Nez Perce

TRIBAL EXECUTIVE COMMITTEE
P.O. BOX 305 • LAPWAI, IDAHO 83540 • (208) 843-2253

December 13, 2018

Submitted via portal: https://www.fs.usda.gov/project/?project=54029

Mr. Keith Lannom, Forest Supervisor
Payette National Forest
U.S. Forest Service
500 North Mission Street, Building 2
McCall, ID 83638

Re: Nez Perce Tribe's Comments on the Granite Meadows Project

Dear Mr. Lannom:

Thank you for the opportunity to comment on the Payette National Forest's ("Forest") proposed Granite Meadows Project ("Project"). According to the scoping materials, the Forest is proposing to improve desired conditions across multiple resource areas within the Project area.

The proposed action includes approximately 25,000 acres of commercial vegetative treatments, 40,000 and 8,000 acres of non-commercial thinning of Forest and non-Forest lands, respectively, and up to 78,000 acres of prescribed fire on Forest and non-Forest land. Proposed actions are designed to reduce fire hazard in the Wildland-Urban Interface ("WUI"), improve the resilience and resistance to wildfire and pathogens, maintain and/or enhance recreation opportunities, restore forest structure, species composition, and tree density, and/or improve wildlife habitat for species of greatest conservation concern within the Project area.

Since time immemorial, the Nez Perce Tribe ("Tribe") has occupied and used over 13 million acres of land now comprising north-central Idaho, southeast Washington, northeast Oregon, and parts of Montana. Tribal members engaged in fishing, hunting, gathering, and pasturing across their vast aboriginal territory. These activities still play—and will continue to play into the future—a major role in the subsistence, culture, religion, and economy of the Tribe.

As the Forest is aware, this Project is located entirely within the Tribe's aboriginal territory subject to the rights the Tribe reserved, and the United States secured, in the Treaty of 1855.[1]

---

[1] Treaty with the Nez Perces, June 11, 1855, 12 Stat. 957.

The Project is also located within the Tribe's area of exclusive use and occupancy, as adjudicated by the Indian Claims Commission,[2] and encompasses areas of cultural and spiritual significance to the Tribe. As a result, the Tribe considers the protection of its Treaty-reserved rights, and other rights and interests, to be a paramount obligation of the Forest when implementing this Project. The Forest has a trust responsibility to ensure that its actions, including implementation of this Project, are fully consistent with the 1855 Treaty, executive orders, departmental regulations, and other federal laws implicating the United States' unique relationship with the Tribe.

Thank you again for the opportunity to provide comments on the Granite Meadows Project. The Tribe's technical comments follow this letter; they reflect the policy views and technical concerns of the Tribe. The Tribe would like to coordinate with Payette Forest staff to schedule a field trip for Tribal staff to the Project area in 2019. You are welcome to contact Amanda Rogerson, Nez Perce Tribe Staff Attorney, at (208) 843-7355 or amandar@nezperce.org, with any questions or concerns.

Sincerely,

Shannon F. Wheeler
Chairman

---

[2] *Nez Perce Tribe v. United States*, Docket #175, 18 Ind. Cl. Comm. 1.

NEZ PERCE TRIBE'S COMMENTS ON
GRANITE MEADOWS PROJECT PROPOSED ACTION
DECEMBER 13, 2018

I. GENERAL COMMENTS

a. The Nez Perce Tribe's Interest in the Granite Meadows Project

Treaty tribes, such as the Nez Perce, have been recognized as managers of their treaty-reserved resources.[3] As a manager, the Tribe has devoted substantial time, effort, and resources to the recovery and co-management of Treaty-reserved resources.

As fiduciary, the United States and all its agencies owe a trust duty to federally recognized tribes to protect their resources.[4] This trust relationship has been described as "one of the primary cornerstones of Indian law,"[5] and has been compared to the relationship existing under the common law of trusts, with the United States as trustee, the tribes as beneficiaries, and the property and natural resources managed by the United States as the trust corpus.[6]

All executive agencies of the United States are subject to the federal trust responsibility to recognize and uphold treaty-reserved rights. Executive agencies must also protect the habitats and resources on which those rights rest, as the right to take fish and other resources reserved by the Tribe presumes the continued existence of the biological conditions necessary to support the treaty-reserved resources.[7]

Forest Service Manual ("FSM") 1563.8b specifically states that the Forest Service "shall administer lands subject to off-reservation treaty rights in a manner that protects Indian tribes' rights and interests in the resources reserved under treaty." Further, FSM 1563.03 directs the Forest Service, among other responsibilities, to "[i]mplement Forest Service programs and activities consistent with and respecting Indian treaty and other reserved rights and fulfilling the Federal Government's legally mandated trust responsibility with Indian Tribes."

II. WILDLIFE COMMENTS

a. Existing and Desired Conditions

A goal of the Payette Forest Plan's Management Direction for Soil Processes and Productivity[8] is to maintain soil productivity and ecological processes where functioning properly and restore

---

[3] *United States v. Washington, 384 F. Supp. 312, 339-40, 403 (W.D. Wash. 1974).*

[4] *See United States v. Cherokee Nation of Oklahoma, 480 U.S. 700, 707 (1987); United States v. Mitchell, 463 U.S. 206, 225 (1983); Seminole Nation v. United States, 316 U.S. 286, 296-97 (1942)..*

[5] Felix Cohen, Handbook of Federal Indian Law 221 (1982).

[6] *See, e.g., Mitchell*, 463 U.S. at 225.

[7] *See Kittitas Reclamation District v. Sunnyside Valley Irrigation District*, 763 F.2d 1032 (9th Cir. 1985), cert. denied, *Sunnyside Valley Irrigation District v. United States*, 474 U.S. 1032 (1985).

[8] Payette National Forest Land and Resource Management Plan ("LRMP"), 2003, page III-19.

soil productivity and ecological processes where currently degraded. What are the existing soil conditions? What impacts will the commercial harvest, non-commercial thinning, and prescribed fire treatments have on vegetation regrowth, soil organic matter inputs, nutrient cycling, and air temperature?

The Tribe encourages the Forest to consider planting climate-adapted seed sources of early seral species (e.g., https://seedlotselectiontool.org/sst/) where appropriate. With respect to whitebark pine, has the Forest conducted an inventory of whitebark pine stands to document age, structure, cone-production potential, and successional stage? The Tribe asks that the Forest assess and report the extent, successional status, and vigor of trees within the Project area. The Tribe recommends that the Forest plant blister-rust resistant stock where natural seed sources have disappeared from the Project area and in areas projected to have suitable climate conditions for future whitebark pine establishment and growth.

b. Non-native Invasive Plant Species

The Tribe is concerned that the commercial, non-commercial thinning, and prescribed fire treatments may cause the establishment and spread of non-native, invasive plant species. Road reconstruction and construction, slash pile burning, and vegetation removal may also provide new ground for the establishment and spread of non-native, invasive plants. The Tribe requests that the Forest take a hard look at the Project's potential direct, indirect, and cumulative impacts on non-native, invasive plants, using best available science.

c. Impacts to Wildlife

The Tribe requests that the Forest evaluate the Project's actions to cavity-nesting wildlife, snag retention and recruitment, old-growth habitat, migratory birds, and sensitive and rare plant species. What are the species of greatest conservation concern within the Project area?

The Tribe requests that the Forest comprehensively evaluate the Project's impacts to big game habitat use, including, but not limited to, security, nutritional capacity, and human disturbance from access routes (all roads and trails). This evaluation should be an analysis of both beneficial and adverse impacts based on the best available scientific information. The Tribe asks that the Forest consider management and biological implications described in Ranglack et al. 2017, Rowland et al. 2018, and Wisdom et al. 2018, and references therein, when describing the affected environment and predicting the environmental consequences of the proposed action and alternatives to big game.

d. Impacts from Livestock Grazing

The Tribe recommends that the Forest defer livestock grazing on Forest, state, and private lands treated with fire until desired vegetative conditions have been met; at a minimum, surviving perennial grasses must have regained productivity and be producing viable seed at levels equal to grasses and forbs in unburned areas. Prior to the resumption of grazing, site-specific monitoring should demonstrate that the plant community and overall site conditions, including, but not limited to, soil and hydrological conditions, have recovered and are trending toward desired condition.

The Tribe requests that the Forest evaluate and report range conditions for the allotments in the Project area. Are resource conditions meeting Forest Plan guidance? The Tribe asks that the analysis incorporate design or mitigation measures to limit possible concurrent activities (e.g. vegetation treatments, prescribed fire, and livestock grazing) that may 1) spread noxious weeds, 2) damage planted seedlings, and 3) degrade resource conditions, such as plant composition, soil stability, and sensitive species viability. In particular, there is evidence of severe impact from livestock grazing along Mud Creek. The Tribe asks that the Forest critically evaluate management strategies, such as a change in seasonal timing or stocking levels, to reduce and minimize further impact from livestock grazing in riparian areas.

According to the proposed action, opportunities to use targeted livestock grazing to reduce fine fuels within the WUI will be explored. The Tribe recommends that the Forest take a hard look at targeted grazing options (e.g., stock type and level, duration, vegetation conditions, and intensity) using the best available science, and adopt specific, standardized guidelines and monitoring protocols for targeted grazing on both Forest and non-Forest lands.

e. Protection for Old Forest and "Legacy Trees"

The Forest needs to determine the best means of protecting old forest and Legacy Trees and of maximizing the retention of large-diameter trees consistent with the goals of the Collaborative Forest Landscape Restoration Program ("CFLRP"). Given the percentage of large tree size classes (overstory trees average 20" diameter or greater) within each Potential Vegetation Group ("PVG") across the Project area,[9] how will the proposed actions impact large-tree-dependent terrestrial species? Are the percentages reported in Tables A-1 through A-3 calculated for a PVG at the HUC10 (5th-field HUC) scale? Do they include forested vegetation in riparian areas?

Legacy Trees have survived stand-replacing natural disturbances and represent some of the best genetics for future seed source. Research has shown that Legacy Trees also provide important habitat elements for many species of wildlife and have a higher level of diversity and richness than control trees.[10]

The goal of protecting Legacy Trees and maximizing retention of large diameter trees is outlined in the CFLRP.[11] It is imperative to find the best means of protecting Legacy Trees and maximizing the retention of large-diameter trees that will become the next generation of Legacy Trees.

III. WATERSHED COMMENTS

a. Watershed Condition

The Tribe is concerned that eight out of eleven subwatersheds in the Project area have a Watershed Condition Framework Rating of "Functioning at Risk" or "Impaired Function."[12] The

---

[9] Granite Meadows Proposed Action, Table A-2, page 14.

[10] http://www.fs.fed.us/psw/publications/4251/mazurek2.pdf.

[11] https://www.fs.fed.us/restoration/documents/cflrp/titleIV.pdf, Section 4003(D).

[12] Granite Meadows Proposed Action, Table A-7, page 18.

Tribe would like to see that the Forest develop the proposed action ("PA") to improve the Watershed Condition of subwatersheds in the Project area.

The Tribe would like the Forest to analyze how the PA will impact watershed health in all subwatersheds of the Project area. For instance, how will the PA change the Watershed Condition Indicator ("WCI") for "Sediment/Turbidity"[13] and "Substrate Embeddedness"[14] in all subwatersheds? How will timber harvest and vegetation treatments change subwatershed WCI for "Change in Peak/Base Flows"[15] through decreased vegetative cover? How will road decommissioning and temporary road construction change subwatershed WCI for "Road Density/Location?"[16] Please explain how vegetation treatments improve subwatershed WCIs for "Disturbance History" given that they increase the Equivalent Clearcut Area ("ECA") and disturb the ground in landslide prone areas? How will vegetation treatments improve subwatershed WCI for "Riparian Conservation Area" ("RCA") through treatments in RCAs?

b. Roads and Road Decommissioning

The Tribe recommends a robust analysis of all of sedimentation from roads physically existing on the landscape, as well as potential sedimentation from log hauling, increased traffic, and temporary road construction associated with the Project. This analysis would provide an overall estimate of the sediment generated by this Project and identify potential problem areas so they can be addressed.

The Tribe recommends that the Forest minimize temporary road construction for this Project. Temporary roads increase ground disturbance and sediment delivery to streams. The Tribe requests that the Forest analyze the impacts of any proposed temporary road construction on terrestrial and aquatic ecosystem health.

The Tribe is supportive of reductions in road densities for watershed health, the removal of older road templates from the landscape, and the elimination of corridors for the dispersal of non-native, invasive plant and insect species. The Tribe, therefore, supports the Forest's proposed 30-35 miles of Forest Road decommissioning,[17] which includes 5 miles within the anadromous, high-priority Brown Creek drainage. The Tribe also recommends, however, that the Forest conduct further road *analysis*, such as Geomorphic Road Analysis and Inventory Package ("GRAIP") surveys, on existing roads to identify specific potential sediment delivery issues.

The PA includes the restoration treatment of an anticipated 50-75 miles of unauthorized routes not needed for future management.[18] The Tribe recommends that the restoration treatment applied be decommissioning through full road recontour.

Road recontouring has a significant positive correlation to the reduction of fine sediments in stream substrate cores.[19] In a 2013 study published in Frontiers of Ecology, two road treatment

---

[13] Payette NF LRMP, 2003, Table B-1, page B-14.

[14] Payette NF LRMP, 2003, Table B-1, page B-15.

[15] Payette NF LRMP, 2003, Table B-1, page B-18.

[16] Payette NF LRMP, 2003, Table B-1, page B-19.

[17] Granite Meadows Proposed Action, page 8.

[18] Granite Meadows Proposed Action, page 9.

[19] McCaffery, M., Switalski, T. A., Eby, L. 2007.

prescriptions were compared for belowground recovery of soil and hydrologic characteristics:[20] fully recontoured (i.e., decommissioned) roads and roads that were simply abandoned (i.e., gated). After 10 years, recontoured roads had carbon storage, nutrient cycling rates, and organic matter quantities similar to never-roaded areas while abandoned roads, after 30-50 years of recovery and revegetation, showed very little carbon storage, soil organic matter, or nitrogen. Results from this study suggest abandoned roads are severely nutrient limited. Recontouring roads also increases infiltration capacity and water storage and decreases runoff time in storm events. Active road recontouring can dramatically accelerate (possibly by hundreds to thousands of years) the recovery of aboveground and belowground properties to conditions found in unroaded areas.

Given the documented benefits, the Tribe recommends full road recontouring as the preferred method of road closure. If funds are not available to fully recontour all roads slated for decommissioning, the Tribe suggests the following priorities in the order they are listed below.

1. Roads that show the highest sediment delivery to streams should be given the highest priority for full road recontouring.
2. Roads in watersheds where Endangered Species Act ("ESA")-listed species are present should take priority over watersheds without ESA-listed species.
3. Roads in RCAs should have high priority for full road recontouring. Considering that roads often wind in and out of RCAs, the Tribe recommends that the management prescription assigned to a portion of road should encompass the entire road.
4. Roads with many stream crossings should rank higher for full road recontouring than roads with fewer stream crossings.
5. Roads with a well-defined road prism should rank higher for recontouring than roads with minimal road compaction.
6. Roads where sensitive wildlife species will be negatively impacted should rank higher for recontouring than roads where sensitive species are not present.

c. Fish Passage Improvements

The Tribe is pleased with the planned improvements at five National Forest System road/stream crossings. The Tribe urges the Forest to also consider appropriate Aquatic Organism Passage ("AOP") structures at each, to restore fish passage and improve hydrologic connectivity. The Tribe recommends bridges and bottomless culverts at all road/stream crossings, rather than hardening for Off Highway Vehicle ("OHV") and cattle use. Cattle and OHV use tends to widen hardened crossings over time, disturbing ground, and destabilizing streambanks.

d. Restoration Opportunities

The Tribe agrees with the PA on the need for streambank and wetland restoration actions in Mud Creek and Sater Meadows.[21] The Tribe supports fence construction, planting native vegetation, and implementation of instream/streambank structures to restore riparian and aquatic ecosystem health. However, the proposal for "streambank stabilization" and "minor channel re-alignment" is vague. The Tribe requests that the Forest describe what streambank stabilization techniques it

---

[20] Lloyd, R. A., Lohse, K. A., Ferre, T. P. A. 2013.

[21] Granite Meadows Proposed Action, page 9.

will used in the Project and justify whether these actions will indeed restore degraded stream channels, wetlands, and riparian habitat. Further, the Tribe requests that the Forest describe how proposed streambank and wetland restoration actions will reverse degradation associated with current or historic grazing.

e. Riparian Conservation Areas ("RCAs")

Riparian areas should only be treated if the treatment will clearly and positively meet RMOs and create positive biological effects. RCA treatments should be light in nature, non-mechanical, non-commercial, and small in terms of acreage, as they are still experimental.

What was the initial project area analysis that indicated a need for vegetative treatments in RCAs? The Tribe has fewer concerns with letting prescribed burns back into RCAs, but cautions against the use of commercial treatments in the outer portions of the RCAs.

The Forest Plan[22] identifies several important considerations when appropriately delineating and designing management activities within or affecting RCAs. These are as follows:

a. *A stream requires predictable and near natural energy and nutrient inputs.*
b. *Many plant and animal communities rely on streamside or wetland forests and vegetation for migratory or dispersion habitat.*
c. *Small streams are generally more affected by hillslope activities than are larger streams.*
d. *As adjacent slopes become steeper, the likelihood of disturbance resulting in discernible instream affects increase.*
e. *Riparian vegetation 1) provides shade to streams channels; 2) contributes large woody debris 3) adds small organic matter; 4) controls sediment inputs from surface erosion; 6) and regulates nutrient and pollutant inputs to streams.*

It is apparent from the available scientific literature that treatments in RCAs are a relatively recent development, are understudied, and have varied biological effects (some positive and some negative).

RCAs are often referred to as buffer zones because they reduce sediment and pollutants from entering water bodies. For this Project, the Forest has proposed treatment within the outer RCA buffer zones using commercial thinning, non-commercial thinning, and burning. The proposed treatments have the ability to negatively impact Large Woody Debris ("LWD") recruitment, increase water temperatures through reduced canopy cover shading, decrease streambank stability through the removal of upland trees just outside of the no-cut zone, hinder fine organic litter from entering streams, alter riparian microclimates, and allow sediment and pollutants to enter water bodies.

In the Forest Plan, under the Management Direction for Soil, Water, Riparian, and Aquatic Resources, number SWST10 Standard states: "Trees or snags that are felled within RCAs must be left unless determined not to be necessary for achieving soil, water, riparian, and aquatic desired conditions. Felled trees or snags left in RCAs shall be left intact unless resource

---

[22] Payette NF LRMP, 2003, Appendix B-36.

protection (e.g., the risk of insect infestation is unacceptable) or public safety requires bucking them into smaller pieces."[23]

Riparian Management Objectives ("RMOs") for this project need to be clearly defined and specifically linked to improving riparian function. This criterion should be more specific than the blanket statement aimed at reducing large scale fires in RCAs and desired conditions.

Ideally, RCA treatments should be covered by burning and non-commercial hand lines. Removal of wood in RCA's should only occur when streams have adequate LWD, as defined by the Forest's Watershed Condition Indicators (>20 pieces per mile, >12 inches in diameter, >35 feet length)[24] and directed by SWST10.

The Tribe is concerned that the use of targeted livestock grazing[25] could cause degradation of aquatic ecosystem health. The Tribe requests that the Forest describe where targeted livestock grazing could occur in the Project and explicitly avoid grazing within RCAs.

f. Cumulative Effects

An individual action may have significant effects when considered in conjunction with the effects of other actions, even when its effects would be insignificant if considered alone. Thus, the Forest needs to take into account and analyze all watersheds encompassed by the Project area in its cumulative effects analysis for this Project. This includes an analysis of the following projects with respect to effects:

1. The Payette National Forest's Lost Creek-Boulder Creek Landscape Restoration Project: The western side of the project area[26] borders the Lost Creek-Boulder Creek Landscape Restoration Project.
2. The Nez Perce-Clearwater National Forests' Windy Shingle Project: This project is a 3,000 acre vegetation treatment approximately five miles west of Riggins, Idaho, in Idaho County. The Nez Perce-Clearwater National Forests began project implementation in 2017 under a Healthy Forests Restoration Act categorical exclusion. Please take note of this project in the Little Salmon watershed, although downstream of the Granite Meadows Project area.
3. Idaho Department of Lands and the Bureau of Land Management ("BLM") conducted salvage harvests in the Hazard Creek area in 2015-2016.
4. Idaho Transportation Department completed curve flattening work on Highway 95.
5. BLM Boulder Vegetation Project proposal includes the lower portion of the Trail Creek subwatershed. The proposal incorporates mechanical treatments on approximately 2,427 acres, prescribed burning on 4,625 acres, construction of 2.41 miles of new road, 11.52 miles of temporary roads, and 0.71 miles of swing trails.
6. The Tepee Spring wildfire happened in 2015 in this area, starting in the lower portion of the Hazard Creek watershed and burning northeast on the east side of Highway 95.

---

[23] Payette NF LRMP, 2003, page III-22.

[24] Payette NF LRMP, 2003, Table B-1, page B-15.

[25] Granite Meadows Proposed Action, page 7.

[26] Granite Meadows Proposed Action, Figure 5, page 33.

IV. CULTURAL RESOURCES

Archaeological surveys are inadequate to identify and evaluate these resources, and the Tribe does not believe that asking Tribal staff in meetings or letters for site information constitutes a good faith effort.

The Tribe therefore urges the Forest to engage the Tribe in ethnographic or traditional use studies to identify sacred sites, traditional cultural properties, and historic properties of religious and cultural significance to Indian tribes for this and future projects, as permitted in the FSM, Section 2367.3:

> The agency official shall use Federal procurement and contracting authority to acquire necessary skills, technical expertise, work capacity, and/or products to complete compliance and stewardship work. Contracting is most appropriate for:
>
> 1. Preparation of Forest cultural resource overviews and ethnographies.

In addition, the Tribe reminds the Forest that the protection of spiritual sites requires more than simple avoidance: the Forest must consider and promote the conditions of solitude and isolation that are integral to the continued use of these places.

V. CONCLUSION

The Tribe shares the Forest's goal of promoting healthy and safe forest conditions in the Project area. Staff look forward to continued coordination and communication about the Project during development. The Tribe would appreciate a field trip for Tribal staff to several representative locations in the Project area in 2019.

VI. REFERENCES

Lloyd, R. A., Lohse, K. A., Ferre, T. P. A. 2013. Influence of road reclamation techniques on forest ecosystem recovery. Frontiers of Ecology and Environment 11(2): 75–81. http://www.esajournals.org/do7i/abs/10.1890/120116.

Mazurek, M. J., Zielinski, W. J.. 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. Forest Ecology and Management 193: 321–334.

McCaffery, M., Switalski, T. A., Eby, L. 2007. Effects of road decommissioning on stream habitat characteristics in the South Fork Flathead River, Montana. Transactions of the American Fisheries Society 136: 553–561.

Ranglack, D. H. [et al.]. 2017. Security areas for elk during archery and rifle hunting seasons. The Journal of Wildlife Management 81(5): 778-91.

Rowland, M. M. [et al.]. 2018. Modeling elk nutrition and habitat use in western Oregon and Washington. Wildlife Monographs 199: 1-69.

Wisdom, M. J. [et al.]. 2018. Elk responses to trail-based recreation on public forests. Forest Ecology and Management 411: 223-233.

Influence of road reclamation techniques on forest ecosystem recovery

Rebecca A Lloyd[1,2*], Kathleen A Lohse[3], and TPA Ferré[4]

Road reclamation has emerged as an integral part of ecological restoration strategies, particularly on public lands. However, there are no consistent techniques for how road reclamation should be implemented to restore ecosystem structure and function. Resource managers are hindered by critical research gaps regarding the linkages between, as well as the effects of different restoration actions on, above- and belowground ecological and hydrological properties. In the western US, we examined how two road reclamation methods (recontouring and abandonment) affect ecosystem properties relative to "never-roaded" areas. Recontoured and abandoned sites displayed similar aboveground properties but exhibited notable differences in belowground properties, including soil hydraulic conductivity, organic matter, total carbon, and total nitrogen, among others. Our findings suggest that recontouring can dramatically accelerate recovery of above- and belowground properties so they resemble never-roaded reference conditions. In contrast, abandoning roads generates above- and belowground properties that follow a different path to recovery.

Front Ecol Environ 2013; 11(2): 75–81, doi:10.1890/120116

Resource managers increasingly rely on restoration activities to accelerate ecosystem recovery and to rehabilitate ecosystem function after a disturbance (Hobbs and Cramer 2008). Although forest and stream restoration in the US has grown into a billion-dollar annual economy (Bernhardt *et al.* 2005), relatively little quantitative information is available regarding the success of restoration projects in rehabilitating ecosystems. Understanding how restoration activities influence the rate of recovery of ecosystem properties is a critical first step toward optimizing restoration efforts (Birch *et al.* 2010).

Ecosystem responses to disturbance and their trajectories toward recovery involve complex biological, chemical, and physical interactions. A growing body of theoretical and empirical research suggests that ecosystems often do not respond smoothly to change, and that ecosystem recovery may require a different pathway back to the initial state, also referred to as reference conditions (Scheffer *et al.* 2009). For example, restoring aboveground forest structure may not be sufficient to allow this ecosystem to return to its original state and function. Other factors, such as belowground soil properties and processes, may affect the pathway to recovery and could result in an alternative final ecosystem state, with ecological composition and functions that differ from unperturbed reference conditions (Kardol and Wardle 2010).

Among the most pressing current challenges facing managers of public lands is how to mitigate the impacts of the many roads that are now surplus to management needs (Leu *et al.* 2008). Concerns over the detrimental effects of erosion and resource damage due to unmaintained roads provided the impetus for most road decommissioning projects on public lands; as a result, most research has focused on mitigation of road-associated sedimentation and hydrologic impacts (Switalski *et al.* 2004). Although identifying erosion and sedimentation impacts is important, this narrow focus may overlook how road decommissioning affects ecological and hydrological linkages that exert critical control over ecosystem recovery. Resource managers developing integrated ecosystem restoration programs have many options for decommissioning a particular road, ranging from passive closure (abandoning the road and allowing revegetation to occur naturally over time; Figure 1) to the most intensive approach (recontouring the existing road and reshaping the hillside to its original contours; Figure 2). However, little information is available to help managers decide how to administer a decommissioning project so as to achieve ecosystem recovery. Failure to understand how different road reclamation treatments influence ecological and hydrological properties may limit the ability to predict whether an ecosystem will recover to a pre-disturbance state or whether it will cross a critical threshold and progress to an alternative state (Suding *et al.* 2004).

Here, we examine the effectiveness of different road decommissioning techniques for rehabilitation of ecological and hydrological systems in densely roaded forest ecosystems. Our overarching hypothesis is that restoration designs that fail to explicitly address both above- and belowground ecosystem structure and function may result in recovery to alternative states that have diminished ecological and hydrological functions relative to a "never-roaded" forest. Figure 3 conceptualizes how recov-

---

[1]*College of Forestry and Conservation, University of Montana, Missoula, MT* [*]*(rebecca.lloyd@umontana.edu)*; [2]*Yellowstone to Yukon Conservation Initiative, Bozeman, MT;* [3]*Department of Biological Sciences, Idaho State University, Pocatello, ID;* [4]*Department of Hydrology and Water Resources, University of Arizona, Tucson, AZ*

Beyond the Frontier: Listen to Rebecca Lloyd discussing this research on *Frontiers'* monthly podcast, at www.frontiersinecology.org.

Figure 1. *Typical abandoned forest roads in the project area, with natural revegation occurring (a) after 10 years and (b) after 30 years.*

ery trajectories toward a desired functional state (ie similar to never-roaded sites) may differ between two methods of restoration: abandoned roads and roads that are actively reclaimed by recontouring. Specifically, we predict that recontouring will accelerate recovery of critical ecosystem properties, such as vegetative succession, soil organic matter (SOM), nutrient stocks, and hydrologic properties of the soil, toward never-roaded reference conditions. We also predict that abandoned roads will recover aboveground vegetative cover similar to that of never-roaded conditions, but belowground characteristics – such as SOM and the ability of water to move through soil – will be diminished as compared with the desired values of never-roaded sites.

Materials and methods

Study area

We integrated our research with a landscape-scale restoration partnership between the Nez Perce Tribe (NPT) and the Clearwater National Forest (CNF) in the upper Lochsa Basin, a tributary of the Clearwater River in northern Idaho, located in the CNF (WebFigure 1). The study area was densely roaded, ranging from 2–24 km of roads per square kilometer (McClelland *et al.* 1997). Roads were built to support timber harvests in the 1950s and 1960s, and have been abandoned for 30–40 years (McClelland *et al.* 1997). To date, this restoration program has decommissioned over 960 km of surplus roads. We established 150-m transects along road treatments to assess how key properties change across a recontour age gradient to show how recovery progresses over time (R1, R5, and R10 represent 1, 5, and 10 years after recontour, respectively) and compared these treatments with never-roaded sites and abandoned sites (a total of 25 road sites). We controlled for other factors (eg geology, topography, climate, and biota) to the best extent possible. The study sites are underlain by the geologic formation known as the Idaho Batholith (McClelland *et al.* 1997). The soils were granitic with a volcanic ash cap generally classified as Andisols (McDaniel and Wilson 2007). The sites experience similar climate, with an average maximum and minimum annual temperature of 28°C and –9°C, respectively, and with a mean annual precipitation of 130 cm (McClelland *et al.* 1997). Slopes ranged from 30–45%.

Aboveground recovery

We followed vegetation data-collection protocols already in use by CNF and the NPT. In brief, we established 150-m line transects that crisscrossed the axis of the road with direction changes every 30 m, and recorded plant functional groups as grass, forb, shrub, tree, or invasive plant every meter and estimated percent cover at five stratified random point locations using 5-m^2 quadrats along each transect. We added transects to compare vegetative succession on roads abandoned for 10 and 30 years (A10 and A30 in Figure 4, respectively).

Belowground recovery

Along each transect, we excavated five soil pits (0.5 m × 0.5 m, to 1-m depth) at stratified random point locations (at 15 m, 30 m, 75 m, 95 m, and 140 m). We collected

A Connor, Clearwater National Forest

Figure 2. *Abandoned roads (a) before recontour, (b) during recontour, and (c) 3 years after recontour.*

soil samples by depth (the upper layer or organic [O] horizons occurred from 0 to 5 cm, the middle layer or mineral [A] horizons occurred from 8 to 40 cm, and the lower layer or C horizons [see description below] occurred below 40 cm); at least three samples were taken in each depth range and homogenized. O horizons consisted of undecomposed to partially decomposed litter. A horizons contained humified organic matter and mineral soil. Horizons with little evidence of soil development and lacking other properties of O, A, or weathered (B) horizons were designated as C horizons (eg a decomposed granitic subsurface horizon). Within each soil pit, we characterized rooting depth and collected soil samples for physical and chemical analysis. For recontoured roads that had negligible profile development in the A horizon, a single homogenized sample from 0.1 to 0.5 m was collected.

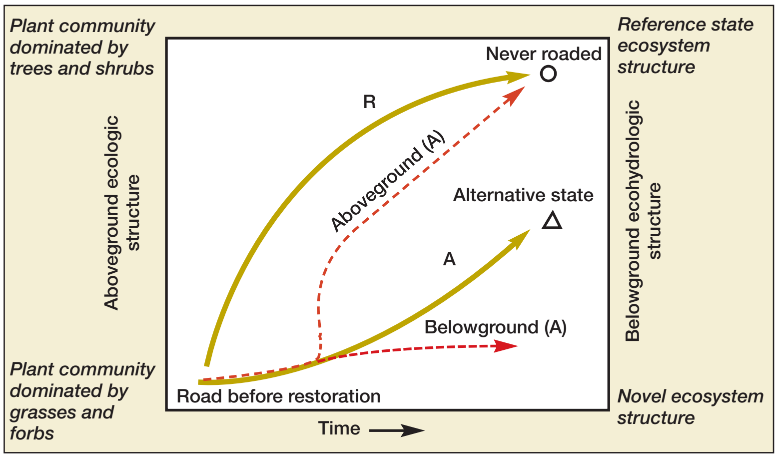


Figure 3. *Coupled ecohydrologic properties will determine ecosystem recovery after road removal. Recontouring roads will accelerate recovery to reference conditions, while abandoning a road may result in decoupling above- and belowground recovery trajectories, resulting in recovery to an alternative functional state. R = recontoured roads; A = abandoned roads. Time represents the years and decades of the recovery period (ie time from the initial restoration treatment). Dashed arrows represent a hypothetical decoupling of above- and belowground recovery trajectories for abandoned roads, whereas solid arrows represent hypothetical recovery trajectories contrasting the two methods of road reclamation (abandon versus recontour).*

Soil biogeochemical and physical properties

Soil cores were processed to determine bulk density (ρ_b) (ie soil mass per unit volume) and other chemical properties following standard protocols (Robertson 1999). We determined saturated hydraulic conductivity (K_s), a quantitative measure of a saturated soil's ability to transmit water, using a Reynold's Tank flow apparatus. Soils were analyzed for SOM content through the use of loss on ignition techniques requiring heating to 360°C for 4 hours (Robertson 1999). We also analyzed 30-mg samples for total carbon (TC) and total nitrogen (TN) using an Elemental Analyzer (Model EA1110, CE Instruments, Wigan, UK). Finally, soils were extracted for nitrogen (N) pools and process rates following methods described in Lohse and Matson (2005). In brief, available soil nitrate (NO_3^-) and ammonium (NH_4^+) pools were determined by extracting soils in 2N potassium chloride (a 1:5 soil-to-extract ratio) upon return from the field and by performing a second extraction after a 7-day aerobic incubation in the laboratory. Net mineralization rates were calculated by subtracting the initial inorganic N (NO_3^- + NH_4^+) from final pools and dividing by the incubation period. Net nitrification was determined by subtracting initial NO_3^- pools from final pools and again dividing by the incubation period. We measured NO_3^--N and NH_4^+-N using a Smartchem Discrete Analyzer (Westco Scientific Instruments, Brookfield, CT).

Data analysis

Data from separate soil pits along the same transect were averaged, and each metric was given one value per transect. We used a one-way analysis of variance (ANOVA) to test for significant differences in means among groups and the Tukey-Kramer post-hoc test to evaluate the significance of differences between each pair of treatment types.

Results

Aboveground recovery

As expected, both abandoned roads and never-roaded reference sites had less bare ground and higher herbaceous cover than recontoured sites (Figure 4). A10 roads had more bare ground (45 ± 8.7%, $F_{5,25} = 3.4$, $P = 0.01$), fewer

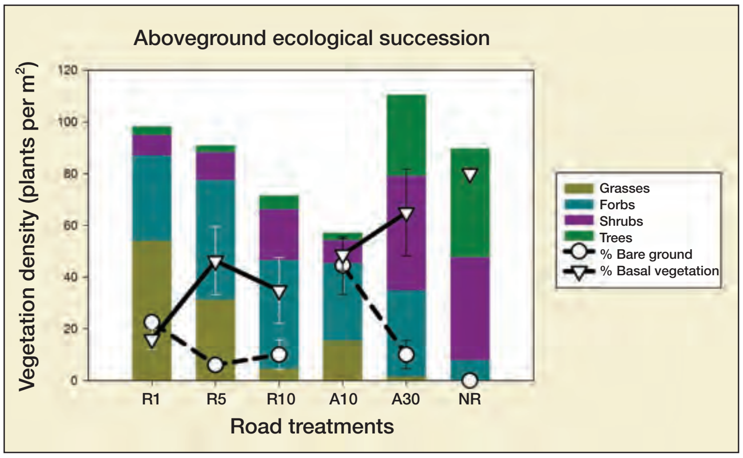


Figure 4. *Changes in plant cover and functional group composition over time and between treatments. R = recontoured; A = abandoned; NR = never roaded. Error bars indicate standard error.*

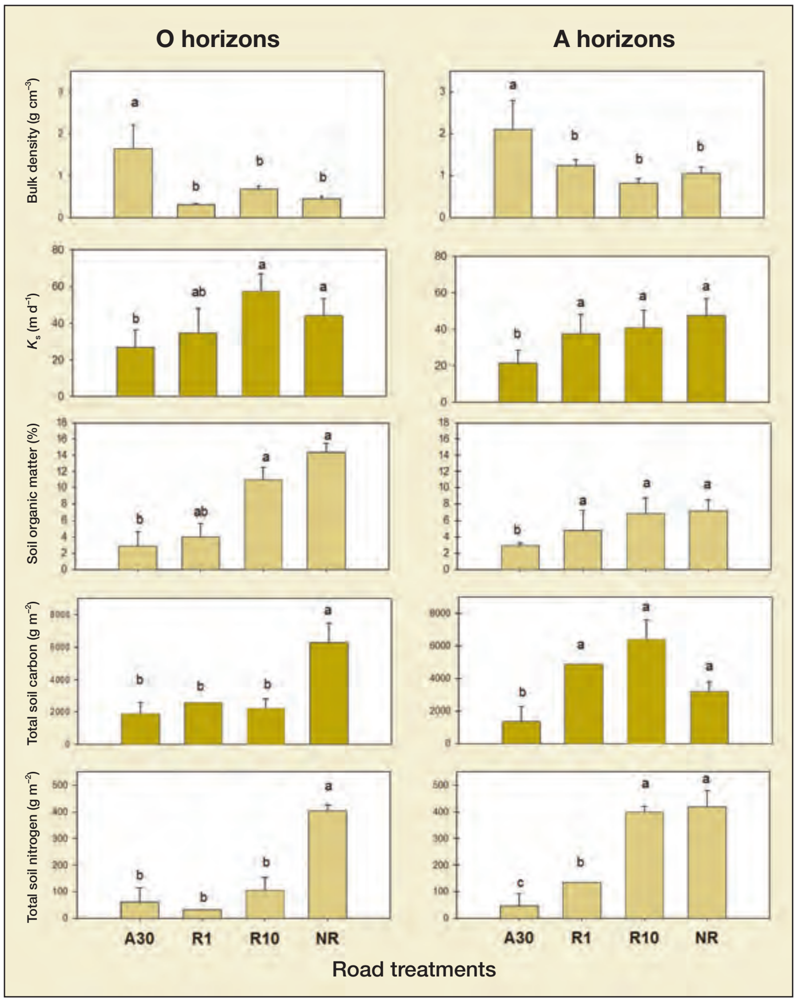


Figure 5. *Compiled results for soil characteristic data, showing differences in values by treatment and compared across two depths in the soil profile. Left panels = O (upper) horizons; right panels = A (lower) horizons. For all treatments,* n = 5, *except R1 where* n = 3; *statistical difference determined by ANOVA with* P < 0.05 *and direction of difference determined by post-hoc Tukey test. Significantly different values are indicated by lowercase letters, where a is greater than b, b is greater than c, and so forth. Error bars indicate standard error.*

shrubs (8 ± 4.7%, $F_{5,25}$ = 5.5, P = 0.009), fewer trees (2.5 ± 0.9%, $F_{5,25}$ = 3.7, P = 0.01), and more grasses (16.4 ± 4%, $F_{5,25}$ = 18.9, P < 0.0001) as compared with never-roaded areas (no bare ground, 39 ± 3.3% shrubs, 42 ± 8% trees, less than 1% grasses). By contrast, A30 roads were not significantly different in shrub and tree density as compared to never-roaded transects, with 23 ± 12% and 22 ± 8% coverage of shrubs and trees, respectively. However, there was significantly more bare ground remaining (10 ± 8%, $F_{5,25}$ = 3.4, P = 0.01) on the oldest abandoned roads (A30).

Average percent of bare ground along recontoured road transects decreased with each successive year after treatment, from 22% in R1 to 10% in R10 (Figure 5). Conversely, percent basal vegetation increased from an average of 16% in R1 to 35% in R10. Concurrently, plant functional groups transitioned from grass- and forb-dominated to higher percentages of shrubs and trees, with cover percentages closer to those of never-roaded areas. R10 roads had more trees (5 ± 2.9%) and shrubs (44 ± 12%, $F_{5,25}$ = 5.5, P < 0.001) than A10 roads and were not significantly different from A30 and never-roaded sites.

Belowground recovery

Soil physical properties and processes

Soils at never-roaded sites were relatively deep (>100 cm), had strong O horizons from 0- to 5-cm depth, and had weak to modest A horizons from 5- to 50-cm depth, overlying a granitic C horizon at 50–100 cm. In contrast, soils on A30 roads were shallow, typically 20- to 25-cm depth, with a weak O horizon in the upper 2 cm, a shallow A horizon, and a granitic C horizon at 25-cm depth. Roots on A30 roads were constrained to the upper 15 cm (10 ± 0.45 cm). In contrast, never-roaded sites and recontoured roads had rooting depths that extended below the limits of soil pit excavations (>60–75 cm).

Average ρ_b and K_s were statistically different among restoration treatment groups, most notably in the A horizons (Figure 5). We used the Hydrus 1-D software (Šimůnek *et al.* 2008) to simulate infiltration capacity and time to runoff generation for each treatment under a typical summer precipitation event, using measured K_s and ρ_b values and soil texture. The simulated time to runoff generation after a 1-hour storm event was significantly different between treatments, with runoff occurring in the first 0.2 hours of the storm on A30 roads and never on R10 roads (WebFigure 2).

Soil biogeochemical properties and processes

Average SOM percent, TC, and TN were significantly different among restoration treatments, with recontoured sites having higher TC and TN as compared to A30 roads in the lower horizons (Figure 5). Summed over the total depth of the sampled soil horizons, soil carbon (C; kg m^{-2}) and soil N (kg m^{-2}) were significantly higher at the recontoured sites (R10 = 17.66 ± 3.5 kg C m^{-2}, 1.03 ± 0.34 kg N m^{-2}) as compared to abandoned sites (A30 = 3.12 ± 0.67 kg C m^{-2}, 0.09 ± 0.03 kg N m^{-2}) but not significantly different from never-roaded areas (19.53 ± 2.34 kg C m^{-2}, 1.23 ± 0.21 kg N m^{-2}) (TC: $F_{2,7}$ = 4.6, P = 0.02; TN: $F_{2,7}$ = 3.1, P = 0.01).

Soil N pools and process rates also varied across restoration treatments, most strongly within the A horizons (Figure 6). Specifically, extractable NH_4^+ pools were significantly higher in the recontoured sites than A30 but not significantly different than never-roaded areas ($F_{4,23}$ = 4.8, P = 0.005). Consistent with these patterns, net mineralization rates in the lower horizons were significantly higher in the recontoured sites as compared to A30 but not in never-roaded sites ($F_{4,23}$ = 3.2, P = 0.01).

Soil C:N ratios were significantly higher along abandoned roads (32:1 ± 15:1) as compared with C:N ratios in never-roaded areas (14:1 ± 5:1) and R10 treatments (21:1 ± 13:1), which were not significantly different (O horizon: $F_{2,7}$ = 19.79, P = 0.0013). The one exception was the lower A horizon of the abandoned roads, which was similar (35:1) to other treatments (lower A horizons: $F_{1,7}$ = 0.52, P = 0.52).

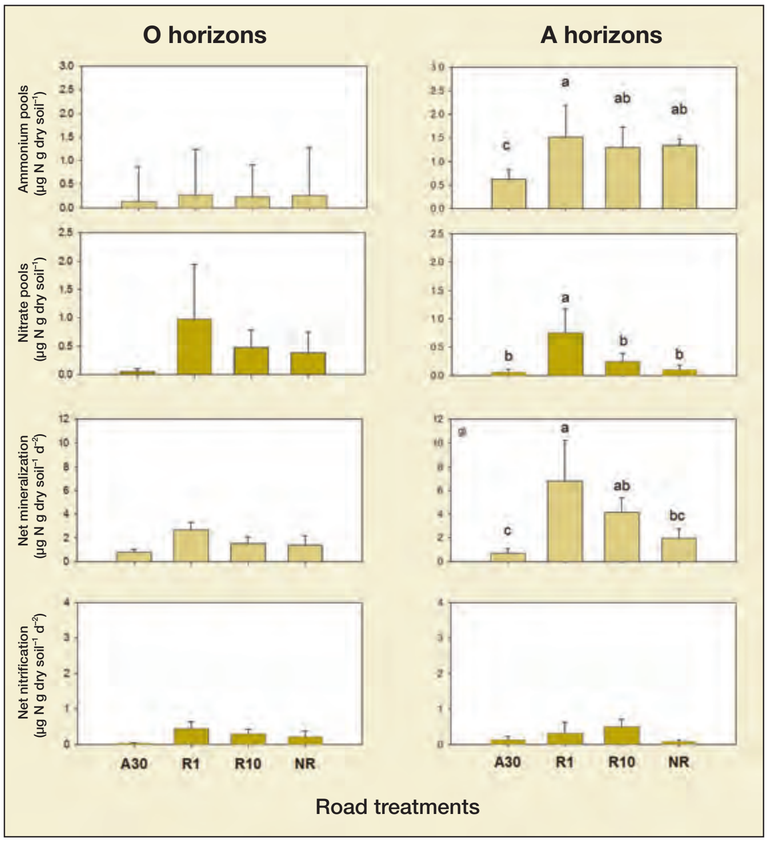


Figure 6. *Nitrogen pools and fluxes compared between upper (left panels) and lower (right panels) soil layers across treatments. Ammonium pools in the surface soil horizons were not significantly different; however, pools in the A (lower) horizons were based on Welch's T test for comparing group means with unequal variances ($F_{3,2}$ = 10.46, P = 0.04); lowercase letters indicate significant differences. The other pools and processes exhibit similar trends in extractable nitrate pools, net mineralization, and rates of net nitrification, with the strongest differences in the A horizon. Error bars indicate standard error.*

Discussion

To our knowledge, this is the first study to evaluate how road restoration treatments influence the recovery of coupled above- and belowground ecosystem structure and processes. We found that patterns of recovery were markedly different among the treatment approaches at the road scale. In practice, resource managers often use restoration of aboveground vegetation structure as the criterion for restoration success. In our study, the trajectory of plant succession on abandoned roads and recontoured roads followed similar trends to other research conducted on passively restored roads (Madej 2001; Foltz *et al.* 2009), although our data suggest that vegetation succession to shrubs and trees may be slower on abandoned roads as compared with recontoured roads. However, ecosystem recovery belowground differed markedly from that aboveground. The strong differences in belowground properties following road abandonment result in an effective decoupling of the recovery trajectories of above- and belowground ecohydrological properties (Figure 3). Together, these findings support the prediction that recontouring accelerates the rehabilitation of key ecohydrologic properties toward reference dynamics.

Results from our study also showed that recontouring increased SOM, TC, and TN pools to levels similar to those of never-roaded sites, while TC and TN pools remained low along abandoned roads. Soil organic matter is a key ecosystem property that exerts control on secondary succession, water-holding capacity, hydraulic properties, and nutrient dynamics. Research quantifying accumulation rates of SOM following disturbance indicates that it can take thousands of years for SOM to accumulate to steady-state levels, particularly in forested ecosystems (Wang *et al.* 1999). In this context, our research suggests that active recontouring can dramatically accelerate the recovery of soil properties by hundreds to thousands of years, as compared with never-roaded reference areas. In contrast, belowground properties and processes along abandoned roads remain in a degraded state even 30 or more years after road closure and revegetation.

The observed differences in hydrologic property recovery were striking, with significantly higher ρ_b, strongly constrained rooting depths, and significantly lower K_s on A30 roads as compared to never-roaded and recontoured sites. Previous research has demonstrated that abandoned roads, even after many years of passive revegetation, have higher soil ρ_b than adjacent never-roaded areas (Luce 1997; Foltz *et al.* 2009). In a study contrasting recontoured roads, roads with their surfaces decompacted only, and recently abandoned roads, Kolka and Smidt (2004) found lower soil ρ_b and less erosion and runoff on treated roads as compared with abandoned roads. Luce (1997) concluded that roads decompacted and left in place have ρ_b values that are initially similar to never-roaded areas, but after only 1 year, recovery is slowed and regresses back to pretreatment states. In contrast to their results, we found that ρ_b values on recontoured roads decreased significantly 1 to 10 years after recontouring, suggesting that this treatment initiates a hydrologic recovery process that may not be possible with less intensive treatments. Modeling how different hydrologic properties may influence runoff and water storage underscores the potential importance of the varied hydrologic recovery trajectories of the two different road treatments. In the modeled response to a typical summer storm (5 cm per hour), runoff occurs within the first 12 minutes of the storm on A30 roads, whereas no runoff occurs within the first hour on R10 roads (WebFigure 2).

In areas with road densities comparable to those within the CNF, different road restoration treatments have implications for C and N storage and cycling at hillslope and watershed scales. In one watershed in the Lochsa Basin, for example, active road recontouring reduced the density of abandoned roads from 2 km per square kilometer to 0.4 km per square kilometer. Extrapolating soil TC estimates to a hillslope, we estimate that soil TC storage was approximately 2.33×10^7 g C per road kilometer (to 25-cm depth) prior to active recontouring. After treatment, we conservatively estimate soil TC storage increased sixfold, to 6.5×10^7 g C per road kilometer (to 25-cm depth). The same trends are seen for soil N. Abandoned roads have approximately 6.96×10^5 g N per road kilometer, and this amount increases by an order of magnitude to 7.16×10^6 g N (to 25-cm depth). These major differences in soil C and N storage have potentially important implications for climate-change mitigation. With thousands of kilometers of roads being recontoured each year across the US, this may represent a substantial C sink, as a result of both higher soil C and increased rooting depth relative to sites that have undergone passive restoration techniques. Thus, road reclamation may serve as an important management approach to mitigate the potential impacts of climate change.

Research shows that complex linkages among subsurface ecosystem properties, including how C and N interact with water storage and runoff to control rates of nutrient cycling, are critical to an ecosystem's post-disturbance recovery (Lohse *et al.* 2009). The major differences in hydrologic function, SOM, soil C, and soil N resulting from the two decommissioning approaches suggest that abandoned roads may be moving to an altered ecosystem state, characterized by diminished capacity for nutrient cycling, water storage, and other key ecosystem functions. Indeed, higher soil C:N, smaller N pools, and decreased C and N process rates seen along the abandoned roads may indicate that these sites are moving toward N limitation. Additional research beyond plant functional groups evaluated in this study is warranted to determine whether these belowground differences in ecological and hydrological processes influence other metrics of aboveground recovery, such as aboveground plant composition, diversity, and productivity. Previous research suggests that differences in N processes and rates may be the strongest control on recovery potential of an ecosystem (Turner *et al.* 2004). The change in functional potential could have cascading consequences for ecosystem recovery and resilience to other disturbances (Suding *et al.* 2004).

Importance

Land management paradigms, particularly on public lands, have shifted from resource extraction to a focus on restoration that will result in ecosystems that are resilient to climate change and other disturbances. To support these efforts, both scientists and managers need more information on how to design restoration efforts that restore ecosystem function. The initial expense of road decommissioning and restoration can be a major issue for managers working with limited budgets. In general, intensive restoration approaches, such as full recontouring, are considerably more expensive than simply abandoning a road. Managers must weigh initial economic costs with both short- and long-term ecosystem benefits.

Although more expensive as compared with road abandonment, recontouring may be the only way to restore both above- and belowground ecosystem processes, accelerating the recovery of these forest ecosystems by decades to millennia. Our findings also suggest that manual groundtruthing or remotely sensed aboveground assessments are inadequate to evaluate the benefits derived from active restoration (Birch *et al.* 2010). Restoration techniques that fail to restore above- and belowground properties and processes may lead to an altered ecosystem with different functional processes and potential (Kardol and Wardle 2010). Further studies are needed to help scientists and managers understand how these differences in ecosystem properties may translate into differences in ecosystem function and how these findings may apply in other landscapes.

Acknowledgements

This research was funded by a University of Arizona (UA) National Science Foundation (NSF) Advance Seed Grant and start up funds provided to KAL by UA. RAL was supported by a US Department of Agriculture Ecohydrology Fellowship, the Nez Perce Tribe (NPT) Watershed Division, a US Forest Service contract, and a US Environmental Protection Agency STAR Fellowship. KAL was supported by the NSF (award number EPS-0814387). We thank the NPT and Clearwater National Forest personnel for collaboration and logistical field support, especially I Jones, E Taylor Jr, D Forestieri, J Crow, A Yearout, L McFarland, A Connor, Steppen, and A Snyder, whose assistance ensured the project's successful completion.

References

Bernhardt ES, Palmer MA, Allan JD, *et al.* 2005. Restoration of US rivers: a national synthesis. *Science* **308**: 636–37.

Birch JC, Newton AC, Aquino CA, *et al.* 2010. Cost-effectiveness of dryland forest restoration evaluated by spatial analysis of ecosystem services. *P Natl Acad Sci USA* **107**: 21925–30.

Foltz RB, Copeland NS, and Elliot WJ. 2009. Reopening abandoned forest roads in northern Idaho, USA: quantification of runoff, sediment concentration, infiltration, and interrill erosion parameters. *J Environ Manage* **90**: 2542–50.

Hobbs RJ and Cramer VA. 2008. Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annu Rev Env Resour* **33**: 39–61.

Kardol P and Wardle DA. 2010. How understanding aboveground–belowground linkages can assist restoration ecology. *Trends Ecol Evol* **25**: 670–79.

Kolka RK and Smidt MF. 2004. Effects of forest road amelioration techniques on soil bulk density, surface runoff, sediment transport, soil moisture, and seedling growth. *Forest Ecol Manag* **202**: 313–23.

Leu MS, Hanser E, and Knick ST. 2008. The human footprint in the West: a large-scale analysis of anthropogenic impacts. *Ecol Appl* **18**: 1119–39.

Lohse KA, Brooks PD, McIntosh JC, *et al.* 2009. Interactions between biogeochemistry and hydrologic systems. *Annu Rev Env Resour* **34**: 65–96.

Lohse KA and Matson PA. 2005. Consequences of nitrogen additions for soil processes and solution losses from wet tropical forests. *Ecol Appl* **15**: 1629–48.

Luce CH. 1997. Effectiveness of road ripping in restoring infiltration capacity of forest roads. *Restor Ecol* **5**: 265–70.

Madej MA. 2001. Erosion and sediment delivery following removal of forest roads. *Earth Surf Proc Land* **26**: 175–90.

McClelland DE, Foltz RB, Wilson WD, *et al.* 1997. Assessment of the 1995 and 1996 floods and landslides on the Clearwater National Forest, part I: landslide assessment. A report to the Regional Forester, Northern Region, US Forest Service. Missoula, MT: USFS.

McDaniel PA and Wilson MA. 2007. Physical and chemical characteristics of ash-influenced soils of inland Northwest forests. Proceedings of RMRS-P-44, Volcanic-ash-derived forest soils of the inland Northwest: properties and implications for management and restoration; 9–10 Nov 2005; Coeur d'Alene, ID.

Robertson GP. 1999. Standard soil methods for long-term ecological research. New York, NY: Oxford University Press.

Scheffer M, Bascompte J, Brock WA, *et al.* 2009. Early-warning signals for critical transitions. *Nature* **461**: 53–59.

Šimůnek J, Šejna M, Saito H, *et al.* 2008. The HYDRUS-1D software package for simulating the movement of water, heat, and multiple solutes in variably-saturated media, Version 4.08, HYDRUS Software Series 3. Riverside, CA: Department of Environmental Sciences, University of California, Riverside.

Suding KN, Gross KL, and Houseman GR. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* **19**: 46–53.

Switalski TA, Bissonette JA, DeLuca TH, *et al.* 2004. Benefits and impacts of road removal. *Front Ecol Environ* **2**: 21–28.

Turner MG, Tinker DB, Romme WH, *et al.* 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* **7**: 751–75.

Wang Y, Amundson R, and Trumbore S. 1999. The impact of land use change on C turnover in soils. *Global Biogeochem Cy* **13**: 47–57.

Effects of Road Decommissioning on Stream Habitat Characteristics in the South Fork Flathead River, Mon....

Article *in* Transactions of the American Fisheries Society · May 2007

DOI: 10.1577/T06-134.1

Transactions of the American Fisheries Society 136:553–561, 2007

DOI: 10.1577/T06-134.1

[Note]

Effects of Road Decommissioning on Stream Habitat Characteristics in the South Fork Flathead River, Montana

MAGNUS MCCAFFERY*
Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812, USA

T. ADAM SWITALSKI
Wildlands CPR, Post Office Box 7516, Missoula, Montana 59807, USA

LISA EBY
Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812, USA

Abstract.—Previous studies have demonstrated the negative effects of roads on stream characteristics important for fish survival; however, few have examined whether decommissioning reverses these adverse impacts. We examined the relationships between the percentage of fine sediment in stream substrate and roads and looked at whether decommissioning had measurable effects on stream habitat in the Flathead National Forest, Montana. We conducted habitat surveys and substrate coring in 12 streams encompassing three watershed treatment types: (1) roadless areas, (2) areas with roads in use, and (3) areas with decommissioned roads. Significant positive correlations were found between the percentage of fine sediment in substrate and various measures of road impact (road density, roads in use, and number of stream crossings). Watersheds with roads in use had higher percentages of fine sediment than those without roads and those with decommissioned roads. Watersheds with high levels of vegetative regrowth on decommissioned roadbeds had a lower percentage of fines in stream sediment. Decommissioning efforts that enhance regrowth may improve stream habitat, although significant effects of these manipulations are difficult to detect through spatial comparisons. Future studies using either before–after or before–after–control designs to evaluate the effects of decommissioning practices on fish and wildlife habitat and populations are needed.

Roads primarily influence salmonid stream habitat by obstructing fish passage and degrading spawning, incubation, and juvenile rearing habitat (Furniss et al. 1991). Improperly designed culverts can impede or preclude fish passage and subsequently fragment aquatic habitat (Wofford et al. 2005). An excess of fine sediments resulting from soil erosion can degrade or completely destroy spawning habitat (e.g., Furniss et al. 1991). The successful incubation of salmonid embryos in stream gravels depends on intragravel water flow to provide oxygen and remove waste products (e.g., Bams 1969). Enhanced levels of fine sediment can reduce intragravel flow, impeding egg development as well as trapping and entombing emerging fry in the gravel (e.g., Phillips et al. 1975). Macroinvertebrate communities also respond negatively to fine sediments, thus influencing food availability for juvenile fish. In addition, excessive sediment delivery can decrease depth and number of pools thereby reducing the physical space available in the streams for rearing and overwintering of juvenile fish. If the riparian zone is compromised, then temperature, shade, and large wood would be altered, further affecting juvenile rearing habitat (Furniss et al. 1991). Although the effects of roads on fish habitat and production in any particular watershed are complex and a function of many interacting factors (Everest et al. 1987), their potential adverse effect on stream fish populations has prompted extensive restoration efforts.

In an attempt to mitigate the negative effects of forest roads the U.S. Forest Service is decommissioning about 3,200 km of roads each year and working to upgrade culverts and passage structures to facilitate fish migration (USFS 2002). Decommissioning roads can include a number of restoration strategies, ranging from blocking access to roads (with a berm or by bridge removal) to a complete removal of the roadbed and recontouring of the road prism to the original natural slope. However, in contrast with the wealth of information on the effects of existing roads (Forman and Deblinger 2000; Haskell 2000; Jones et al. 2000; Trombulak and Frissell 2000), almost no information exists on the effectiveness of road removal. Relatively few studies have documented that road decommissioning reduces road-related erosion (Kolka and Smidt 2001; Luce 1997; Madej 2001) and studies that have examined the effects of road decommissioning on wildlife are rarer still (Switalski et al. 2004). These studies have primarily examined decommissioning

---

* Corresponding author: magnus.mccaffery@umontana.edu

Received June 11, 2006; accepted December 18, 2006

actions involving complete road removal and recontouring in highly erodible landscapes. Few published studies have focused on the effects of road decommissioning on fish habitat and species in Montana (but see Wegner 1999). Given the variation in geomorphology and related underlying erodibility of the landforms and soil across the country, as well as the variety of types of road decommissioning activities, the evaluation of various road decommissioning actions across multiple geographic areas is necessary for us to determine the effects of restoration efforts on fish and wildlife.

In Montana, bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisii* are two native coldwater salmonid species of conservation concern. Connectivity between high-quality stream spawning and foraging habitats is necessary for migratory life history forms of both bull trout and westslope cutthroat trout to complete their life cycles. Although many factors have contributed to the decline of these species, habitat degradation and fragmentation are two primary concerns in their conservation (Fraley and Shepard 1989; Lee et al. 1997; Liknes and Graham 1988; Rieman et al. 1997). Roads have been implicated in the degradation of bull trout habitat; forest roads are negatively correlated with bull trout stream use, abundance, and spawning activity (Baxter et al. 1999; Dunham and Rieman 1999). In addition, there is evidence of a significant inverse relationship between the percentage of fine sediment in the substrate and survival to the emergence of westslope cutthroat and bull trout embryos in incubation tests (Weaver and White 1985; Weaver and Fraley 1991).

On the Flathead National Forest, Montana, road decommissioning typically refers to blocking road entrances with earthen berms, which allows for natural revegetation and soil stabilization. In fish-bearing streams culverts are typically removed and stream banks recontoured. In some cases road entrances are gated. In addition to increased connectivity associated with culvert removal, road decommissioning is expected to reduce the delivery of sediment to streams, thus increasing the quality of spawning and rearing habitat for trout.

We evaluated streams within the Flathead National Forest that comprised three treatment types: (1) roadless watersheds; (2) watersheds with main roads still in public use but often with spurs that are decommissioned, gated, or both; and (3) watersheds with decommissioned roads (bermed and culverts removed). We did not consider roads that were only seasonally gated as decommissioned. We addressed two questions. First, is there a relationship between substrate composition (percentage of fine sediment) and road density? Second, if so, does road decommissioning have measurable effects on the percentage of fine sediment and other stream habitat characteristics that are important to fish?

Study Area

Research was conducted in the Flathead National Forest in northwestern Montana. As part of the Northern Continental Divide Ecosystem, the Flathead National Forest's 2.3 million acres is considered to be 47% wilderness and is one of the few forests left in the contiguous U.S. where a full complement of native trout species remains. Streams were sampled in the southern half of the Forest in the South Fork Flathead River Basin (Figure 1). This basin is bounded to the east by the Bob Marshall Wilderness Complex and to the west by the Swan Mountains and primarily comprises sedimentary rock with dense stands of coniferous forest that exhibit historical clear-cut logging and associated roads.

Of the 6,100 km of roads on the Flathead National Forest, 544 km have been decommissioned and an additional 612 km are slated for decommissioning (U.S. Forest Service, Flathead National Forest, unpublished database for road decommissioning projects). The effects that these roads have on aquatic habitat vary and are based on (1) watershed characteristics and geomorphology (e.g., slope and soil type, land use, road density and use); (2) proximity of the road to the stream (riparian buffers, number of road crossings); and (3) stream characteristics (the power of the stream to move or flush sediment from system [e.g. Duncan and Ward 1985; Luce et al. 2001]). Similarly, influences of road decommissioning will vary depending on the location and quantity of the decommissioned roads in the watershed as well as how and when they were decommissioned.

We chose 12 study streams with fairly similar watershed and stream size and gradient characteristics, which controlled for differences in stream power and watershed size while exhibiting differences in watershed road treatments (Table 1). Twin Creek had a significantly larger watershed area, but had characteristics similar to our other streams. Study watersheds generally had roads that paralleled the stream with a riparian buffer greater than 20 m. To minimize confounding effects, watersheds of study streams did not have recent (within 5 years) wildfires or timber sales within the watershed. Three watersheds had roads-in-use (Wheeler, Emery, and Quintonkon creeks), while three watersheds had entirely roadless watersheds (Riverside, Tin, and Twin creeks) to provide reference stream conditions. Of the six watersheds containing decommissioned roads, two streams had all roads within their watershed decommissioned (Slide Creek and Connor Creek) and the

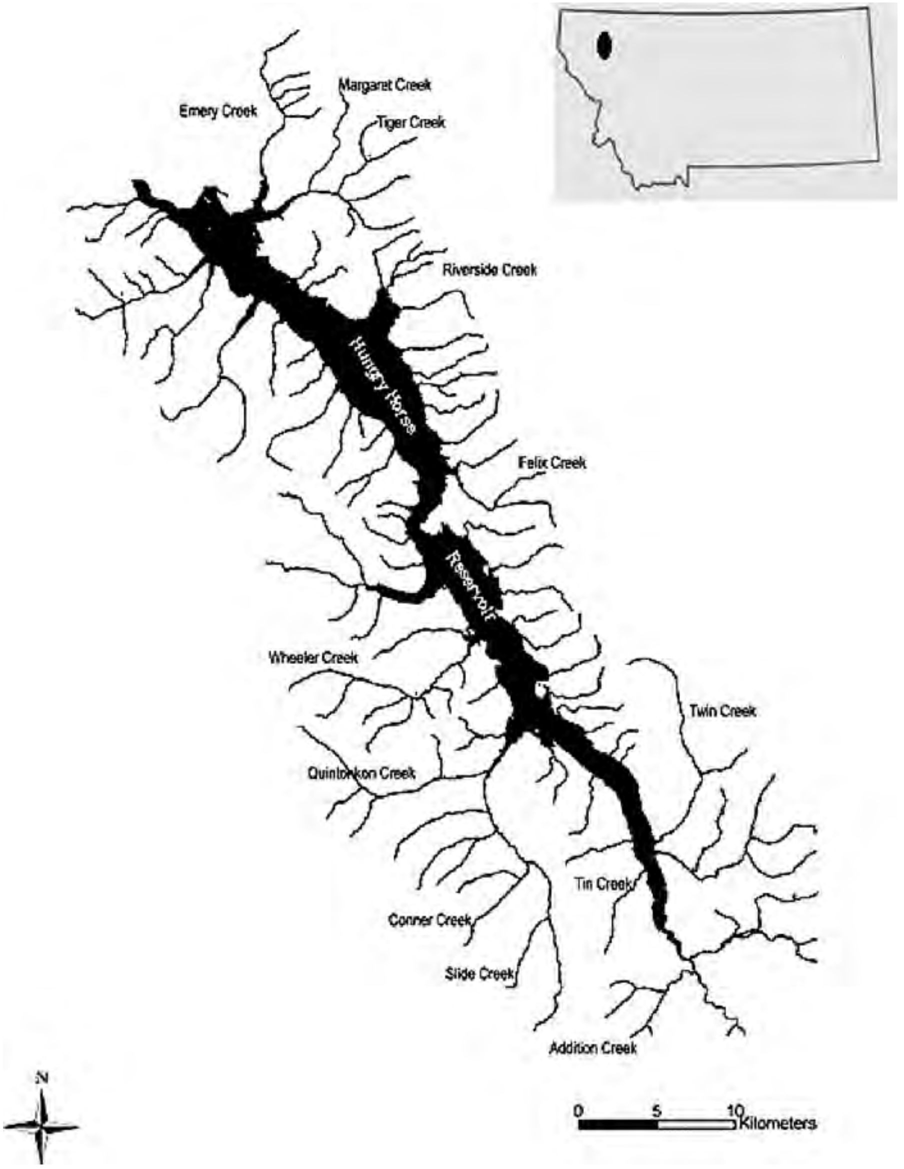


FIGURE 1.—Study area located in the Flathead National Forest (Hungry Horse and Spotted Bear Ranger Districts) in northwestern Montana. All of the study streams were tributaries to the South Fork of the Flathead River at or near Hungry Horse Reservoir.

remaining four watersheds contained a mix of road treatments (bermed with regrowth, as well as gated roads in administrative use; Table 1).

Methods

Basic road surveys were conducted to verify our categorization of roads within the different treatments. Watershed treatments were characterized as roadless, roads in use, or decommissioned. If they were decommissioned we qualitatively assessed the level of vegetative regrowth (sparse grass, dense grass, shrubs, or trees), and noted any signs of road activity (e.g., motorized vehicle tracks) for the primary road adjacent to the stream. We separated our decommissioned road treatments based on the level of revegetation of the primary road in the watershed. Conner, Slide, and Tiger creeks all had grass, bushes, and trees on the primary road and were classified as high

TABLE 1.—Stream and watershed habitat characteristics for 12 watersheds studied in the South Fork Flathead River basin.

Stream	Level of regrowth on decommissioned roads	Elevation (m)	Incline (%)	Total road density (km/km^2)	Road-in-use density (km/km^2)	Number of road crossings	Distance from Hungry Horse, Montana (km)	Watershed area (km^2)
Wheeler	Open road	1,364	3	0.61	0.24[a]	16	63	46.26
Emery	Open road	1,202	2	1.58	0.28	30	14	38.54
Quintonkon	Open road	1,223	2	0.69	0.25	15	70	55.45
Addition	Low	1,323	2	0.22	0.01[b]	4	93	38.87
Felix	High	1,139	2	1.51	0.00	4	46	19.91
Tiger	Low	1,234	2	0.13	0.00	0	21	17.46
Margaret	Low	1,295	5	0.67	0.00	3	19	10.42
Slide	High	1,347	2	0.33	0.00	0	84	12.90
Conner	High	1,299	2	0.53	0.07[c]	3	80	17.60
Riverside	Roadless	1,163	3	0.00	0.00	0	31	14.79
Tin	Roadless	1,184	2	0.02[d]	0.00	0	84	16.88
Twin	Roadless	1,113	2	0.00	0.00	0	79	116.92

[a] Seasonal closures.
[b] Gated during this study (summer 2004); decommissioned at the end of summer 2004.
[c] Bridge out at Sullivan Creek so no road in use in Conner watershed.
[d] Main road at base of watershed downstream from sampling.

regrowth watersheds. Other decommissioned watersheds (Addition, Margaret, and Felix) exhibiting only sparse grass were grouped together into a low regrowth category.

To quantify the influence that roads have on a watershed, we calculated a series of road-related variables for each of our watersheds. Both total road density (for all classes of roads) and the density of roads currently in use within each study watershed were calculated from U.S. Forest Service geographical information systems (GIS) road layers using the distance tool in ArcMap at a resolution of 1:24,000. Similarly, distance along roads between the stream access point to the closest town (Hungry Horse, Montana) was established as a surrogate measure of accessibility and hence traffic volume (Table 1). In addition, we noted any road crossings (e.g., bridge, culvert) in the field and used a Flathead National Forest map (scale: 1:126,720) to estimate the number of roads crossing streams within each watershed (Table 1).

Approximately 300 m of each stream was sampled both in the summer (June–July) and fall (September–November) of 2004, except at Wheeler Creek, which was only sampled in the fall. The lower half of each stream was divided into contiguous 100-m sections and three of these sections were randomly selected for sampling.

During summer sampling we performed habitat surveys (Overton et al. 1997). Proceeding upstream, we described each channel habitat unit (riffle, run, or pool) and measured its length (m), mean wetted width (m), middle depths of riffles (cm) and maximum depth of pools (cm). In each section we measured average incline and elevation, visually estimated bank stability, quantified large wood, and estimated canopy cover. Channel incline was assessed with a compass, elevation was obtained using a Garmin global positioning system (GPS), and canopy cover was estimated with a Moosehorn densitometer (80 readings along eight different cross-sectional transects per section). The stability of stream banks was rated on a scale from 1 to 4 as follows: 1 = banks were stable, less than 5% of the bank having signs of erosion or bank failure absent or minimal; 2 = banks were moderately stable, with infrequent, small areas (5–30% of bank in reach) indicative of erosion; 3 = banks were moderately unstable, 30–60% of the bank showing signs of erosion resulting in high erosion potential during floods; and 4 = banks were unstable, eroded areas being seen frequently along straight sections and bends (60–100% having erosional banks). We deployed a temperature logger (ibuttons, Maxim Dallas semiconductor) in each section to collect water temperature data every 90 min.

During fall sampling we measured pool habitat characteristics and performed substrate coring in study sections. Pool frequency and depth were analyzed for differences among the three treatment types using a Kruskal–Wallis test (Zar 1999). Ten substrate cores (McNeil core samples) per stream were collected in the lower two sections (five per section) to measure substrate composition and fine sediments. All cores were collected in flowing water, over cobble substrate, and at a pool–riffle break (as suggested by OPSW 1999). Cores were taken to a depth of 15 cm into the substrate. Oven-dried core samples were weighed after being shaken through sieves with mesh sizes of 75, 50, 25, 19, 12.5, 9.5, 6.3, 4.75, and 2.0 mm and 850, 425, and 63 μm. An average of 3.8 kg ± 0.058 (mean ± SE) of substrate was collected per core. Since fine

TABLE 2.—Characteristics of streams surveyed in the South Fork Flathead River basin (LWD = large woody debris, ND = no data).

Stream	Temperature (°C)	LWD/100 m		Bank stability[a]	Riffle area (%)	Average width (m)	Midstream depth (cm)	Pool frequency (per 100 m)	Maximum pool depth (cm)	Sediment <6.3 mm (%)
		Singles	Aggregates							
Wheeler	ND	6.8	1.9	1.0	85.9	8.9	35.3	1.2	89.5	23.88
Emery	7	23.1	8.0	1.0	89.1	4.4	29.7	4.7	67.3	34.22
Quintonkon	7	5.7	1.0	1.1	97.6	7.7	32.7	1.2	89.5	20.42
Addition	ND	16.8	4.2	1.1	83.0	6.7	52.7	6.1	79.7	22.02
Felix	9	11.4	3.0	1.6	97.9	5.7	19.3	3.0	71.7	20.64
Tiger	9	6.6	2.0	1.0	97.7	4.6	23.0	5.5	58.3	18.49
Margaret	8	15.7	4.0	1.0	97.9	3.8	22.3	6.1	59.3	20.78
Slide	8	12.1	3.9	1.3	94.9	5.0	27.7	3.0	77.7	14.81
Conner	10	3.0	1.6	1.1	96.2	5.4	29.0	3.7	54.3	14.45
Riverside	ND	8.9	5.0	1.0	58.1	4.9	38.8	7.4	66.3	21.36
Tin	8	7.8	1.5	1.1	97.3	4.8	33.7	4.0	61.7	13.36
Twin	10	0.0	0.0	1.1	83.2	9.3	31.7	3.0	77.7	18.53

[a] Scale = 1 to 4; see text for details.

material disturbed by coring typically remains in suspension within the corer and is often not included in the captured substrate, we improved our estimate of the fine particle component by agitating the remaining sediment within the core and extracting three 150-mL subsamples of water to measure suspended sediment. The height of the water within the corer was measured and converted to a volume based on a depth-to-volume curve produced in the laboratory specifically for this corer. These subsamples were returned to the laboratory where the sediment was settled and measured in Imhoff cones. The volume of fine sediment was then multiplied by the volume of water in the corer to determine the total fines. These wet volumes of fine sediment were then converted to a dry weight using a conversion factor developed by Shepard and Graham (1982) allowing us to add these measures of fine sediment to the fraction of our substrate composition data that was less than 63 μm in size.

Substrate composition was expressed as the percentage of substrate particles (SP) smaller than 6.3 mm. This is the size fractionation used to assess spawning habitat for both bull trout and westslope cutthroat trout (e.g., Shepard and Graham 1982; Weaver and Fraley 1991; 1993). We compared percent of substrate particles less than 6.3 mm among treatment types with a Kruskal–Wallis nonparametric analysis of variance (ANOVA) (Zar 1999). We examined correlations in our dataset associated with roads and watersheds. After eliminating highly correlated variables a step-wise multiple linear regression was used to evaluate which watershed characteristics (e.g., road crossings, watershed area) best predicted the percent of fine substrate. Finally, watersheds with decommissioned roads were analyzed using a stepwise multiple regression analysis to examine whether level of regrowth, number of road crossings, or watershed area explained a significant amount of variation in the percentage of substrate composed of fine sediment (Zar 1999).

Results

Stream Habitat Characteristics

Overall, stream sections were of similar size and gradient, and the habitat was dominated by riffles. Bank stability was high in all streams (Table 2).

Substrate Composition and Road Impacts

To investigate how roads affect the substrate composition of our study streams, we examined whether there was a correlation between the percentage of fine sediment (%SP < 6.3 mm) in the substrate and total road density, density of roads in use, distance from the closest town (Hungry Horse), and the number of road–stream crossings within the watershed. There was a significant positive relationship between percentage of fine sediment and road density (Pearson correlation = 0.36; $P = 0.038$, $n = 12$), roads in use (Pearson correlation = 0.43; $P = 0.021$, $n = 12$), and the number of road–stream crossings (Pearson correlation = 0.84; $P = 0.001$, $n = 12$, Figure 2). Furthermore, there was a negative trend but nonsignificant correlation (Pearson correlation = −0.573; $P = 0.051$, $n = 12$) between percentage of fine sediment in the substrate and potential road use (i.e., distance from Hungry Horse). These measures of watershed road characteristics were all significantly correlated with each other making it impossible to separate their potential effects. Given the extent of the riparian buffers (typically >20 m) in these watersheds, personal observations of erosion at road crossings during the road surveys and the high correlation of road–stream crossings with percentage of fine sediment, we used number of road–stream crossings for our analyses to detect potential effects of decommissioning roads.

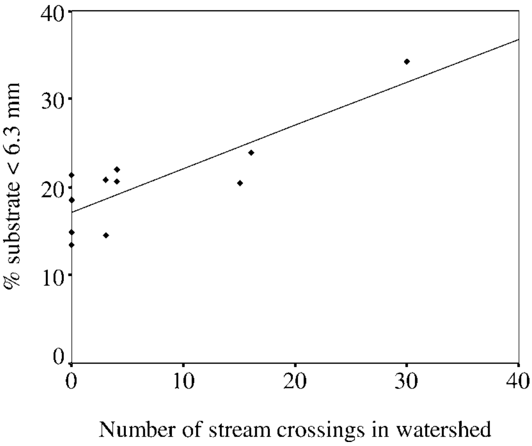


FIGURE 2.—Relationship between the percentage of substrate particles less than 6.3 mm in size and the number of stream crossings in the watershed ($r^2 = 0.70$, $P = 0.001$). Strong positive correlations were also found among total road density, the density of roads in use, and stream crossings.

Watershed Treatment Comparisons

There were no statistically significant differences in the number of pools per 100 m ($P = 0.981$) or maximum pool depth among our three treatment groups ($P = 0.207$; Table 2).

Watersheds with roads in use had the highest median percentage of substrate particles of less than 6.3 mm in stream cores and decommissioned and roadless watersheds exhibited similar percentages of fine sediment in stream cores, although the differences were not statistically significant (Kruskal–Wallis test: $\chi^2 = 3.15$, df = 2, $P = 0.20$; Figure 3a). Watersheds with decommissioned roads were tested for differences in percentage of fine sediment versus number of road crossings, watershed size, and amount of regrowth on roads. Percentage of fine sediment in stream substrate within the decommissioned watersheds was not significantly related to number of road crossings or watershed size. However, there was a significant effect of the level of regrowth with fine sediment (regrowth = 0.019, number of road crossings $P = 0.385$, area $P = 0.852$, final regression $F = 14.67$, $P = 0.02$, df = 5), whereby decommissioned roads with high levels of regrowth appeared to have a lower percentage of fine sediment in the stream substrate (Mann–Whitney test: $Z = -1.96$, $P = 0.05$; Figure 3b).

Discussion

Road building leads to increased sedimentation and a reduction in fish habitat quality (Gucinski et al. 2001; for reviews, see Meehan 1991; Trombulak and Frissell 2000) and areas without roads are often strongholds for native fish communities (Lee et al. 1997; Baxter et al. 1999). The percentage of substrate particles less than a given size for a specific species or guild is often considered the best indicator of fish habitat degradation from roads (Young et al. 1991). In this study, watersheds that had higher total road density, roads in use, and road–stream crossings exhibited higher percentages of fine sediment compared with those watersheds that had lower levels of road influence (Figures 2, 3a). These general trends tentatively support expectations about the relationship among roads, substrate composition, and potential for spawning success.

Other studies have found that as traffic increases, there are concomitant increases in sediment yields from roads (e.g., Reid and Dunne 1984). Using the distance along roads of each creek from the town of Hungry Horse as a surrogate measure of road use by vehicles, we found no significant relationship between increased percentage of fine sediment and increased potential traffic. Upon examination of our watersheds, we found that Emery Creek, which probably has the heaviest traffic volume given its relative accessibility (Table 1), exhibits the highest percent composition of fine sediment.

Having established a relationship between road density and crossings and fine sediment composition in streams (Figure 2), we examined whether road decommissioning is correlated with a lower percentage of fine sediment in stream substrate. We did not see significant differences among our three treatment groups. Watersheds with roads in use had higher levels of fine sediment in the substrate than either those without roads or those with decommissioned roads, but the high amount of fine sediment in Emery Creek had a large influence on these trends (Table 2).

Our lack of statistically significant results among treatments may stem from the combination of confounding factors and low power. For instance, in May 2004 (several weeks before sampling), our study area experienced a 14-year peak flood event with discharges approximately 50% higher than mean annual peak flow levels. This may have influenced our streams by flushing fine sediment from our study sites, thereby affecting our ability to detect differences in chronic sediment loading in these watersheds (U.S. Geological Survey, gauging station 12359800, South Fork Flathead River at Twin Creek near Hungry Horse).

There was a significant difference in the percentage of fine sediment in the substrate of streams with different levels of regrowth on decommissioned roads. Streams associated with watersheds containing a high amount of regrowth, whereby a mixture of trees, shrubs, and grasses had established themselves on the

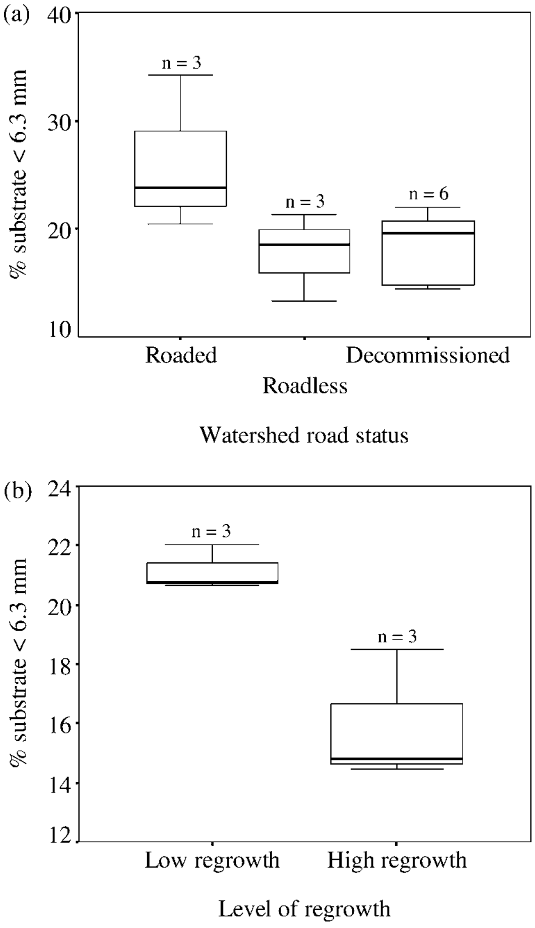


FIGURE 3.—Box plots showing **(a)** the percentage of fine substrate for each road treatment type ($\chi^2 = 3.15$, df $= 2$, $P = 0.20$) and **(b)** the percent of fine substrate with respect to the level of roadbed regrowth within decommissioned road treatments ($Z = -1.96$, $P = 0.05$). High regrowth refers to old roadbeds with a mixture of trees, shrubs, and grasses, while low regrowth refers to sparse grass. The heavy lines within the boxes represent the median values, the lower and upper boundaries of the boxes the 25th and 75th percentiles, and the whiskers the 10th and 90th percentiles.

old road, had lower percentages of fine sediment in the substrate than did those watersheds with only sparse grass (Figure 3b). Thus, as decommissioned roads become increasingly revegetated over time, the amount of fine sediment loading is reduced to the levels that existed before the roads were built.

The few studies in which road decommissioning has been shown to have large beneficial effects for fish habitat were conducted in areas with more erosive soils or higher susceptibility to mass wasting. The soils in the Flathead National Forest are not as erosive as some granitic soils where many of the most obvious road sedimentation problems exist (e.g., Clearwater National Forest, Megahan and Kidd 1972). However, large flood events and culvert blow-outs are not uncommon in this forest.

Our results suggest that road decommissioning that results in vegetative regrowth reduces fine sediment in streams, thereby conferring positive effects on stream habitat for bull and cutthroat trout in the Flathead National Forest. Other studies have demonstrated how upgrading passage barriers (e.g., perched culverts) can result in recolonization by juvenile bull trout (USFWS 2002). Bull trout populations also increased following full recontouring of the streams and culvert removals on the nearby Kootenai National Forest (Wegner 1999); a 48% decline in fine sediment and a 16% increase in bull trout redds was observed in the 5 years following decommissioning. Our study has attempted to elucidate differences in substrate composition associated with different road treatment types and levels of regrowth associated with decommissioning actions. Based on our results, we suggest that decommissioning roads that lead to high levels of revegetation probably reduces the amount of fine sediment in streams.

While road decommissioning appears to be an effective tool with which to mitigate many of the negative effects of roads on fish habitat, care must be taken when designing studies to demonstrate its effects. Given our estimated variance, detecting statistical significance would require large-effect sizes (~30–40% change in percentage of fine substrate), as well as large sample sizes ($n \geq 25$ streams). With the large amount of spatial variation in sedimentation that we observed among watersheds, even after controlling for watershed and stream characteristics, we recommend study designs in which streams serve as their own controls, that is, either replicated before–after or replicated before–after–control impact designs, to evaluate the effects of road decommissioning (Roni et al. 2005).

Acknowledgments

Funding provided by the Yellowstone to Yukon Conservation Science Grants Program. We thank J. Fox, E. Dallalio, and D. Bixby for data collection, R. Wahl, S. Amish, and three anonymous reviewers for review comments, as well as P. Van Eimeren and D. Mucklow from the Flathead National Forest for other support.

References

Bams, R. A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravels. Pages 71–87 *in* T. G.

Northcote, editor. Symposium on salmon and trout in streams. MacMillan, Vancouver.

Baxter, C. V., C. A. Frissell, and F. R. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. Transactions of the American Fisheries Society 128:854–867.

Duncan, S. H., and J. W. Ward. 1985. The influence of watershed geology and forest roads on the composition of salmon spawning gravel. Northwest Science 59:204–213.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642–655.

Everest, F. H., R. L. Beschta, J. D. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. *In* E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fisheries interactions. University of Washington, Contribution 57, Seattle.

Forman, R. T. T., and R. D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conservation Biology 14:36–46.

Fraley, J. J., and B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake River system, Montana. Northwest Science 63:133–143.

Furniss, M. J., T. D. Roelofs, and S. C. Yee. 1991. Road construction and maintenance. W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19, Bethesda, Maryland.

Gucinski, H., M. J. Furniss, R. R. Ziemer, and M. H. Brookes. 2001. Forest roads: a synthesis of scientific information. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Haskell, D. G. 2000. Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian Mountains. Conservation Biology 14:57–63.

Jones, J. A., F. J. Swanson, B. C. Wemple, and K. U. Snyder. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14:76–85.

Kolka, R., and M. Smidt. 2001. Revisiting forest road retirement. Water Resources Impact 3:15–16.

Lee, D. C., J. Sedell, B. Rieman, R. Thurow, and J. Williams. 1997. Broad-scale assessment of aquatic species and habitats. Pages 1057–1496 *in* T. M. Quigley and S. J. Arbelbinde, editors. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great basins, volume 3. U.S. Forest Service General Technical Report PNW-GTR-405.

Liknes, G. A., and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. Pages 53–60 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Luce, C. H. 1997. Effectiveness of road ripping in restoring infiltration capacity of forest roads. Restoration Ecology 5:265–275.

Luce, C. H., B. E. Rieman, J. B. Dunham, J. L. Clayton, J. G. King, and T. A. Black. 2001. Incorporating aquatic ecology into decisions on prioritization of road decommissioning. Water Resources Impact 3:8–14.

Madej, M. A. 2001. Erosion and sediment delivery following removal of forest roads. Earth Surface Processes and Landforms 26:175–190.

Meehan, W. R., editor. 1991. Influences of forest and rangeland management on salmonid fisheries and their habitats. American Fisheries Society, Bethesda, Maryland.

Megahan, W. F., and W. J. Kidd. 1972. Effects of logging and logging roads on erosion and sediment deposition from steep terrain. Journal of Forestry 70:136–141.

OPSW (Oregon Plan for Salmon and Watersheds). 1999. Water quality monitoring, technical guidebook, version 2.0. OPSW, Corvallis.

Overton, C. K., S. P. Wollrab, B. C. Roberts, and M. A. Radko. 1997. R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory procedures handbook. U.S. Forest Service General Technical Report INT-GTR 346.

Phillips, R. W., R. L. Lantz, E. W. Claire, and J. R. Morning. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104:462–466.

Reid, L. M., and T. Dunne. 1984. Sediment production from forest road surfaces. Water Resource Research 20:1753–1761.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River basin. North American Journal of Fisheries Management 17:1111–1125.

Roni, P., M. C. Liermann, C. Jordan, and E. A. Steel. 2005. Steps for designing a monitoring and evaluation program for aquatic restoration. Pages 13–34 *in* P. Roni, editor. Monitoring stream and watershed restoration. American Fisheries Society, Bethesda, Maryland.

Shepard, B. B., and P. J. Graham. 1982. Monitoring spawning gravel bed material used by bull trout on the Glacier View District, Flathead National Forest. Montana Fish, Wildlife and Parks, Completion Report, Kalispell.

Switalski, T. A., J. A. Bissonette, T. H. DeLuca, C. H. Luce, and M. A. Madej. 2004. Benefits and impacts of road removal. Frontiers in Ecology and the Environment 2:21–28.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

USFS (U.S. Forest Service). 2002. Report of the Forest Service: fiscal year 2001. USFS, Washington, D.C.

Weaver, T., and J. J. Fraley. 1991. Fisheries habitat and fish populations. Flathead Basin Forest Practices, Water Quality and Fisheries Cooperative Program. Flathead Basin Commission, Kalispell, Montana.

Weaver, T., and J. J. Fraley. 1993. A method to measure emergence success of westslope cutthroat trout fry from varying substrate compositions in a natural stream channel. North American Journal of Fisheries Management 13:817–822.

Weaver, T., and R. G. White. 1985. Coal Creek fisheries monitoring study III. Montana State Cooperative Fisheries Research Unit, Quarterly Progress Report, Bozeman.

Wegner, S. 1999. Monitoring of watershed restoration activities: Quartz Creek–Middle Kootenai bull trout recovery area. Pages 317–324 *in* D. S. Olsen and J. P. Potyondy, editors. Proceedings of the Bozeman Specialty Conference on Wildland Hydrology. American Water Resources Association, Middleburg, Virginia.

Wofford, J. E. B., R. E. Gresswell, and M. A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15:628–637.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. North American Journal of Fisheries Management 11:339–346.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey.

Modeling relationships between landscape-level attributes and snorkel counts of chinook salmon and steelhead parr in Idaho

William L. Thompson and Danny C. Lee

Abstract: Knowledge of environmental factors impacting anadromous salmonids in their freshwater habitats, particularly at large spatial scales, may be important for restoring them to previously recorded levels in the northwestern United States. Consequently, we used existing data sets and an information-theoretic approach to model landscape-level attributes and snorkel count categories of spring–summer chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) parr within index areas in Idaho. Count categories of chinook salmon parr were negatively related to geometric mean road density and positively related to mean annual precipitation, whereas those for steelhead parr were negatively related to percent unconsolidated lithology. Our models predicted that chinook salmon parr would be in low count categories within subwatersheds with >1 $km \cdot km^{-2}$ geometric mean road densities and (or) <700 mm mean annual precipitation. Similarly, steelhead parr were predicted to be in low count categories in subwatersheds with >30% unconsolidated lithology. These results provide a starting point for fish biologists and managers attempting to map approximate status and quality of rearing habitats for chinook salmon and steelhead at large spatial scales.

Résumé : La connaissance des facteurs environnementaux influant sur les salmonidés anadromes dans leurs habitats dulcicoles, particulièrement aux grandes échelles spatiales, peut être importante pour le rétablissement des populations aux niveaux observés dans le passé dans le nord-ouest des États-Unis. Ainsi, nous avons utilisé des ensembles de données déjà existants et une approche basée sur la théorie de l'information pour relier des attributs du paysage avec l'abondance des tacons de saumon quinnat (*Oncorhynchus tshawytscha*) et de saumon arc-en-ciel (*Oncorhynchus mykiss*), dénombrés dans l'eau par plongée au tuba, dans des secteurs témoins de l'Idaho. Les catégories d'abondance des tacons de saumon quinnat étaient corrélées négativement avec la moyenne géométrique de la densité des routes et corrélées positivement avec les précipitations anuelles moyennes, tandis que celles des tacons de saumon arc-en-ciel étaient corrélées négativement avec le pourcentage de matière non consolidée. Nos modèles prévoient que les tacons de saumon quinnat seraient peu abondants dans les bassins secondaires où les moyennes géométriques de la densité des routes sont >1 $km \cdot km^{-2}$ et (ou) les précipitations annuelles moyennes sont <700 mm. De même, ils prévoient que les tacons de saumon arc-en-ciel seraient peu abondants dans les bassins secondaires où le pourcentage de matière non consolidée est >30%. Ces résultats peuvent servir de point de départ aux biologistes et aux gestionnaires responsables de la faune ichthyenne qui veulent établir des cartes représentant l'état et la qualité approximatifs des habitats où se développent le saumon quinnat et le saumon arc-en-ciel couvrant de grandes régions.

[Traduit par la Rédaction]

Introduction

Numbers of anadromous salmonids have greatly decreased from previously recorded levels for many stocks in the northwestern United States (Nehlsen et al. 1991). For instance, numbers of salmon and steelhead in the Columbia Basin have decreased sharply from an estimated 10–16 million adults to about 1.5–4.0 million adults during this century (Northwest Power Planning Council 1986). One factor thought to be influencing these declines is loss or degradation of freshwater spawning and rearing habitats (Nehlsen et al. 1991). Unfortunately, empirical data supporting this assertion at the landscape or basinwide scale are lacking in the published literature because fishery research has traditionally been conducted on smaller spatial scales (Schlosser 1991; but see Dunham and Rieman 1999; Torgersen et al. 1999). Thus, there is a need for empirically based models to investigate relationships between large-scale habitat and land management attributes and numbers of anadromous salmonids in their rearing environments (e.g., Bradford et al. 1997). These models could be used to predict status and quality of salmon spawning and rearing habitats across an area of interest as well as serve to highlight possible factors affecting population status and trends.

Availability of broadscale habitat and land management data generated by the recent interior Columbia Basin assessment (Quigley and Arbelbide 1997) and a 10-year data set of

Received May 20, 1999. Accepted May 31, 2000.
J15149

W.L. Thompson[1] and D.C. Lee.[2] USDA Forest Service, Rocky Mountain Research Station, 316 East Myrtle Street, Boise, ID 83702, U.S.A.

[1] Author to whom all correspondence should be addressed. e-mail: bthompson02@fs.fed.us

[2] Present address: USDA Forest Service, Sierra Nevada Conservation Framework, 801 I Street, Sacramento, CA 95814, U.S.A.

spring–summer chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) parr counts obtained from streams across Idaho (Hall-Griswold and Petrosky 1996) provided an opportunity to build large-scale predictive models based on empirical data. Consequently, we applied the latest information-theoretic modeling techniques (Buckland et al. 1997; Burnham and Anderson 1998) to investigate possible relationships between broadscale habitat and land management attributes and snorkel counts of spring–summer chinook salmon and steelhead parr within index streams in the Snake River drainage in Idaho. This geographical area is of particular importance because the indigenous stocks of spring–summer chinook salmon and steelhead have been listed as threatened under the Endangered Species Act (Federal Register 1997, 1998*a*). Due to various shortcomings with the snorkel count data, emphasis of this paper is as much on the approach to extract information from this broadscale but problematic data set as it is on interpretation of model results. We emphasize that the information-theoretic approach to model building, model selection, and model averaging applied in this paper is relevant to any study requiring a statistically based modeling approach.

Materials and methods

Snorkel count data set

The Idaho Department of Fish and Game (IDFG) and several cooperating agencies conducted snorkel counts of juvenile chinook salmon and steelhead (i.e., parr) in the Salmon River, Clearwater River, and lower Snake River drainages in Idaho during 1986–1995 (Hall-Griswold and Petrosky 1996) (Fig. 1). Abundance indices were obtained via snorkel counts by divers swimming approximately 100 m upstream within stream sections. One to five divers were used depending on stream size (Petrosky and Holubetz 1986). Stream sections were chosen based on a variety of criteria such as access, existence of previous counts, and perceived quality of rearing habitat (J. Hall-Griswold, IDFG, Stanley, Idaho, personal communication). Thus, selection of stream sections was nonrandom, but these sections represented a spectrum of habitats, stocks, and production types (i.e., wild (native) and natural (having a previous hatchery influence); Rich and Petrosky 1994). Although an attempt was made to survey the same sections over time, location and size (length and width) of snorkeled sections often varied among years mainly due to loss of previous section boundary markers, difficulties in relocating inadequately described sections, loss of access, and annual differences in stream flows. Further, not all sections were surveyed every year because of personnel, funding, and logistical constraints (J. Hall-Griswold, IDFG, Stanley, Idaho, personal communication). Finally, some stream sections were stocked with hatchery fish to better evaluate population responses of parr to mitigation measures (Petrosky and Holubetz 1986).

Subsetting the snorkel count data set

We only analyzed counts from stream sections where mitigation measures and stocking were not applied (see Rich and Petrosky 1994, their appendix B) because of confounding effects of those factors on the relationship between landscape-level variables and fish abundance. In addition, we limited our analyses to counts conducted when the water temperature exceeded 9°C because of the low detectability of fish below this temperature (Thurow 1994), which also would have had a confounding effect on the relationship between landscape attributes and snorkel counts.

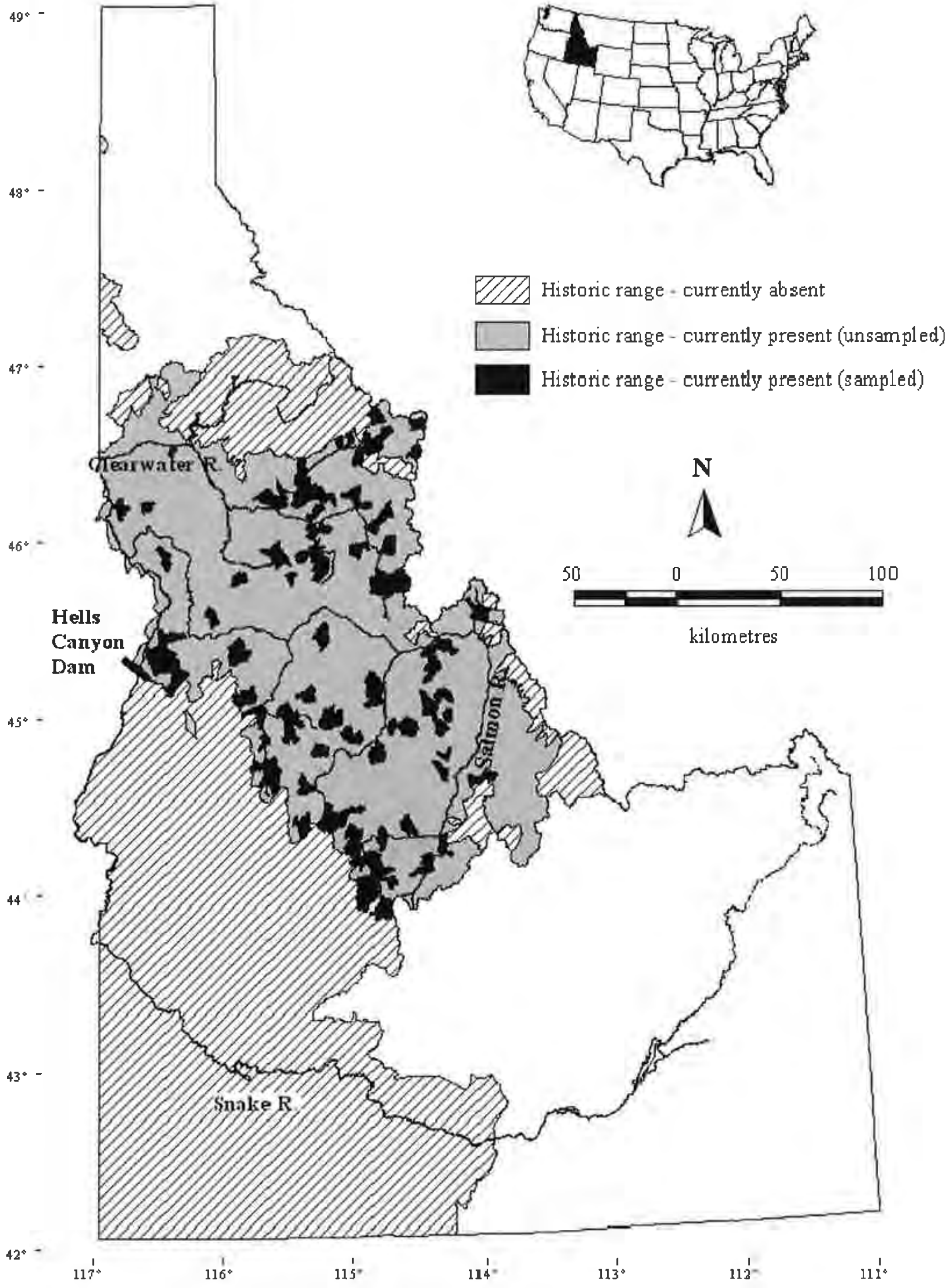
Because snorkel counts were uncorrected for incomplete detectability of fish within sections and therefore contained an unknown amount of bias (e.g., Rodgers et al. (1992) reported that only 40% of fish were detected during their snorkel counts), we pooled them into two categories in an attempt to alleviate detrimental effects of this bias on interpretation of model results. Categories were defined based on fish density indices and habitat ratings used by IDFG to categorize quality of rearing habitat; these values were 0.12 parr$\cdot$m^{-2} for chinook salmon and 0.06 parr$\cdot$m^{-2} for steelhead (Hall-Griswold and Petrosky 1996). Counts were divided by estimated area of each snorkeled stream section to provide a common unit of comparison with the IDFG ratings. Snorkel counts per unit area at or below 0.12 parr$\cdot$m^{-2} for chinook salmon or 0.06 parr$\cdot$m^{-2} for steelhead were placed into category 1, whereas higher counts per unit area were placed into category 2. This approach may lessen effects of bias, for instance, when two stream sections have the same actual densities of chinook salmon parr (e.g., 0.06 parr$\cdot$m^{-2}) but different detection rates of individuals (e.g., 40 and 80%). In this case, if observed counts were used, one section would be improperly modeled with twice the observed count than the other section, which could lead to spurious model results. Conversely, results of both counts would be placed into the same count category under the categorization approach described above. Note, however, that categorization still could lead to misclassification of stream sections (and spurious results), depending on the detectability of fish within a given section and how close the count per unit area was to the cutoff value used in the categorization.

We pooled seasonal runs for both species because sample sizes were inadequate to model these data separately. Although peaks in average counts per unit area differed slightly between runs for both species in two years during 1986–1990, their 90% confidence intervals broadly overlapped. We also included both wild and natural populations in our analyses. Further, we concentrated on counts from C channels for chinook salmon and B channels for steelhead because these were their optimal habitats (Hall-Griswold and Petrosky 1996) and therefore should have supported higher densities of parr. C channels occurred in low-gradient (<2% slope) terrain, whereas B channels were those in moderate-gradient (2–4% slope) terrain (Rosgen 1985, 1996). Finally, data from the year with the highest average counts per unit area for each species were used in our investigation of landscape linkages. We did this to maximize our ability to detect a difference between better and lower quality sites, where quality was defined in terms of fish counts per unit area during years of high fish numbers. Preliminary analyses suggested that average counts per unit area of fish were similar between better quality sites and lower quality sites during years of low counts, whereas these sites were much more distinct during years of high counts (J. Peterson, Rocky Mountain Research Station, Boise, Idaho, unpublished data). Difficulties associated with site identification, nonrandom site selection, incomplete time series of surveys, and counting bias precluded use of typical methods for modeling time series data.

Landscape habitat and anthropogenic data

Landscape-level data were compiled by Lee et al. (1997) and defined at the subwatershed scale, which is about 7800 ha on average within the Columbia Basin. These variables were categorized as either physiographic and geophysical or as anthropogenic (Table 1). One of the anthropogenic variables, management cluster, was categorical (i.e., each subwatershed was assigned the predominant category) and was generated by Lee et al. (1997) from results of a cluster analysis of variables representing land-type classification, management classification, ownership, percent grazed, and percent wilderness (for details, see Lee at al. 1997). We further pooled these results into four broad categories for simplicity (Ta-

Fig. 1. Mapping of historical and current range of chinook salmon and steelhead in Idaho, U.S.A. (Lee et al. 1997). Dark areas are subwatersheds containing stream sections that were sampled for chinook salmon parr during 1987 and steelhead parr during 1990.



ble 1). This variable is an index to potential effects of land use and land management practices on adjacent streams and stream fish populations.

Modeling approach

We employed the information-theoretic approach to model building and selection suggested by Akaike (1973) and extended by Burnham and Anderson (1998). First, a global (i.e., overall; Burnham and Anderson 1998) logistic regression model was constructed with count category as the dichotomous response and landscape-level habitat and anthropogenic covariates that were deemed ecologically most relevant as predictors. Choice of predictors was based on results from Lee et al. (1997) and subject area experts familiar with the study area. We then assessed the fit of the global model via the Hosmer–Lemeshow goodness-of-fit (GOF) test and checked the Pearson χ^2 residuals for obvious outliers (i.e., >2; Hosmer and Lemeshow 1989). An outlier was dropped from

Table 1. Category and description of covariates used in modeling landscape (subwatershed scale) habitat and land management attributes (Lee et al. 1997) with count categories of chinook salmon and steelhead parr.

Category	Model covariate	Description
Physiographic and geophysical	Precip	Mean annual precipitation (mm) based on the PRISM model (Daly et al. 1994)
	Sumtemp	Mean annual maximum summer temperature (°C)
	Slope	% of subwatershed with slopes >50%
	Mafic	% of subwatershed with mafic lithology
	Unconsol	% of subwatershed with unconsolidated lithology
Anthropogenic	Georoad	Geometric mean road density (km·km^{-2})
	Mngclus	Management cluster variable containing four land use and ownership categories: (1) HIF (high impact forest): high impact, grazed USDA Forest Service forest (2) MF (managed forest): moderate to high impact, ungrazed USDA Forest Service forest (3) W (wilderness): USDA Forest Service wilderness (4) R (rangeland): USDI BLM rangelands and moderate impact, grazed USDA Forest Service rangeland

analysis if its inclusion caused serious model lack of fit (see below). The Hosmer–Lemeshow GOF statistic was generated by ordering observations by their event probabilities, grouping them into a 2 × g table (where g is number of groups; for the grouping procedure, see Hosmer and Lemeshow 1989), and calculating a Pearson χ^2 GOF statistic for this table. Low P values ($P < 0.10$) indicated model lack of fit. If the global model adequately fitted the data, we constructed a subset of candidate models from it that represented ecologically meaningful combinations of the landscape covariates. Each subsetted model was assumed to provide an adequate fit if the global model did so (Burnham and Anderson 1998).

Model selection was performed using a modification of Akaike's information criterion (AIC) (Akaike 1973; Burnham and Anderson 1998). An extension of likelihood theory, AIC is an estimate of the relative distance between model pairs (Burnham and Anderson 1998), where distance refers to the Kullback–Leibler distance of information theory (Kullback and Leibler 1951). The Kullback–Leibler distance is a measure of the degree of information loss when a model is used to approximate reality (Cover and Thomas 1991; Burnham and Anderson 1998). Specifically, AIC is defined as

$$\mathrm{AIC} = -2\ \ln(L(\hat{\theta}\,|\,\mathrm{data})) + 2k$$

where $\ln(L(\hat{\theta}|\,\mathrm{data}))$ is the maximized log-likelihood over the unknown model parameters (θ) given the data and k is the number of estimable parameters in the model (Buckland et al. 1997; Burnham and Anderson 1998). We used the small sample adjustment to the AIC that also corrects for overdispersion in count data, called QAICc. This statistic is calculated as

$$\mathrm{QAICc} = \frac{-2\ln(L(\hat{\theta}\,|\,\mathrm{data}))}{\hat{c}} + 2k + \frac{2k(k+1)}{n-k-1}$$

where $\hat{c}$ is the χ^2 GOF statistic for the global model and n is sample size (Burnham and Anderson 1998). Overdispersion refers to instances where sampling (observed) variance exceeds the theoretical variance of the underlying model (e.g., binomial model) and is commonly present in count data (Burnham and Anderson 1998). We used $\hat{c}$ to adjust for overdispersion in parameter estimates for each candidate model as well.

Models with lower QAICc values are considered better approximating models than those with higher values. However, QAICc is a relative statistic. The meaningful quantity for comparing candidate models is the difference between a particular model's QAICc value and the lowest QAICc value from all models; this difference is referred to as ΔQAICc (Burnham and Anderson 1998). The relative plausibility or weight of evidence of each model, given the data (w_i), can then be computed as

$$w_i = \frac{e^{(-\Delta \mathrm{QAICc}_i/2)}}{\sum_{r=1}^{R} e^{(-\Delta \mathrm{QAICc}_r/2)}}$$

where $\Delta\mathrm{QAICc}_i$ is the ΔQAICc value for the ith model in a set of R candidate models (Buckland et al. 1997). These w_i, or model weights, also can be used in model averaging. Instead of assuming a single "best" model and using its parameter estimates to make inferences, we based our inferences and predictions on a composite model generated from the w_i weighted average of parameter estimates for each landscape covariate from the set of candidate models (for details on model averaging, see Burnham and Anderson 1998). Model averaging incorporates both uncertainty related to model selection and uncertainty associated with parameter estimates within each candidate model. Inference based on a single model will lead to underestimates of variance and hence poor confidence interval coverage for parameter estimates unless its w_i is much higher (see below) than that of all other competing models (Burnham and Anderson 1998). Our composite models (one each for chinook salmon and steelhead data) only contained landscape covariates within candidate models whose w_i were at least one tenth of the maximum w_i, which is comparable with the minimum cutoff point (i.e., 8 or 1/8) suggested by Royall (1997) as a general rule-of-thumb for evaluating strength of evidence.

Interpreting model results

Data for landscape covariates were standardized so that their coefficients could be interpreted on a common scale. We also computed an odds ratio for each covariate by using its unstandardized coefficient, e.g., raising the coefficient to base "e" or e^{β_1}, to facilitate interpretation of the magnitude of its effect on parr densities. As given, these odds ratios are based on a single unit change, whereas larger (or smaller) units of change may be more ecologically interpretable. Therefore, we multiplied relevant unstandardized coefficients by a constant (C) whose magnitude reflected a more meaningful interpretation than a single unit change (e.g., $e^{C\beta_1}$; Hosmer and Lemeshow 1989). We obtained an initial estimate of the magnitude of the constant for each covariate based on the difference represented in two standard deviations from its mean as computed from the database compiled by the interior Columbia Basin assessment (Lee et al. 1997). Then, we consulted with subject area experts familiar with the study area to fine-tune these estimates. For example, the model coefficient for percentage of subwatershed containing >50% slopes (Slope) was multiplied by 10 because a 10% change in Slope from one subwatershed to another had more meaning, in terms of physical processes potentially affecting the streams and fish therein, than a single unit (1%) change in Slope. However, we also present unstandardized coeffi-

Table 2. Model selection results for logistic regression models containing landscape habitat predictor variables and count categories of chinook salmon parr sampled during 1987 (n = 37 subwatersheds (72 stream sections)).

Candidate model	QAICc	ΔQAICc	ΔQAICc weight	% of maximum ΔQAICc weight
Precip, Slope, Georoad	46.50	0	0.379	100
Precip, Mafic	48.48	1.98	0.141	37.2
Precip	48.77	2.27	0.122	32.2
Precip, Slope, Mafic	49.15	2.65	0.101	26.6
Precip, Slope, Unconsol, Georoad	49.16	2.66	0.101	26.6
Precip, Unconsol	50.07	3.57	0.064	16.9
Georoad	51.72	5.22	0.028	7.4
Precip, Slope, Unconsol	51.98	5.48	0.024	6.3
Sumtemp	53.50	7.00	0.011	2.9
Slope, Mafic	53.87	7.37	0.010	2.6
Sumtemp, Mafic	54.19	7.69	0.008	2.1
Global Model	54.94	8.44	0.006	1.6
Slope, Georoad, Mngclus	56.87	10.37	0.002	0.5
Mngclus	58.05	11.55	0.001	0.3
Slope, Mngclus	58.44	11.94	0.001	0.3
Georoad, Mngclus	58.60	12.10	0.001	0.3
Unconsol, Georoad, Mngclus	61.42	14.92	<0.001	<0.1

cients and their standard errors for those interested in interpreting odds ratios based on a single unit change.

We did not simply rely on statistical significance to interpret model results because an odds ratio could be small enough to be considered ecologically unimportant but still be statistically significant (Yoccoz 1991). Note that statistical significance can be construed if the confidence interval for an odds ratio does not include 1; this is equivalent to testing, say, $\beta_1 = 0$, which can be respecified in terms of an odds ratio, $e^{\beta_1} = e^0 = 1$. We evaluated ecological importance of each covariate in the composite model by computing 90% confidence intervals for the scaled odds ratios (e.g., $e^{C\hat{\beta} \pm 1.64 C \widehat{\mathrm{SE}}(\hat{\beta}1)}$, where $z_{0.95} = 1.64$; Hosmer and Lemeshow 1989) and interpreting magnitudes of the values contained within these intervals (Gerard et al. 1998). A confidence interval that only contained values whose sizes were considered meaningful indicated an ecologically important relationship between the covariate and parr count categories. Conversely, an interval that only contained values whose magnitudes were considered of minimal importance indicated a covariate exhibiting a weak relationship with parr count categories. Finally, a confidence interval that contained values for odds ratios either on both sides of 1 or whose range included both ecologically important and unimportant magnitudes indicated inconclusive results due to imprecision from inadequate sample sizes.

We computed the predicted probability ($\hat{p}$) that a subwatershed had a low count category of parr (category 1) or a moderate to high count category of parr (category 2) using the formula $\hat{p} = \frac{1}{1 + e^{(-\beta_0 - \tilde{\beta}\tilde{X})}}$, where β_0 is the model intercept, $\tilde{B}$ is the vector of slope estimates, and $\tilde{X}$ is the vector of predictor variables (Hosmer and Lemeshow 1989). A Pearson correlation (r) was then calculated between predicted probability and predictor variable(s) with an ecologically important relationship with parr count category in both the chinook salmon and the steelhead composite models. If more than one predictor variable was ecologically important, we used the additional predictors as a basis for stratification for the correlation analysis. For instance, if composite model results indicated that both geometric mean road density and mean annual precipitation had ecologically important relationships with chinook salmon parr count categories, correlations were computed between predicted probability and mean annual precipitation for subwatersheds with both low and medium to high geometric mean road densities.

The SAS statistical package (SAS Institute Inc. 1996) was used for all of our analyses. Both the type I error rate (α) for GOF tests and the confidence coefficient for confidence intervals were set at 0.10 prior to analyses.

Results

We used data from 1987 for chinook salmon and from 1990 for steelhead because these years contained both the highest average parr counts per unit area and the narrowest confidence intervals of these estimates for each species. After removing one obvious outlier whose inclusion caused a serious model lack of fit, the global model for chinook salmon adequately fitted the data (Hosmer–Lemeshow GOF statistic = 6.06, 7 df, $P = 0.53$). The global model for steelhead also adequately fitted the data (Hosmer–Lemeshow GOF statistic = 9.81, 7 df, $P = 0.20$) and had no obvious outliers.

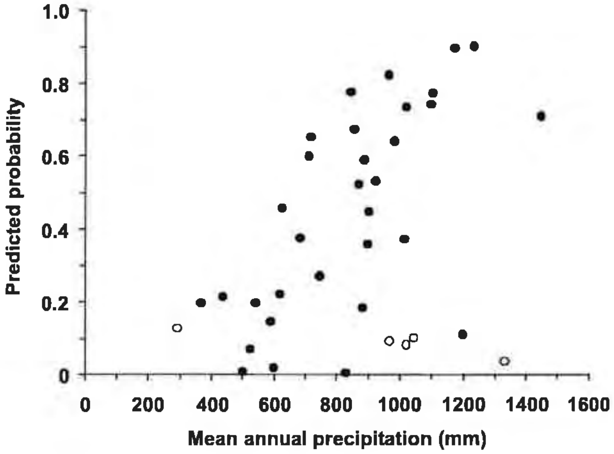
For the chinook salmon parr data, the candidate model containing mean annual precipitation, percentage of subwatershed containing >50% slopes, and geometric mean road density was nearly three times more plausible than the next best approximating model (Table 2). The composite habitat model for the chinook salmon data contained three covariates that were statistically significant, two of which had a fairly strong relationship with parr count categories (Table 3). Geometric mean road density exhibited a negative relationship with chinook salmon parr count categories in that moderate to high counts of parr were 1.33 (1/0.750) times less likely to occur in subwatersheds with every increase in 1 $\mathrm{km \cdot km^{-2}}$ road densities. Conversely, moderate to high counts of chinook salmon parr were at least 1.29 times more likely to occur in subwatersheds with every 200-mm increase in mean annual precipitation. The lower bound of the odds ratio for percent slope >50% in a subwatershed was statistically significant but of trivial magnitude (Table 3).

Table 3. Model-averaged results of composite models for chinook salmon and steelhead.

Species	Model parameter	Estimated coefficient (SE)	Standardized coefficient	OR unit change	Estimated OR	90% CI for OR	
						Lower	Upper
Chinook salmon	Intercept	−2.336 (1.531)	—	—	—	—	—
	Precip	0.004 (0.002)	0.658	200	2.164	1.293	3.622
	Slope	−0.125 (0.073)	−0.598	10	0.286	0.086	0.948
	Mafic	−1.490 (1.114)	−0.512	10	<0.001	<0.001	28.992
	Unconsol	0.008 (0.024)	0.079	10	1.080	0.723	1.612
	Georoad	−1.023 (0.448)	−0.624	1	0.360	0.172	0.750
Steelhead	Intercept	−1.357 (1.728)	—	—	—	—	—
	Precip	0.002 (0.001)	0.300	200	1.350	0.922	1.975
	Sumtemp	0.274 (0.140)	0.259	2	1.728	1.092	2.735
	Slope	−0.018 (0.028)	−0.085	10	0.833	0.525	1.324
	Mafic	0.026 (0.009)	0.390	10	1.300	1.120	1.509
	Unconsol	−0.107 (0.044)	−0.645	10	0.342	0.167	0.701
	Georoad	0.191 (0.250)	0.131	1	1.210	0.803	1.824

Note: Model parameters whose 90% confidence intervals (CI) for their estimated odds ratios (OR) do not include 1 are statistically significant.

Fig. 2. Relationship between mean annual precipitation and geometric mean road density (open circles indicate low density and solid circles indicate medium to high density) and predicted probability ($\hat{p}$) of a subwatershed containing either low (e.g., $\hat{p} \le 0.5$) or moderate to high (e.g., $\hat{p} > 0.5$) count categories of chinook salmon parr.



Evidence was inconclusive for the remaining covariates in the composite habitat model for chinook salmon.

Subwatersheds with low geometric mean road density (<1 km·km^{-2}; adapted from Lee et al. 1997) had a strong positive correlation (r = 0.643, n = 32) between mean annual precipitation and predicted probability of chinook salmon parr count category, whereas those with medium to high road density (≥1 km·km^{-2}) had a very strong negative correlation (r = −0.874, n = 5) between these variables. The five subwatersheds containing medium to high geometric mean road densities had predicted probabilities close to 0, which indicated that these subwatersheds were classified as containing low count categories of chinook salmon parr regardless of mean annual precipitation levels (Fig. 2).

For the steelhead parr data, the model containing mean annual precipitation and percent unconsolidated lithology was the best approximating model but was only slightly more plausible than the next highest ranked model (Table 4). The composite habitat model contained three covariates whose odds ratios were statistically significant (Table 3) but only one (percent unconsolidated lithology) had a fairly strong relationship with parr count categories. That is, moderate to high counts of steelhead parr were at least 1.43 (1/0.701) times less likely to occur in subwatersheds with every 10% increase in unconsolidated lithology than low densities. Thus, there was a negative relationship between steelhead parr counts and unconsolidated lithology.

Both mean annual maximum summer temperature and percent mafic lithology had a small positive relationship with moderate to high counts of steelhead parr. Moderate to high steelhead parr counts were at least 1.09 times more likely to occur in subwatersheds with every increase in 2°C mean annual maximum summer temperature and at least 1.12 times more likely to occur in subwatersheds with every increase in 10% mafic lithology (Table 3). Information on all other covariates in the composite habitat model was inconclusive.

Subwatersheds with <10% unconsolidated lithology had a weakly to moderately negative correlation (r = −0.343, n = 69) with predicted probability of steelhead parr count category, whereas those with >10% unconsolidated lithology exhibited an extremely strong negative correlation (r = −0.996, n = 10) with these predicted probabilities. Using the typical 0.5 cutoff for categorizing predicted probabilities (Hosmer and Lemeshow 1989), the five subwatersheds with >30% unconsolidated lithology would be classified as containing low count categories of steelhead parr (Fig. 3).

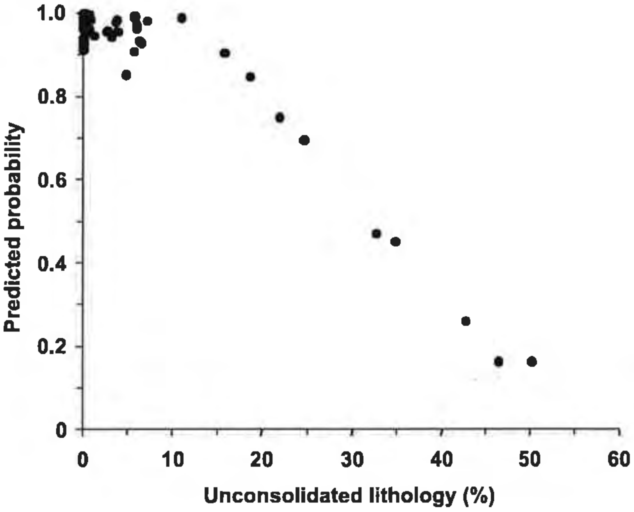
Discussion

Results generated from our analyses must be viewed within the limitations of the parr monitoring and landscape habitat data sets. First, our analyses suffered from the fact that our objective differed from the one originally set forth in the parr monitoring project, and therefore, we subsetted the data accordingly. Second, problems with study design, particularly the unknown impact of bias generated from the nonrandom selection of stream sections and counts uncor-

Table 4. Model selection results for logistic regression models containing landscape habitat predictor variables and count categories of steelhead parr sampled during 1990 (n = 79 subwatersheds (155 stream sections)).

Candidate model	QAICc	ΔQAICc	ΔQAICc weight	% of maximum ΔQAICc weight
Precip, Unconsol	81.51	0	0.280	100
Precip, Mafic	82.10	0.59	0.208	74.3
Precip, Slope, Unconsol	82.96	1.45	0.136	48.6
Sumtemp, Mafic	83.23	1.72	0.119	42.5
Precip, Slope, Mafic	84.28	2.77	0.070	25.0
Precip, Slope, Unconsol, Georoad	84.90	3.39	0.051	18.2
Unconsol, Georoad, Mngclus	85.76	4.25	0.034	12.1
Slope, Mafic	85.82	4.31	0.033	11.8
Sumtemp	86.39	4.88	0.024	8.6
Georoad	87.05	5.54	0.018	6.4
Precip	88.30	6.79	0.009	3.2
Global Model	88.58	7.07	0.008	2.9
Precip, Slope, Georoad	89.44	7.93	0.005	1.8
Mngclus	91.89	10.38	0.002	0.7
Georoad, Mngclus	92.76	11.25	0.001	0.4
Slope, Mngclus	94.13	12.62	<0.001	0.2
Sumtemp, Mngclus	94.73	13.22	<0.001	0.1

Fig. 3. Relationship between percent unconsolidated lithology and predicted probability ($\hat{p}$) of a subwatershed containing either low (e.g., $\hat{p} \le 0.5$) or moderate to high (e.g., $\hat{p} > 0.5$) count categories of steelhead parr.



rected for incomplete detectability of individuals within sections, compelled us to further subset and pool the data. In the latter case, simply modeling raw counts with covariates thought to influence detectability of fish within sampled sections will not correct for sampling bias but will only reflect how well the covariates relate to the biased counts. The matter of confounding still exists. Such a modeling approach would only be valid if (*i*) the nature and magnitude of the counting bias were known for single or repeated counts or (*ii*) repeated counts were conducted on each stream section and the true abundance did not change among counts. Changes in both abundance and covariate values across repeated counts produce confounding between biased counts and covariates. Third, by scaling up to the subwatershed level, we assumed that sampled stream sections were an adequate representation of chinook salmon or steelhead populations for all relevant stream sections within their respective subwatersheds.

Because of various difficulties inherent in the data, in this paper we placed as much emphasis on our analytic approach as we did on interpretation of results. Our procedure for subsetting and modeling a problematic data set should be of interest to fishery biologists, especially because snorkel counts are so commonly used in stream fish studies. We stress, however, that there is no substitute for proper study design and statistically sound sampling methods. It is more preferable to model counts directly than to lose information by pooling data. Nonetheless, we deemed the potential for spurious results due to biased counts to be far more serious than loss of information due to pooling data.

The modeling component of our analyses, in particular, has applications well beyond those used in this paper. AIC-based model selection has a strong theoretical basis (for details, see Burnham and Anderson 1998) and, as such, represents a fundamental departure from traditional methods of model building and variable selection based on null hypothesis testing (e.g., various stepwise and all subset selection procedures). Further, model averaging explicitly incorporates model selection uncertainty into model parameter estimates and also provides a statistically rigorous means to handle the common situation where there is no single model that is clearly better than other models. Ideally, construction of the global and candidate set of models would occur during the design stage of a study and be dictated by the research or management questions being addressed as well as existing information from previous studies. It is important to remember that AIC-based model selection will only choose the best approximating model in the candidate set; it will not correct for poor data or model choice. No analytical methods exist that can completely rescue a data set generated from an inadequately designed study.

Within the boundaries of inference allowed by the data set, there were some notable patterns that emerged between parr count categories and various landscape attributes. For instance, the negative relationship between geometric mean road density and count categories of chinook salmon may be of particular interest to land managers who are charged with ensuring the persistence of anadromous salmonid populations. Particular attention should be paid to those subwatersheds with >1 km·km^{-2} geometric mean road densities. Lee et al. (1997) also reported a negative relationship between road densities and fish population status in the Columbia Basin. Unfortunately, the correlative nature of the data is insufficient for identifying the important drivers behind this relationship. Nevertheless, these findings are noteworthy with respect to the recent road closure policy proposed by the USDA Forest Service (Federal Register 1998*b*).

The fairly strong positive influence of mean annual precipitation on count categories of chinook salmon parr may be related to the positive impact that stream discharge typically has on survival rates of anadromous salmonids (Gibson and Myers 1988; Bradford 1994; Fukushima and Smoker 1997). However, other factors related to high stream flows may be influencing chinook salmon parr numbers as well, such as lower predation rates (Bradford 1994), increased rearing habitat (Bradford 1994), and decreased egg mortality due to freezing (Gibson and Myers 1988).

Model results also infer that surrounding lithology may be especially important to steelhead parr numbers, even on a landscape scale. The fairly strong negative relationship between unconsolidated lithology and steelhead parr count categories could be related to sedimentation. An unconsolidated lithology is one that tends to slough off more than other more consolidated lithologies and hence would contribute more sediment inputs into surrounding streams, which could adversely affect parr survival (Crouse et al. 1981; Waters 1995). Conversely, a mafic lithology contains a strong alkaline component, and hence, its inputs may be tied to higher alkalinity in streams, which has been previously related to increased fish productivity (Scarnecchia and Bergersen 1987; Waters et al. 1993; Kwak and Waters 1997). This idea is consistent with the positive relationship between average maximum summer temperature (which was within the range of tolerance for steelhead) and steelhead parr count categories, where elevated summer temperature may increase primary production in a stream or parr metabolism and growth rates.

Our composite model results represent an initial approximation for fishery biologists and managers interested in mapping approximate status and quality of rearing habitats for chinook salmon and steelhead in relevant areas of Idaho. Assuming that our count categories provide an adequate index of density, subwatersheds with medium to high (>1 km·km^{-2}) geometric mean road densities and (or) low (<700 mm) mean annual precipitation levels may indicate low densities of chinook salmon parr, whereas subwatersheds with high percentages (>30%) of unconsolidated lithologies may indicate low densities of steelhead parr. These models could be updated and refined as more and better information became available and then used to help evaluate possible factors affecting salmonid population status and trends. If additional population data are collected, an effort should be made to collect them at the same spatial scale as the predictor variables.

There are probably factors unrelated to habitat that may be affecting status and distribution of these two species in Idaho. For example, deleterious effects of dams on access to spawning and rearing areas, stock productivity, and survival rates could be the overriding factors influencing parr numbers (or even presence) (Schaller et al. 1999). A number of subwatersheds may have an inherent capacity to support high parr densities, based on landscape-level habitat attributes, but may lack proper access for anadromous salmonids (e.g., blockage of the upper Snake River drainage by Hells Canyon Dam). In any event, identifying cause and effect relationships between anthropogenic variables (e.g., road density, land management practices, and dams) and parr numbers will require carefully planned, well-funded, large-scale field experiments.

Acknowledgments

R. King, M. Jones, C. Paulsen, C. Petrosky, and two anonymous reviewers provided many helpful comments on earlier drafts of this manuscript. We thank J. Hall-Griswold and C. Petrosky of the IDFG for allowing access to the parr monitoring data set as well as providing background on the General Parr Monitoring Program. J. Peterson conducted a preliminary descriptive analysis of the data set and offered helpful suggestions for its more detailed analysis. We gratefully acknowledge D. Myers for generating the study area map. This work was funded by the U.S. Department of Energy, Bonneville Power Administration, under Project 92-32 and the USDA Forest Service, Rocky Mountain Research Station.

References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *In* Second International Symposium on Information Theory. *Edited by* B.N. Petrov and F. Csaki. Akademiai Kiado, Budapest, Hungary. pp. 267–281.

Bradford, M.J. 1994. Trends in the abundance of chinook (*Oncorhynchus tshawytscha*) of the Nechako River, British Columbia. Can. J. Fish. Aquat. Sci. **51**: 965–973.

Bradford, M.J., Taylor, G.C., and Allan, J.A. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Trans. Am. Fish. Soc. **126**: 49–64.

Buckland, S.T., Burnham, K.P., and Augustin, N.H. 1997. Model selection: an integral part of inference. Biometrics, **53**: 603–618.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cover, T.M., and Thomas, J.A. 1991. Elements of information theory. John Wiley & Sons, New York.

Crouse, M.R., Callahan, C.A., Malueg, K.W., and Dominguez, S.E. 1981. Effects of fine sediments on growth of juvenile coho salmon in laboratory streams. Trans. Am. Fish. Soc. **110**: 281–286.

Daly, C., Neilson, R.P., and Phillips, D.L. 1994. A statistical–topographic model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteorol. **33**: 140–158.

Dunham, J.B., and Rieman, B.E. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecol. Appl. **9**: 642–655.

Federal Register. 1997. Endangered and threatened species: listing of several evolutionary significant units (ESUs) of west coast steelhead. Fed. Regist. **62**(159): 43 937 – 43 954.

Federal Register. 1998*a*. Endangered and threatened species: withdrawal of proposed rule to list Snake River spring/summer chinook and fall chinook salmon as endangered. Fed. Regist. **63**(7): 1807–1811.

Federal Register. 1998*b*. Administration of the forest development transportation system. Fed. Regist. **63**(18): 4350–4351.

Fukushima, M., and Smoker, W.W. 1997. Determinants of stream life, spawning efficiency, and spawning habitat in pink salmon in the Auke Lake system. Can. J. Fish. Aquat. Sci. **54**: 96–104.

Gerard, P.D., Smith, D.R., and Weerakkody, G. 1998. Limits of retrospective power analysis. J. Wildl. Manage. **62**: 801–807.

Gibson, R.J., and Myers, R.A. 1988. Influence of seasonal river discharge on survival of juvenile Atlantic salmon, *Salmo salar.* Can. J. Fish. Aquat. Sci. **45**: 344–348.

Hall-Griswold, J.A., and Petrosky, C.E. 1996. Idaho habitat/natural production monitoring. Part 1. U.S. Dep. Energy Bonneville Power Admin. Annu. Rep. 1995, Project 91-73. Available on the Internet at <http://www.efw.bpa.gov/Environment/EW/EWP/DOCS/REPORTS/HABITAT/withpdf.htm>

Hosmer, D.W., Jr., and Lemeshow, S. 1989. Applied logistic regression. John Wiley & Sons, New York.

Kullback, S., and Leibler, R.A. 1951. On information and sufficiency. Ann. Math. Stat. **22**: 79–86.

Kwak, T.J., and Waters, T.F. 1997. Trout production dynamics and water quality in Minnesota streams. Trans. Am. Fish. Soc. **126**: 35–48.

Lee, D.C., Sedell, J.R., Rieman, B.E., Thurow, R.F., Williams, J.E., Burns, D., Clayton, J., Decker, L., Gresswell, R., House, R., Howell, P., Lee, K.M., Macdonald, K., McIntyre, J., McKinney, S., Noel, T., O'Connor, J.E., Overton, C.K., Perkinson, D., Tu, K., and Van Eimeren, P. 1997. Broadscale assessment of aquatic species and habitats. *In* An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great basins. Vol. III. *Edited by* T.M. Quigley and S.J. Arbelbide. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-405, Portland, Oreg. pp. 1057–1713. Available on the Internet at <http://www.fs.fed.us/pnw/int_col.htm>

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Washington, and Idaho. Fisheries (Bethesda), **16**(2): 4–21.

Northwest Power Planning Council. 1986. Compilation of information on salmon and steelhead losses in the Columbia River Basin. Northwest Power Planning Council, Portland, Oreg.

Petrosky, C.E., and Holubetz, T.B. 1986. Idaho habitat evaluation for off-site mitigation record. U.S. Dep. Energy Bonneville Power Admin. Annu. Rep. 1985, Project 83-7, Portland, Oreg.

Quigley, T.M., and Arbelbide, S.J. (*Technical Editors*). 1997. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great basins. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-405, Portland, Oreg. Available on the Internet at <http://www.fs.fed.us/pnw/int_col.htm>

Rich, B.A., and Petrosky, C.E. 1994. Idaho habitat and natural production monitoring. Part 1. U.S. Dep. Energy Bonneville Power Admin. Annu. Rep. 1992, Project 91-73, Portland, Oreg.

Rodgers, J.F., Solazzi, M.F., Johnson, S.L., and Buckman, M.A. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. N. Am. J. Fish. Manage. **12**: 79–86.

Rosgen, D.L. 1985. A stream classification system. *In* Riparian ecosystems and their management: reconciling conflicting uses. *Edited by* R.R. Johnson, C.D. Ziebell, D.R. Palton, P.F. Ffolliott, and R.H. Hamre. USDA For. Serv. Gen. Tech. Rep. RM-120, Fort Collins, Colo. pp. 91–95.

Rosgen, D.L. 1996. Applied river morphology. Wildland Hydrology, Pagosa Springs, Colo.

Royall, R.M. 1997. Statistical evidence: a likelihood paradigm. Chapman and Hall, New York.

SAS Institute Inc. 1996. SAS/STAT software: changes and enhancements, through version 6.11. SAS Institute Inc., Cary, N.C.

Scarnecchia, D.L., and Bergersen, E.P. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. N. Am. J. Fish. Manage. **7**: 315–330.

Schaller, H.A., Petrosky, C.E., and Langness, O.P. 1999. Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. Can. J. Fish. Aquat. Sci. **56**: 1031–1045.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. BioScience, **41**: 704–712.

Thurow, R.F. 1994. Underwater methods for study of salmonids in the Intermountain West. USDA For. Serv. Gen. Tech. Rep. INT-GTR-307, Ogden, Utah.

Torgersen, C.E., Price, D.M., Li, H.W., and McIntosh, B.A. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecol. Appl. **9**: 301–319.

Waters, T.F. 1995. Sediment in streams: sources, biological effects and control. Am. Fish. Soc. Monogr. No. 7.

Waters, T.F., Kaehler, J.P., Polomis, J.T., and Kwak, T.J. 1993. Production dynamics of smallmouth bass in a small Minnesota stream. Trans. Am. Fish. Soc. **122**: 588–598.

Yoccoz, N.G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. Bull. Ecol. Soc. Am. **72**: 106–111.

Available online at www.sciencedirect.com

SCIENCE DIRECT®

ELSEVIER

Forest Ecology and Management 193 (2004) 321–334

Forest Ecology and Management

www.elsevier.com/locate/foreco

Individual legacy trees influence vertebrate wildlife diversity in commercial forests

M.J. Mazurek*, William J. Zielinski

US Forest Service, Pacific Southwest Research Station, 1700 Bayview Dr., Arcata, CA 95521, USA

Received 15 October 2003; received in revised form 14 December 2003; accepted 7 January 2004

Abstract

Old-growth forests provide important habitat elements for many species of wildlife. These forests, however, are rare where lands are managed for timber. In commercial forests, large and old trees sometimes exist only as widely-dispersed residual or legacy trees. Legacy trees are old trees that have been spared during harvest or have survived stand-replacing natural disturbances. The value of individual legacy trees to wildlife has received little attention by land managers or researchers within the coast redwood (*Sequoia sempervirens*) region where 95% of the landscape is intensively managed for timber production. We investigated the use of individual legacy old-growth redwood trees by wildlife and compared this use to randomly selected commercially-mature trees. At each legacy/control tree pair we sampled for bats using electronic bat detectors, for small mammals using live traps, for large mammals using remote sensor cameras, and for birds using time-constrained observation surveys. Legacy old-growth trees containing basal hollows were equipped with 'guano traps'; monthly guano weight was used as an index of roosting by bats. The diversity and richness of wildlife species recorded at legacy trees was significantly greater than at control trees (Shannon index = 2.81 versus 2.32; species = 38 versus 24, respectively). The index of bat activity and the number of birds observed was significantly greater at legacy trees compared to control trees. We found no statistical differences between legacy and control trees in the numbers of small mammals captured or in the number of species photographed using remote cameras. Every basal hollow contained bat guano and genetic methods confirmed use by four species of bats. Vaux's swifts (*Chaetura vauxi*), pygmy nuthatches (*Sitta pygmaea*), violet-green swallows (*Tachycineta thalassina*), and the long-legged myotis (*Myotis volans*) reproduced in legacy trees. As measured by species richness, species diversity, and use by a number of different taxa, legacy trees appear to add significant habitat value to managed redwood forests. This value probably is related to the structural complexity offered by legacy trees. The presence of a basal hollow, which only occur in legacy trees, was the feature that appeared to add the greatest habitat value to legacy trees and, therefore, to commercial forest stands. The results of our study call for an appreciation for particular individual trees as habitat for wildlife in managed stands. This is a spatial resolution of analysis that, heretofore, has not been expected of managers. The cumulative effects of the retention of legacy trees in commercial forest lands could yield important benefits to vertebrate wildlife that are associated with biological legacies.

Keywords: Biodiversity; Legacy tree; Biological legacy; Forest management; Managed forests; Northwestern California; Redwood; *Sequoia sempervirens*; Basal hollows; Wildlife communities; Bats; Small mammals; Birds

1. Introduction

The conservation of old-growth forests has received much attention in recent decades with the heart of the

---

* Corresponding author. Tel.: +1-707-825-2995; fax: +1-707-825-2901.
E-mail address: mmazurek@fs.fed.us (M.J. Mazurek).

0378-1127/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2004.01.013

debate focusing on the value of old-growth as habitat for wildlife. Structural components of old-growth forests, such as snags, living trees with decay, hollows, cavities and deeply furrowed bark, provide habitat for many species (Bull et al., 1997; Laudenslayer, 2002). However, remnant old-growth trees and snags are rare in landscapes that are intensively managed for wood products. Homogenous young stands lacking structural and compositional complexity reduce the habitat value for species associated with old-growth forests (McComb et al., 1993; Carey and Harrington, 2001). The value of individual old-growth structures to wildlife in managed landscapes has received little attention by land managers or researchers (Hunter and Bond, 2001).

In some forest ecosystems, lands managed for timber production occupy all but a small portion of the landscape. In coast redwood (*Sequoia sempervirens*) forests, only 3–5% of the original old-growth redwood forest remains, largely as fragments scattered throughout a matrix of second and third-growth forests (Fox, 1996; Thornburgh et al., 2000). The remnants vary in size from large, contiguous forest patches protected in state and federal parks to patches of only a few hectares in size, to individual legacy trees in managed stands. Individual old-growth trees that have, for one reason or another been spared during harvest, or have survived stand-replacing natural disturbances, are referred to as ‘‘legacy’’ trees (Franklin, 1990). We define legacy trees as having achieved near-maximum size and age, which is significantly larger and older than the average trees on the landscape. This distinguishes them from other ‘residual’ trees, which may also have been spared from harvest but are not always larger and older than the average trees in the landscape.

The rarity of old-growth forests in managed landscapes combined with the rising economic value of old-growth redwood increases the likelihood that legacy stands and individual legacy trees will be harvested. At this time, there is no specific requirement for the retention of legacy trees during timber harvests on private or public lands in California. Exceptions occur on lands owned by companies that are certified as sustainable forest managers (Viana et al., 1996; SmartWood Program, 2000) and as such, are required to maintain and manage legacy old-growth trees.

A number of studies have demonstrated the importance of legacy and residual trees to wildlife. In Douglas-fir (*Pseudotsuga menziesii*) forests, flying squirrel abundance and nest locations were most often found in second-growth forests containing residual trees (Carey et al., 1997; Wilson and Carey, 2000). In addition, horizontal structural complexity increased in stands containing residuals (Zenner, 2000). In eastern hardwood forests, residual trees provided important habitat elements to forest birds in regenerating clear-cut stands (Rodewald and Yahner, 2000). In young and homogenous stands of regenerating redwood forests, residual old-growth legacy trees appear to be important roosting, foraging, resting, and breeding sites for spotted owls (*Strix occidentalis*), fishers (*Martes pennanti*), bats, Vaux’s swifts (*Chaetura vauxi*), and marbled murrelets (*Brachyramphus marmoratus*) (Folliard, 1993; Klug, unpublished data; Thome et al., 1999; Zielinski and Gellman, 1999; Hunter and Mazurek, in press). In the preceding studies, the value of legacy structures was identified only as a consequence of studies on the individual species of wildlife. Our goal was instead to focus our research effort on the rare habitat element itself (the legacy tree) and determine how a variety of wildlife taxa may use it, compared to commercially-mature trees in the same stand.

2. Methods

2.1. Study area

The research was conducted during 2001 and 2002 in Mendocino County, California, in the central portion of the redwood range (Sawyer et al., 2000) in the Northern California Coast ecoregion (Bailey, 1994). The study area was approximately 1750 km^2 in size and included lands owned and managed by the Mendocino Redwood Company (MRC), the California Department of Forestry and Fire Protection-Jackson State Demonstration Forest (JSDF), and Hawthorne Timber Company (HTC)/Campbell Timberland Management (Campbell). These landowners manage approximately 65% of all coast redwood timberlands in Mendocino County.

MRC lands comprise 94,089 ha of timberlands in Mendocino and Sonoma Counties and are certified as sustainable under the Forest Stewardship Council and the Smart Wood Programs (Certificate No. SW-FM/COC-128). HTC/Campbell land includes 74,264 ha of commercial redwood forest. JDSF is 20,639 ha of primarily second and third-growth redwood and Douglas-fir forests. Silvicultural prescriptions for each of the ownerships include about equal measures of even and uneven-aged harvest.

Elevations ranged from 44 to 576 m. Seasonal temperatures range from 18.2 to 9.4 °C in summer and from 13.3 to 5.5 °C in winter. Forests in this region are dominated by coast redwood. Other common trees species include Douglas-fir, grand fir (*Abies grandis*), tan oak (*Lithocarpus densiflora*), bigleaf maple (*Acer macrophyllum*), and Pacific madrone (*Arbutus menziesii*).

2.2. Site and tree selection

For the purposes of our research, we defined a legacy tree as any old-growth redwood tree that was >100 cm diameter at breast height (dbh) and possessed at least some of the following characteristics: deeply furrowed bark, reiterated crown, basal fire-scars, platforms, cavities, and one or more ‘dead-tops’. Many legacy trees also had basal hollows (‘goose pens’) but absence of this trait did not exclude a tree from consideration. Legacy trees were represented by other species than coast redwood (e.g. Douglas-fir) but were not included in this study.

Thirty legacy trees were discovered using information provided by the landowners/managers and by our own reconnaissance. For a legacy tree to be selected for study the stand surrounding it must not have undergone timber operations at least 1 year prior to sampling nor could the stand have been proposed for alteration during the course of the study. The most recent harvest method varied from stand to stand but the majority of stands ($n = 27$) had been harvested under some type of selection method.

Legacy trees included those with and without basal hollows. Basal hollows occur as a result of periodic fires that produce repeated scarring and healing (Finney, 1996). To qualify as a hollow, the internal height must have been greater than the external height of the opening. Otherwise, the structure was considered a fire-scar when the cambium of the tree showed clear signs of effects from fire. We assumed that legacy trees did not need to have basal hollows to be of value to wildlife, therefore 15 legacy trees were selected that contained hollows and 15 did not.

The first step in selecting a control tree was by locating several ($\text{range} = 3-10$) of the largest commercially-mature trees from 50 to 100 m of a legacy tree. The set of candidates was reduced by eliminating from consideration all trees that did not share the same general environmental features with the legacy tree (i.e., similar distance to water and roads, similar slope and aspect). One control tree was randomly selected from the candidates that remained.

2.3. Wildlife sampling

2.3.1. General

An initial inspection was conducted of all trees that contained basal hollows ($n = 15$) and fire-scars ($n = 14$) by examining the interior of the hollow or fire-scar using a flashlight. These surveys were conducted during the initial portion of the study so as to not interfere with protocols designed to sample focal taxa (i.e., bats, small mammals). The hollow ceiling was searched for bats and nests of birds and mammals. The interior substrate of the hollow or fire-scar was inspected for evidence of use (e.g., feces, feathers, hair, prey remains, rest sites). Legacy and control trees were also visited regularly during the application of taxa-specific survey methods. Each time a tree was visited, field personnel would conduct an initial inspection for signs of use by wildlife.

2.3.2. Bats

We used Anabat II bat detectors (Titley Electronics, Australia) to record bat vocalizations at the trees, following the methods of Hayes and Hounihan (1994). The total number of vocalizations (‘bat passes’: Krusic et al., 1996; Hayes, 1997) was used to compare activity in the immediate vicinity of the legacy and control trees. To account for temporal variation in bat detections, we used a paired design and sampled simultaneously at the legacy and control trees at each site (Hayes, 1997). Bat detectors were located between 5 and 10 m from the trees, placed 1.4 m above the ground and at a 45° angle directed at the tree, a configuration that maximizes detection rates (Weller and Zabel, 2002). Each pair was sampled four times for two consecutive nights each ($\text{total} = 8$ nights), between either June (2002) or July (2001) and September.

Guano sampling occurred only at trees with basal hollows, using guano collection methods outlined by Gellman and Zielinski (1996). In addition to sampling guano in the 15 legacy trees with basal hollows, we also installed traps in three legacy trees with fire-scars. The oven-dried weight of guano served as a monthly index of bat use. A sample of 100 guano pellets was selected and subjected to genetic analysis to identify species. Species-specific genetic markers were developed from a 1.56 kilobase region of mitochondrial DNA spanning the majority of the 12S and 16S ribosomal RNA genes (Zinck et al., in press). We selected pellets for analysis by choosing one pellet from each tree sampled each year, and then selecting one pellet per tree sampled each season (i.e., spring and summer) until we reached 100 pellets. All trees sampled contributed at least one pellet for analysis. Eight species that occur in our study area can be identified using this method and one group of three species (*Myotis evotis*, *M. lucifugus*, and *M. thysanodes*) can be distinguished from others but not from each other (J. Zinck, pers. comm.).

2.3.3. *Small mammals*

We sampled non-volant mammals using live traps. Each tree selected for study was sampled using six Sherman live traps (8 cm × 9 cm × 23 cm) and two Tomahawk live traps (13 cm × 13 cm × 41 cm) placed at the base. Also, two Sherman traps and one Tomahawk trap were elevated 1.5 m and attached to the sides of the tree in an attempt to capture arboreal mammals. Traps contained seed bait and a small amount of polyester batting for insulation and bedding. We recorded the species, age, sex, reproductive status, and weight (g) of each mammal captured. A small amount of fur was clipped from the rear hindquarter (on the left if captured at the legacy tree; on the right if captured at the control) to distinguish individuals. Two, 5-day trapping sessions were conducted at each tree between June and August.

2.3.4. *Time-constrained visual observation*

Time-constrained observations were conducted from May to September. We observed each legacy and control tree for evidence of use or occupancy by wildlife. In 2001 we conducted one 30 min observation session in each of the three time intervals: (1) 2 h centered at dawn, (2) mid-day centered between 1100 and 1400 h, and (3) 2 h prior to sunset. In 2002, we conducted one 30 min observation session within 2 h of sunrise and sunset. All wildlife observed on, or within 5 m of the tree was recorded. Each time an animal was observed, the observer would note one occurrence (incident) per individual, the species, the amount of time spent at the tree, and the activity. Observations were categorized as perching, fly/perch, foraging, roosting, fledging, or 'present' (for non-avian species).

2.3.5. *Remote photographic sampling*

Animals present at the base of each tree were photographed using a remotely-triggered camera system (Trailmaster TM550, Trailmaster Infrared Trail Monitors, Lenexa, KS). The combination infrared and activity sensors and cameras were directed at the base of each tree from a distance of a few meters. We restricted the field of view of the sensor such that only animals directly in front of the tree base would be detected. Cameras were checked one day after installation and then approximately every 5 days for 3 weeks. Cameras operated simultaneously at each legacy and control tree in a pair. Each photo of an animal was considered a single detection, but we excluded all but one of a set of photographs of the same species taken consecutively during any 24 h period. This eliminated instances where animals would be present at the tree for several hours. We also excluded photographs of all small mammal species that were captured during the trapping sessions. All cameras operated during April–September.

2.4. *Vegetation sampling*

We collected physical measurements of each tree and of all basal hollows using variables described in Gellman and Zielinski (1996). We also measured vegetation attributes in the immediate vicinity of a random sample of 15 pairs of trees to determine whether the structure of the vegetation surrounding legacy and control trees differed. If such differences existed, it is possible that they would affect the use of the trees by wildlife, independent of the characteristics of the legacy and control trees themselves. We used variable-radius plot methods to estimate basal area (20-factor prism), and each tree that was included in the prism sample was also identified to species and its diameter, height, and condition was recorded. Within an 11.3 m fixed radius plot, and centered on the legacy or control tree, all logs >25.4 cm diameter were recorded by species and their length and diameter measured. Canopy, shrub, herbaceous, and ground cover (duff and downed wood) were estimated visually within a 5 m fixed radius plot.

2.5. Species diversity

We used the Shannon index (Magurran, 1988, p. 34) to characterize the diversity of species detected at legacy and control trees. Diversity indices were calculated separately for the results from the small mammal sampling, time-constrained observation surveys, remote camera surveys, and for these three survey methods combined. We used the number of individuals captured (small mammal surveys), the number of detections (camera surveys) and the number of incidents (visual observation surveys) to calculate the proportion of individuals observed for all species. Our diversity calculations for the visual observation surveys (both individual and combined with the two other surveys) excluded species that were engaged in nesting activities that included frequent forays to and from a nest site (i.e., pygmy nuthatches (*Sitta pygmaea*) and violet-green swallows (*Tachycineta thalassina*)). We also calculated species evenness, a measure of the ratio of observed diversity to maximum diversity (Pielou, 1969), for each survey type described above.

2.6. Statistical analyses

Species diversity indices were statistically compared using the methods of Hutcheson (1970), which calculates a variance for each diversity statistic then provides a method of calculating *t*-values to test for significant differences between samples (Magurran, 1988, p. 35). Small mammal trapping, time-constrained observation and remote photograph (medium and large mammals only) data were analyzed using matched-pair *t*-tests. We were unable to normalize the results of the camera (all animals) data and thus used a non-parametric signed-rank test (*S*) to compare the number of detections by photograph at legacy and control trees. We used a mixed-effects analysis of variance model to compare bat detections between legacy and control trees.

Vegetation characteristics in the immediate vicinity of the legacy and control tree were compared using either *t*-tests (continuous variables) or χ^2-tests (categorical variables). All statistical analyses were conducted using SAS, Version 8.2 (SAS Institute, 2001, Cary, NC). Statistical significance was implied if *P* was <0.05.

3. Results

As expected, legacy trees were larger in diameter (mean dbh = 293 cm (S.D. = 82.3)) and height (mean = 53 m (S.D. = 14.8)) than the control trees (mean dbh = 73 cm (S.D. = 15.2), mean height = 32 m (S.D. = 10.2)). However, the mean diameter of control trees was 72.5 cm dbh, which is considered a commercially-mature size (R. Shively, pers. comm., 2001, Mendocino Redwood Company).

3.1. General wildlife observations

Initial examinations of the trees indicated that most of the hollows and fire-scars in legacy trees ($n = 19$; 63%) had evidence of small mammal use on the basis of the discovery of feces, food remains, or nest evidence (usually dusky-footed wood rat *Neotoma fuscipes* middens, $n = 5$). One hollow contained four roosting bats and six hollows (40%) contained guano, evidence of bat use. Four hollows or fire-scarred legacy trees (13%) had evidence of use (i.e., claw marks) by large mammals and feces or nests indicated that 10 legacy trees (33%) were used by birds.

The general inspection of trees resulted in several noteworthy observations of reproductive activity:

(1) On 16 June 2002, two adult pygmy nuthatches were observed repeatedly entering and exiting a cavity in a legacy tree. The birds were observed entering the cavity with food, which was followed by vocalizations of young.
(2) A legacy tree contained a large cavity that was occupied by barn owls (*Tyto alba*) during both years of the study. Fresh feces and food pellets were observed during each visit to the tree.
(3) On 16 July 2002, violet-green swallows were observed repeatedly entering and exiting a cavity in a legacy tree. These behaviors, and the time of

year, suggest the birds were nesting within the cavity.

(4) Vaux's swifts nested for two consecutive years in the basal hollow of a legacy tree.

(5) On 23 July 2002 a large number of bats was observed in a hollow that had conspicuous guano accumulation and in which was discovered, on 31 July 2001, a dead juvenile long-legged myotis. Collectively, this evidence suggests that this legacy tree was used as a maternity colony.

3.2. Bats

3.2.1. Acoustic sampling

We recorded a total of 10,799 bat passes over the two sample years. The mean index of bat activity was significantly greater at the legacy trees compared to the control trees ($F_{1,45.7} = 17.66, P < 0.0001$) (Fig. 1). The mean index of bat activity at legacy trees with and without hollows was 34.8 (S.D. = 33.4, $n = 15$) and 22.6 (S.D. = 15.9, $n = 15$), respectively, a difference that was not statistically significant ($t = 1.27$, $P = 0.21$).

3.2.2. Guano sampling

We collected guano monthly from July to October 2001 and April to October 2002. All hollows and fire-scars showed evidence of bat use during some portion of the survey period. Average guano weight declined from August to October during both years (Fig. 2).

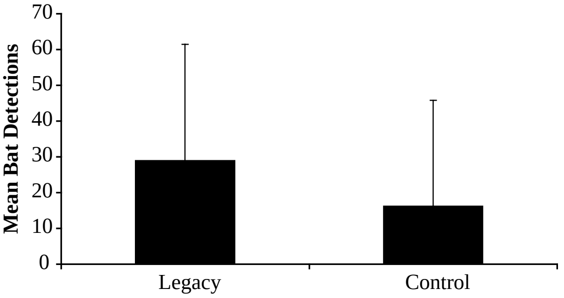


Fig. 1. Mean bat detections and standard deviation for legacy and control trees ($F_{1,45.7} = 17.66$, $P < 0.0001$) in Mendocino County, California, 2001 and 2002.

Sixty-eight of the 100 guano samples submitted for analysis amplified adequate amounts of DNA for species analysis. Four species were verified to use legacy trees, with the long-legged myotis the most common (46%) (Table 1). The California myotis (*Myotis californicus*) was the species detected at the greatest number of hollow-bearing trees (73%) and the total number of trees (hollow-bearing and fire-scarred (66%)). The big brown bat (*Eptesicus fuscus*) and the California myotis were the only species identified from the four guano samples that originated from fire-scars (Table 1).

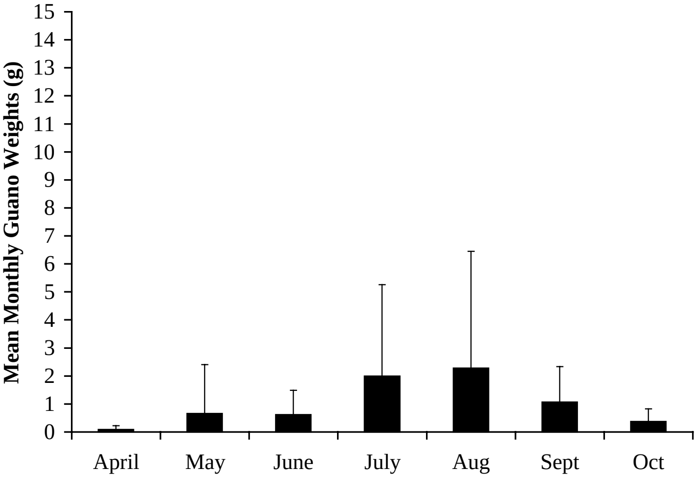


Fig. 2. Mean monthly guano weights (g) and standard deviation (April–October) at 14 hollow-bearing trees in Mendocino County, California, 2001 and 2002.

Table 1
Number of 68 guano samples collected from 15 basal hollows and three fire-scars that could be identified to species

Species	Guano sample		Hollows		Fire-scars		Trees total	
	Number	Percentage of samples	Number	Percentage of hollows	Number	Percentage of fire-scars	Number	Percentage of trees total
Big brown bat (*E. fuscus*)	9	13	5	33	3	100	8	44
California myotis (*M. californicus*)	17	25	11	73	1	33	12	66
Myotis 3[a]	11	16	5	33	0	0	5	27
Long-legged myotis (*Myotis volans*)	31	46	9	60	0	0	9	50

[a] *Myotis lucifugus*, *M. evotis*, and *M. thysanodes* are not currently distinguishable, but guano from these three species can be distinguished from other species.

3.3. Small mammal sampling

There was a slightly greater number of total small mammal captures at legacy trees compared to control trees (Table 2). There was also a greater number of individuals captured at the legacy trees compared to control trees, though this relationship was not statistically different ($t = 0.5$, $P = 0.62$). Two of the insectivores (shrew mole (*Neurotrichus gibbsi*) and Trowbridge's shrew (*Sorex trowbridgii*)) were the only species of small mammals that appeared to be trapped more commonly at the base of legacy trees.

3.4. Observation surveys

Each legacy and control tree was sampled at least twice, resulting in a total of 132 surveys and 114.5 h of survey effort (Table 3). There was a significantly greater number of incidents ($t = 16.6$, $P < 0.0001$) and time spent ($t = 4.05$, $P = 0.0004$) at legacy trees compared to control trees (Table 3). Wildlife (primarily birds) was observed about nine times as frequently at legacy trees compared to control trees and there were also more species observed at legacy trees compared to control trees (Table 4).

Of the activities observed, 82% was either perching or flying. There was twice as much foraging activity at legacy trees (22 incidents) compared to control trees (10 incidents). Woodpeckers, nuthatches, and some swallows were observed only at legacy trees; acorn woodpeckers used a legacy tree as a food storage location (i.e., granary). The majority of individuals observed were pygmy nuthatches, violet-green swallows, or unknown passerines.

Remote cameras operated a total of 1278 survey hours. We photographed 18 species at legacy and control trees; 13 species were detected only as a result of the camera surveys (Table 5). The total number of photographic detections was 38 at legacy trees (mean = 1.4, S.D. = 2.4, $n = 27$) and 17 at control

Table 2
Summary of small mammal captures by species at study sites in Mendocino County, California, 2001 and 2002

Species	Total captures		Total individuals captured		Individuals captured at both legacy and control pair
	Legacy	Control	Legacy	Control	
Trowbridge's shrew (*S. trowbridgii*)	33	18	30	16	0
Fog shrew (*S. sonomae*)	2	4	2	3	0
Shrew mole (*N. gibbsii*)	5	0	5	0	0
Short-tailed weasel (*Mustela erminea*)	0	1	0	1	0
Dusky-footed wood rat (*N. fuscipes*)	62	88	23	37	0
Redwood (yellow-cheeked) chipmunk (*Tamias ochrogenys*)	93	51	39	31	3
Deer mouse (*Peromyscus maniculatus*)	150	133	67	61	1
Western red-backed vole (*Clethrionomys californicus*)	20	37	13	19	0
Total	365	332	179	168	4

Table 3
Summary of visual observation results[a]

Tree type	Total			Survey period					
	Total survey effort (h)	min/h	Number of incidents	a.m.		Mid		p.m.	
				min/h	Number of incidents	min/h	Number of incidents	min/h	Number of incidents
Legacy	57.5	0.0998	188	0.1035	170	0.002	4	0.1938	14
Control	57.0	0.0105	34	0.0143	27	0.003	6	0.0024	1

[a] Total survey effort, duration (min/h of survey effort) that individuals were observed and the total number of incidents of wildlife observed for three time periods; a.m. (within 2 h of sunrise), mid (2 h centered around mid-day) and p.m. (2 h within sunset).

trees (mean = 0.63, S.D. = 1.3, $n = 27$); the means were not statistically different ($S = 37.5$, $P = 0.10$). When we restricted detections to include only medium and large mammals the total numbers of detections were 14 (mean = 0.52, S.D. = 0.64) and 10 (mean = 0.37, S.D. = 0.88) at legacy and control trees respectively, but were not statistically different ($t = 0.78$, $P = 0.44$).

Table 4
Species observed at legacy and control trees and the number of incidents (number of times a species was observed) during time-constrained visual observations in Mendocino County, California, 2001 and 2002

	Legacy	Control
Species at legacy only		
Acorn woodpecker	12	0
Common raven	2	0
Downy woodpecker	1	0
Hairy woodpecker	3	0
Northern flicker	2	0
Osprey	1	0
Pygmy nuthatch	25	0
Red-breasted nuthatch	1	0
Turkey vulture	1	0
Unknown flycatcher	1	0
Unknown owl	1	0
Unknown swallow	11	0
Unknown woodpecker	4	0
Vaux's swift	3	0
Violet-green swallow	52	0
Winter wren	2	0
Species at control only		
Golden-crowned kinglet	0	1
Hutton's vireo	0	8
Species at both legacy and control		
Brown creeper	4	2
Chestnut-backed chickadee	4	2
Hermit warbler	1	1
Pacific-slope flycatcher	1	1
Redwood chipmunk	1	1
Steller's jay	10	7
Unknown passerine	44	10
Western gray squirrel	1	1

3.5. Vegetation sampling

There were no differences in the vegetation characteristics in the area immediately surrounding the legacy and control trees. Basal areas, tree diameters, tree heights, log volumes, canopy cover, shrub cover, and herbaceous cover were statistically indistinguishable (Table 6). In addition, there were no significant

Table 5
List of species and the number of detections (photographs) at legacy and control trees during remote camera surveys in Mendocino, California, 2002[a]

	Legacy	Control
Species at legacy only		
Bat (species unknown)	1	0
Brush rabbit (*Sylvilagus bachmani*)	7	0
Sonoma vole (*Arborimus pomo*)	1	0
Winter wren (*Troglodytes troglodytes*)	1	0
Species at control only		
Gray fox (*Urocyon cinereoargenteus*)	0	2
Raccoon (*Procyon lotor*)	0	1
Species at legacy and control		
Black bear (*Ursus americanus*)	4	1
Black-tailed deer (*Odocoileus hemionus*)	1	1
Bobcat (*Lynx rufus*)	4	1
Douglas' squirrel (*Tamiasciurus douglasii*)	5	4
Spotted skunk (*Spilogale gracilis*)	1	1
Striped skunk (*Mephitis mephitis*)	4	3
Western gray squirrel (*Sciurus griseus*)	9	3

[a] Each detection represents only one photo per species per tree per 24 h period.

Table 6
Means and standard deviations (S.D.) for habitat variables sampled in the immediate vicinity of legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Vegetation characteristic	Tree type				t	P
	L		C			
	Mean	S.D.	Mean	S.D.		
Basal area (m^2/ha)	55.6	22.5	56.8	27.5	0.17	0.87
Tree dbh (cm)	46.7	23.2	49.2	23.6	0.38	0.71
Tree height (m)	24.6	7.7	26.2	8.3	0.87	0.40
Log volume (m^2)	1.27	1.4	0.79	0.86	1.08	0.30
Canopy cover (%)	83.6	7.6	84.4	8.2	0.42	0.68
Shrub cover (%)	12.8	16.5	16.1	21.2	0.63	0.54
Herbaceous cover (%)	24.9	36.8	16.7	23.6	1.19	0.30

[a] Legacy and control trees were excluded from calculations. t-values and P-values are from the results of matched-pair t-tests.

Table 7
Frequency of occurrence for habitat variables sampled in the immediate vicinity of legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Vegetation characteristic		Frequency for tree type		χ^2	P
		L	C		
Tree species	Coast redwood	22	22	2.03	0.36
	Other conifer	15	12		
	Hardwood	20	10		
Tree condition	Live	40	33	2.42	0.3
	Declining	13	5		
	Dead	4	5		
Log species	Coast redwood	31	27	0.63	0.73
	Other conifer	10	9		
	Hardwood	4	6		
Log condition	Class 1	2	1	1.05	0.9
	Class 2	8	8		
	Class 3	15	11		
	Class 4	13	12		
	Class 5	7	9		
Downed wood	High	7	8	0.13	0.72
	Low	8	7		
Duff	High	13	12	NA	NA
	Low	2	3		

[a] Legacy and control trees were excluded from calculations. Statistical values are from χ^2 goodness of fit tests.

differences in tree species, tree condition, log species, log condition, the amount of duff, or the amount of downed wood (Table 7). Thus, we concluded that there were no systematic differences in the physiognomy of vegetation surrounding legacy trees when compared to control trees.

3.6. Diversity indices

The number and diversity of species using legacy trees was greater than those using control trees using data from only the time-constrained observation surveys, or when we combined the results from the time-constrained observation surveys, camera surveys, and small mammal trapping (Table 8). Species richness was about 1.5 times as great at legacy trees ($n = 38$) than at control trees ($n = 24$) for all surveys. Using data from the timed observation surveys only, the species richness was more than twice as great at legacy

Table 8
Number of individuals (small mammals) or detections (other taxa), species richness, evenness and diversity indices by survey method for legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Survey method	Tree type	Number of individuals or detections	Richness (number of species)	Evenness	Shannon diversity index	t statistic	d.f.	P
Observation	L	111	22	0.73	2.25	2.13	95	0.05–0.02
	C	34	10	0.82	1.88			
Trailmaster	L	38	11	0.88	2.11	0.64	54	>0.5
	C	17	9	0.93	2.04			
Mammal trapping	L	179	7	0.82	1.60	0.26	350	>0.25
	C	168	7	0.82	1.58			
Overall	L	328	38	0.77	2.81	5.05	481	<0.001
	C	219	24	0.73	2.32			

[a] Tests statistics refer to the Shannon diversity indices.

trees ($n = 22$) than at control trees ($n = 10$). The Shannon diversity indices were statistically higher at legacy trees (2.81) than control trees (2.32) for the combined surveys and for the observational surveys (human observer) (Table 8), but we did not find differences in the richness or diversity of small mammals captured in traps or for the species detected by cameras, when these data sets were analyzed separately (Table 8). Evenness was greater at legacy trees compared to control trees for the combined surveys only (Table 8).

4. Discussion

As measured by species richness, species diversity, and use by a number of different taxa, legacy trees appear to add important foraging and breeding habitat value to redwood forests managed for timber. The use of legacy trees by wildlife was demonstrated by evidence of their nesting, roosting and resting; behaviors which were not observed at control trees. This difference is probably related to the structural complexity offered by redwood legacy trees (Bull et al., 1997; Laudenslayer, 2002). Control trees were smooth-boled with very few large horizontal limbs, few cavities, and no basal hollows. Legacy trees possess these structural features, which probably account for their greater attractiveness to a variety of wildlife species.

The presence of a basal hollow, which only occur in legacy trees, was the feature that appeared to add the greatest habitat value to legacy trees and, as a result, to commercial forest stands. However, we did not sample specifically for wildlife that may benefit from the presence of large horizontal branches (e.g. platform nesting wildlife). Basal hollows were used by every taxa sampled, but appear to be particularly important to bats and birds. In addition to the fact that guano was collected at every hollow we sampled, individual bats were observed in hollows, and reproduction was documented. Use of basal hollows by bats has been observed in other redwood regions (Gellman and Zielinski, 1996; Zielinski and Gellman, 1999; Purdy, 2002) and there are several previous reports of basal hollows used by bats for reproduction (Rainey et al., 1992; Mazurek, in press). Hollows also appear to be important nest sites for some bird species, in particular Vaux's swifts (Hunter and Mazurek, in press). Because roost and nest availability can limit the populations of birds and bats (Humphrey, 1975; Kunz, 1982; Brawn and Balda, 1988; Christy and West, 1993; Raphael and White, 1984), basal hollows may play a critical role in the redwood region if they provide roost and nest sites in forests that are otherwise deficient. The increased use of legacy trees by insectivorous birds and bats may also be because the rugosity of the bark may harbor a greater diversity and abundance of insects (Ozanne et al., 2000; Willett, 2001; Summerville and Crist, 2002). Bark gleaners, such as brown creepers (*Certhia americana*), have been correlated with the abundance of spiders and other soft-bodied arthropods that are significantly associated with bark furrow depth (Mariani and Manuwal, 1990); this may also explain the disproportionate use of legacy trees by nuthatches and woodpeckers. Finally, basal hollows not only benefit the wildlife that use them but the trees in which they are found. The feces of animals that are attracted to hollows can be an important source of nutrients for trees that may be on nutrient-poor sites (Kunz, 1982; Rainey et al., 1992).

The mammal data (bats excluded) did not suggest a disproportionate association with either legacy or control trees. Possible exceptions include two insectivores, which were captured more at legacy trees, and the dusky-footed woodrat, whose nests were found in five of 15 basal hollows. Shrew moles are associated with older forests (Raphael, 1988; Carey and Johnson, 1995) and are infrequently found in logged areas (Tevis, 1956). Several studies also found that Trowbridge's shrews have a similar association with mature forest conditions (Gashwiler, 1970; Hooven and Black, 1976; Carey and Johnson, 1995).

The camera data did not reveal disproportionate use of legacy trees by mammals. Relatively few mammalian carnivores were detected at either type of tree, perhaps because some species (i.e., the marten (*Martes americana*) and the fisher (*M. pennanti*)) are sensitive to forest habitat loss and fragmentation (Buskirk and Powell, 1994) and have been either extirpated from the region or are very rare (Zielinski et al., 1995, 2001). With the exception of the two insectivores and wood rats, none of the non-volant mammals we sampled appeared to be strongly associated with the legacy trees. Unlike the passerine birds, which use the structurally complex bark of legacy trees for foraging and cavities for nesting, and the bats, which roost in hollows and bark crevices, our data do not indicate that legacy trees have exceptional value for rodents or for the species of carnivorous mammals that still occur in the region.

Our conclusions about the value of legacy trees to wildlife in the redwood region are supported by the results of studies on individual species of wildlife elsewhere. Legacy trees (also described as old-growth residuals) are used by northern (*Strix occidentalis caurina*) and California (*S. o. occidentalis*) spotted owls for nesting and roosting (Moen and Gutiérrez, 1997; Irwin et al., 2000). Fishers use legacy conifers, and residual hardwoods, as daily rest sites in public Douglas-fir forests (Seglund, 1995) and private redwood forests (R. Klug, pers. comm.). Flying squirrels were twice as abundant when legacy trees were retained in managed areas (Carey, 2000) and their diet was found to be more diverse in legacy stands (Carey et al., 2002).

Our work was directed at assessing the value of individual *legacy* trees in stands, but there is a considerable body of research on the related question of what value *residual* trees and patches have in maintaining wildlife diversity in forests. Residual structures may not be as old as the legacy structures we studied, but they can add important structural diversity to which many species of wildlife respond. Songbirds in a variety of coniferous mixed, and hardwood forest types have benefited from the retention of residual trees (Hobson and Schieck, 1999; Rodewald and Yahner, 2000; Schieck et al., 2000; Tittler et al., 2001; Whittman et al., 2002; Zimmerman, 2002). Southern red-backed voles (*Clethrionomys gapperi*), a late-successional associated forest species, are also more common in harvested areas as the basal area in residual trees increases (Sullivan and Sullivan, 2001). The retention of residual structure during logging appears to have benefits to wildlife, but additional research will be necessary to distinguish the effects of retaining commercially mature—but relatively young—trees for wildlife from retaining and managing legacy trees, which are typically much older.

The goal of this study was to document the pattern and frequency of use of legacy and control trees so that we might better understand how young and old elements are used within the matrix of commercial redwood forests. To do so we compared the occurrence of species and individuals, but did not evaluate how individual trees contribute to *survival* or *reproduction* (i.e., fitness) of individual species. Measures of abundance, or indices of abundance, are not sufficient to completely evaluate the effects of variation in habitat on wildlife populations; in some cases they can even mislead because not all places where animals occur are suitable for reproduction (Van Horne, 1983). Our observations of reproductive behavior by a number of birds and at least one species of bat, however, suggest that legacy trees may influence the fitness of some species as well. We also believe that the potential survival value of access to legacies was probably underestimated in our study because we evaluated use only during the climatically benign summer months. We expect that benefits of access to legacy trees would be the greatest during the winter when they would be used as refuges from inclement weather (e.g., Carey, 1989).

If legacy trees provide one of the few choices for nesting and reproductive sites, and they are rare, then it is possible that they may be easily located and searched by predators making them population 'sinks' (Pulliam, 1988). Tittler and Hannon (2000) did not find increased predation in this respect, but their study evaluated residual trees, which were more numerous and probably not as distinctive and obvious foraging locations as are the more structurally distinctive redwood legacy trees. It is clear, however, that the risks that wildlife may be subjected to when using, and perhaps congregating at, legacy structures will need to be evaluated with respect to the benefits.

5. Conclusions

Our traditional view of conservation reserves is of large protected areas. However, few landscapes provide us with the opportunity to preserve large tracts of land and we must consider conserving biodiversity within the matrix of multiple use lands (Lindenmayer and Franklin, 1997). Given the fragmented nature of mature forests in the redwood region, remnant patches of old-growth and individual legacy trees may function as 'mini-reserves' that promote species conservation and ecosystem function. Legacy structures increase structural complexity in harvested stands and, as a result, can provide the 'lifeboats' for species to re-establish in regenerating stands (Franklin et al., 2000). Although the lifeboat function may not be entirely fulfilled for vertebrates with large area needs, these habitat elements may make it possible for some species to: (1) breed in forest types where they may otherwise be unable, and (2) secure a greater number of important refuges from climatic extremes and predators. In addition, these functions may allow legacy trees to provide some measure of habitat connectivity ('stepping stones') to larger more contiguous tracts of old-growth forests (Tittler and Hannon, 2000; Noss et al., 2000).

Because of their rarity in commercial forests, the first step in the management of legacy trees is to determine their locations and protect them from logging or from physical degradation of the site. Because legacy redwoods with basal hollows are even more rare, locating and protecting these should be the highest priority. In addition, the circumstances that lead to their genesis will be difficult to recreate, especially on commercial timberland. Hollows form by repeated exposure of the base of trees to fire (Finney, 1996), and because most fires on private land are suppressed, prescribed fire would need to be repeatedly applied to trees that would be designated as 'future legacies' and which would be excluded from harvest in perpetuity. We hasten to add, however, that legacy trees without basal hollows appear to have significant benefits to wildlife. Even without management to encourage basal hollows we suggest that managers plan for the recruitment of trees that are destined to become legacies. This will require their protection over multiple cutting cycles. We expect that new silvicultural methods will be required to prescribe the process of identifying, culturing, and protecting residual legacy trees. Although we do not believe that any one tree will protect a species, we do believe that the cumulative effects of the retention, and recruitment, of legacy and residual trees in commercial forest lands will yield important benefits to vertebrate wildlife and other species of plants and animals that are associated with biological legacies.

The results of our study beg us to consider habitat at a spatial scale that is smaller than that of habitat patches or remnant stands; we conclude that *individual trees* can have very important values to wildlife. More research would be helpful, however, to specify the level of individual tree retention required to maintain biodiversity in managed lands (Lindenmayer and Franklin, 1997). It would help to know, for example, whether the fitness of individual species, and the diversity of wildlife communities, is greater in landscapes in which legacy trees are common compared to landscapes with very few legacy trees. It is possible that because legacy trees are rare—despite their apparent values to wildlife—that they do not affect wildlife diversity or productivity over large areas. It would also advance our knowledge to determine whether legacy trees in legacy-rich landscapes can function to maintain connectivity between protected stands of mature and old-growth forests. If so, the landscape context will be an important component of managing residual legacy trees and planning their recruitment across landscapes. For now, however, this study makes clear that protecting legacy trees will protect important habitat features that receive disproportionate use by many wildlife species. The protection and management of these trees can enhance wildlife conservation on lands where the opportunities to do so can be limited.

Acknowledgements

This work was funded by the USDA Forest Service, Redwood Sciences Laboratory, Save-the-Redwoods League, Mendocino Redwood Company, Bat Conservation International, California Department of Forestry and Fire Protection, Jackson State Demonstration Forest, and the USDI Fish and Wildlife Service, Arcata, CA. We thank M. Escobar, T. Zarubin, L. Hagenauer, and J. Bailey for assistance in the field. We thank the landowners and managers for the opportunity to conduct this study on their respective properties. We thank M. Goldstein, formerly of MRC, for helping to establish the foundation for the project. J. Werren and R. Knickerbocker provided GIS support and B. Howard provided database management support. J. Baldwin and L. Olivier provided statistical support. S. O'Connor helped transcribe our acoustic tapes. We appreciate the assistance of Dr. Jan Zinck, Portland State University, for conducting the genetic analysis on bat guano samples. Special thanks to J. Hunter and M. Bond for providing the inspiration to embark on this research. J. Franklin and A. Carey

provided helpful comments on earlier versions of the manuscript.

References

Bailey, R.G., 1994. Descriptions of the Ecoregions of the United States, 2nd ed. Miscellaneous Publication No. 1391. Forest Service, US Department of Agriculture, Washington, DC (revised).

Brawn, J.D., Balda, R.P., 1988. Population biology of cavity-nesters in northern Arizona: do nest sites limit breeding densities? Condor 90, 61–71.

Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and logs important to wildlife in the interior Columbia River basin. General Technical Report No. PNW-GTR-391. USDA Forest Service, 55 pp.

Buskirk, S.W., Powell, R.A., 1994. Habitat ecology of fishers and American martens. In: Buskirk, S.W., Harestad, A.S., Raphael, M.G., Powell, R.A. (Eds.), Martens, Sables and Fishers: Biology and Conservation. Comstock Publishing Associates, Cornell University Press, Ithaca, NY, pp. 283–296.

Carey, A.B., 1989. Wildlife associated with old-growth forests in the Pacific Northwest. Nat. Areas J. 9, 151–162.

Carey, A.B., 2000. Effects of new forest management strategies on squirrel populations. Ecol. Appl. 10, 248–257.

Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-growth forests. Ecol. Appl. 5, 336–352.

Carey, A.B., Wilson, T.M., Maguire, C.C., Biswell, B.L., 1997. Dens of northern flying squirrels in the Pacific Northwest. J. Wildl. Manage. 61, 684–699.

Carey, A.B., Harrington, C.A., 2001. Small mammals in young forests: implications of management for sustainability. For. Ecol. Manage. 154, 289–309.

Carey, A.B., Colgan, W., Trappe, J.M., Molina, R., 2002. Effects of forest management on truffle abundance and squirrel diets. Northw. Sci. 76, 148–157.

Christy, R.E., West, S.D., 1993. Biology of bats in Douglas-fir forests. General Technical Report No. PNW-GTR-308. USDA Forest Service, 28 pp.

Finney, M.A., 1996. Development of fire-scar cavities on old-growth coast redwood. In: Leblanc, J. (Ed.), Coast Redwood Forest Ecology and Management. University of California, Berkeley, CA, pp. 96–98.

Folliard, L., 1993. Nest site characteristics of northern spotted owls in managed forests of northwest California. M.S. Thesis. University of Idaho, Moscow, ID, 106 pp.

Fox, L., 1996. Current status and distribution of coast redwood. In: Leblanc, J. (Ed.), Coast Redwood Forest Ecology and Management. University of California, Berkeley, CA, pp. 18–19.

Franklin, J.F., 1990. Biological legacies: a critical management concept from Mount St. Helens. Trans. N. Am. Wildlands Nat. Resour. Conf. 55, 216–219.

Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D., 2000. Threads of continuity. Conserv. Biol. Pract. 1, 9–16.

Gashwiler, J.S., 1970. Plant and mammal changes on a clearcut in west central Oregon. Ecology 51, 1018–1026.

Gellman, S.T., Zielinski, W.J., 1996. Use by bats of old-growth redwood hollows on the north coast of California. J. Mammal. 77, 255–265.

Hayes, J.P., 1997. Temporal variation in the activity of bats and the design of echolocation-monitoring studies. J. Mammal. 78, 514–524.

Hayes, J.P., Hounihan, P., 1994. Field use of the Anabat II bat detector system to monitor bat activity. Bat Res. News 35, 1–3.

Hobson, K.A., Schieck, J., 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecol. Appl. 9, 849–863.

Hooven, E.F., Black, H.C., 1976. Effects of some clearcutting practices on small-mammal populations in western Oregon. Northw. Sci. 50, 189–208.

Humphrey, S.R., 1975. Nursery roosts and community diversity of nearctic bats. J. Mammal. 56, 321–346.

Hunter, J.E., Bond, M.L., 2001. Residual trees: wildlife associations and recommendations. Wildl. Soc. Bull. 29, 995–999.

Hunter, J.E., Mazurek, M.J., in press. Characteristics of trees used by nesting and roosting Vaux's swifts nest in northwestern California. West. Birds.

Hutcheson, K., 1970. A test for comparing diversities based on the Shannon formula. J. Theoret. Biol. 29, 151–154.

Irwin, L.L., Rock, D.F., Miller, G.P., 2000. Stand structures used by northern spotted owls in managed forests. J. Raptor Res. 34, 175–186.

Krusic, R.A., Yamasaki, M., Neefus, C.D., Pekins, P.J., 1996. Bat habitat use in White Mountain National Forest. J. Wildl. Manage. 60, 625–631.

Kunz, T.H., 1982. Roosting ecology of bats. In: Kunz, T.H. (Ed.), Ecology of Bats. Plenum Press, New York, pp. 1–55.

Laudenslayer, W.F., 2002. Cavity-nesting bird use of snags in eastside pine forests of northeastern California. In: Laudenslayer, W.F., Shea, P.J., Valentine, V.E., Weatherspoon, C.P., Lisle, T.E. (Tech. Coords.), Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, Reno, NV, November 2–4, 1999. General Technical Report No. PSW-GTR-181. USDA Forest Service, pp. 223–236.

Lindenmayer, D.B., Franklin, J.F., 1997. Managing stand structure as part of ecologically sustainable forest management in Australian mountain ash forests. Conserv. Biol. 11, 1053–1068.

Magurran, A., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, NJ, 177 pp.

Mariani, J.M., Manuwal, D.A., 1990. Factors influencing brown creeper (*Certhia americana*) abundance patterns in the southern Washington Cascade range. Stud. Avian Biol. 13, 53–57.

Mazurek, M.J., in press. Townsend's big-eared bat maternity colony uses old-growth redwood basal hollows in Grizzly Creek State Park, California. Northw. Nat.

McComb, W.C., McGarigal, K.M., Anthony, R.G., 1993. Small mammals and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, in western Oregon. Northw. Sci. 67, 7–15.

Moen, C.A., Gutiérrez, R.J., 1997. California spotted owl habitat selection in the central Sierra, Nevada. J. Wildl. Manage. 61, 1281–1287.

Noss, R.F., Strittholt, J.R., Heilman, G.E., Frost, P.A., Sorensen, M., 2000. Conservation planning in the redwood region. In: Noss, R.F. (Ed.), The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. Island Press, Covelo, CA, pp. 201–228.

Ozanne, C.M.P., Speight, M.R., Hambler, C., Evans, H.F., 2000. Isolated trees and forest patches: patterns in canopy arthropod abundance and diversity in *Pinus sylvestris* (Scots pine). For. Ecol. Manage. 137, 53–63.

Pielou, E.C., 1969. An Introduction to Mathematical Ecology. Wiley/Interscience, New York, 286 pp.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.

Purdy, D., 2002. Bat use of old-growth redwood basal hollows: a study of capture methods and species use of redwoods. M.S. Thesis. Humboldt State University, Arcata, CA, 51 pp.

Rainey, W.E., Pierson, E.D., Colberg, M., Barclay, J.H., 1992. Bats in hollow redwoods: seasonal use and role in nutrient transfer into old-growth communities. Bat Res. News 33, 71.

Raphael, M.G., 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. In: Szaro, R.C., Severson, K.E., Patton, D.R. (Tech. Coords.), Proceedings of the Symposium on the Management of Amphibians, Reptiles, and Small Mammals in North America. General Technical Report No. RM-166. USDA Forest Service, pp. 23–31.

Raphael, M.G., White, M., 1984. Use of snags by cavity-nesting birds in the Sierra–Nevada. Wildl. Monogr. 86, 1–66.

Rodewald, A.D., Yahner, R.H., 2000. Bird communities associated with harvested hardwood stands containing residual trees. J. Wildl. Manage. 64, 924–932.

SAS Institute, 2001. The SAS System for Windows, Version 8.2. SAS Institute Inc., Cary, NC.

Sawyer, J.O., Sillett, S.C., Popenoe, J.H., LaBanca, A., Sholars, T., Largent, D.L., Euphrat, F., Noss, R.F., VanPelt, R., 2000. Characteristics of redwood forests. In: Noss, R.F. (Ed.), The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. Island Press, Covelo, CA, pp. 39–80.

Schieck, J., Stuart-Smith, K., Norton, M., 2000. Bird communities are affected by amount and dispersion of vegetation retained in mixedwood boreal forest harvest areas. For. Ecol. Manage. 126, 239–254.

Seglund, A.E., 1995. The use of resting sites by the pacific fisher. M.S. Thesis. Humboldt State University, Arcata, CA, 66 pp.

SmartWood Program, 2000. Forest management public summary for Mendocino Redwood Company. SmartWood Program, New York, NY, 38 pp.

Sullivan, T.P., Sullivan, D.S., 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. J. Appl. Ecol. 38, 1234–1252.

Summerville, K.S., Crist, T.O., 2002. Effects of timber harvest on forest lepidoptera: community, guild and species responses. Ecol. Appl. 12, 820–835.

Tevis, L., 1956. Responses of small mammal populations to logging of Douglas-fir. J. Mammal. 37, 189–196.

Thome, D.M., Zabel, C.J., Diller, L.V., 1999. Forest stand characteristics and reproduction of northern spotted owls in managed north-coastal California forests. J. Wildl. Manage. 63, 44–59.

Thornburgh, D.A., Noss, R.F., Angelides, D.P., Olson, C.M., Euphrat, F., Welsh, H.J., 2000. Managing redwoods. In: Noss, R.F. (Ed.), The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. Island Press, Covelo, CA, pp. 229–262.

Tittler, R., Hannon, S.J., 2000. Nest predation in and adjacent to cutblocks with variable tree retention. For. Ecol. Manage. 136, 147–157.

Tittler, R., Hannon, S.J., Norton, M.R., 2001. Residual tree retention ameliorates short-term effects of clear-cutting on some boreal songbirds. Ecol. Appl. 11, 1656–1666.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47, 893–901.

Viana, V.M., Ervin, J., Donovan, R.Z., Elliott, C., Gholz, H., 1996. Certification of Forest Products: Issues and Perspectives. Island Press, Washington, DC, 261 pp.

Weller, T.J., Zabel, C.J., 2002. Variation in bat detections due to detector orientation in a forest. Wildl. Soc. Bull. 30, 922–930.

Whittman, R.M., McCracken, J.D., Francis, C.M., Gartshore, M.E., 2002. The effects of selective logging on nest-site selection and productivity of hooded warblers. Can. J. Zool. 80, 644–654.

Willett, T.R., 2001. Spiders and other arthropods as indicators in old-growth versus logged redwood stands. Restor. Ecol. 9, 410–420.

Wilson, S.M., Carey, A.B., 2000. Legacy retention versus thinning: influences on small mammals. Northw. Sci. 74, 131–145.

Zenner, E.K., 2000. Do residual trees increase structural complexity in Pacific Northwest coniferous forests? Ecol. Appl. 10, 800–810.

Zielinski, W.J., Kucera, T.E., Barrett, R.H., 1995. The current distribution of fishers in California. Cal. Fish Game 81, 104–112.

Zielinski, W.J., Gellman, S.T., 1999. Bat use of remnant old-growth redwood stands. Conserv. Biol. 13, 160–167.

Zielinski, W.J., Slauson, K.M., Carroll, C.R., Kent, C.J., Kudrna, D.G., 2001. Status of American martens in coastal forests of the Pacific states. J. Mammal. 82, 478–490.

Zimmerman, K.L., 2002. Sustaining biological diversity in managed sub-boreal spruce landscapes: residual habitat strategies for cavity nesting species. M.S. Thesis. University of Northern British Columbia, Canada.

Zinck, J.M., Duffield, D.A., Ormsbee, P.C., in press. Primers for identification and polymorphism assessment of Verpertilionid bats in the Pacific Northwest. Mol. Eco. Notes.

Effects of Road Decommissioning on Stream Habitat Characteristics in the South Fork Flathead River, Mon....

Article *in* Transactions of the American Fisheries Society · May 2007

DOI: 10.1577/T06-134.1

Magnus Mccaffery
Turner Endangered Species Fund

Transactions of the American Fisheries Society 136:553–561, 2007

DOI: 10.1577/T06-134.1

[Note]

Effects of Road Decommissioning on Stream Habitat Characteristics in the South Fork Flathead River, Montana

MAGNUS MCCAFFERY*
Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812, USA

T. ADAM SWITALSKI
Wildlands CPR, Post Office Box 7516, Missoula, Montana 59807, USA

LISA EBY
Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812, USA

Abstract.—Previous studies have demonstrated the negative effects of roads on stream characteristics important for fish survival; however, few have examined whether decommissioning reverses these adverse impacts. We examined the relationships between the percentage of fine sediment in stream substrate and roads and looked at whether decommissioning had measurable effects on stream habitat in the Flathead National Forest, Montana. We conducted habitat surveys and substrate coring in 12 streams encompassing three watershed treatment types: (1) roadless areas, (2) areas with roads in use, and (3) areas with decommissioned roads. Significant positive correlations were found between the percentage of fine sediment in substrate and various measures of road impact (road density, roads in use, and number of stream crossings). Watersheds with roads in use had higher percentages of fine sediment than those without roads and those with decommissioned roads. Watersheds with high levels of vegetative regrowth on decommissioned roadbeds had a lower percentage of fines in stream sediment. Decommissioning efforts that enhance regrowth may improve stream habitat, although significant effects of these manipulations are difficult to detect through spatial comparisons. Future studies using either before–after or before–after–control designs to evaluate the effects of decommissioning practices on fish and wildlife habitat and populations are needed.

Roads primarily influence salmonid stream habitat by obstructing fish passage and degrading spawning, incubation, and juvenile rearing habitat (Furniss et al. 1991). Improperly designed culverts can impede or preclude fish passage and subsequently fragment aquatic habitat (Wofford et al. 2005). An excess of fine sediments resulting from soil erosion can degrade or completely destroy spawning habitat (e.g., Furniss et al. 1991). The successful incubation of salmonid embryos in stream gravels depends on intragravel water flow to provide oxygen and remove waste products (e.g., Bams 1969). Enhanced levels of fine sediment can reduce intragravel flow, impeding egg development as well as trapping and entombing emerging fry in the gravel (e.g., Phillips et al. 1975). Macroinvertebrate communities also respond negatively to fine sediments, thus influencing food availability for juvenile fish. In addition, excessive sediment delivery can decrease depth and number of pools thereby reducing the physical space available in the streams for rearing and overwintering of juvenile fish. If the riparian zone is compromised, then temperature, shade, and large wood would be altered, further affecting juvenile rearing habitat (Furniss et al. 1991). Although the effects of roads on fish habitat and production in any particular watershed are complex and a function of many interacting factors (Everest et al. 1987), their potential adverse effect on stream fish populations has prompted extensive restoration efforts.

In an attempt to mitigate the negative effects of forest roads the U.S. Forest Service is decommissioning about 3,200 km of roads each year and working to upgrade culverts and passage structures to facilitate fish migration (USFS 2002). Decommissioning roads can include a number of restoration strategies, ranging from blocking access to roads (with a berm or by bridge removal) to a complete removal of the roadbed and recontouring of the road prism to the original natural slope. However, in contrast with the wealth of information on the effects of existing roads (Forman and Deblinger 2000; Haskell 2000; Jones et al. 2000; Trombulak and Frissell 2000), almost no information exists on the effectiveness of road removal. Relatively few studies have documented that road decommissioning reduces road-related erosion (Kolka and Smidt 2001; Luce 1997; Madej 2001) and studies that have examined the effects of road decommissioning on wildlife are rarer still (Switalski et al. 2004). These studies have primarily examined decommissioning

---

* Corresponding author: magnus.mccaffery@umontana.edu

Received June 11, 2006; accepted December 18, 2006

actions involving complete road removal and recontouring in highly erodible landscapes. Few published studies have focused on the effects of road decommissioning on fish habitat and species in Montana (but see Wegner 1999). Given the variation in geomorphology and related underlying erodibility of the landforms and soil across the country, as well as the variety of types of road decommissioning activities, the evaluation of various road decommissioning actions across multiple geographic areas is necessary for us to determine the effects of restoration efforts on fish and wildlife.

In Montana, bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisii* are two native coldwater salmonid species of conservation concern. Connectivity between high-quality stream spawning and foraging habitats is necessary for migratory life history forms of both bull trout and westslope cutthroat trout to complete their life cycles. Although many factors have contributed to the decline of these species, habitat degradation and fragmentation are two primary concerns in their conservation (Fraley and Shepard 1989; Lee et al. 1997; Liknes and Graham 1988; Rieman et al. 1997). Roads have been implicated in the degradation of bull trout habitat; forest roads are negatively correlated with bull trout stream use, abundance, and spawning activity (Baxter et al. 1999; Dunham and Rieman 1999). In addition, there is evidence of a significant inverse relationship between the percentage of fine sediment in the substrate and survival to the emergence of westslope cutthroat and bull trout embryos in incubation tests (Weaver and White 1985; Weaver and Fraley 1991).

On the Flathead National Forest, Montana, road decommissioning typically refers to blocking road entrances with earthen berms, which allows for natural revegetation and soil stabilization. In fish-bearing streams culverts are typically removed and stream banks recontoured. In some cases road entrances are gated. In addition to increased connectivity associated with culvert removal, road decommissioning is expected to reduce the delivery of sediment to streams, thus increasing the quality of spawning and rearing habitat for trout.

We evaluated streams within the Flathead National Forest that comprised three treatment types: (1) roadless watersheds; (2) watersheds with main roads still in public use but often with spurs that are decommissioned, gated, or both; and (3) watersheds with decommissioned roads (bermed and culverts removed). We did not consider roads that were only seasonally gated as decommissioned. We addressed two questions. First, is there a relationship between substrate composition (percentage of fine sediment) and road density? Second, if so, does road decommissioning have measurable effects on the percentage of fine sediment and other stream habitat characteristics that are important to fish?

Study Area

Research was conducted in the Flathead National Forest in northwestern Montana. As part of the Northern Continental Divide Ecosystem, the Flathead National Forest's 2.3 million acres is considered to be 47% wilderness and is one of the few forests left in the contiguous U.S. where a full complement of native trout species remains. Streams were sampled in the southern half of the Forest in the South Fork Flathead River Basin (Figure 1). This basin is bounded to the east by the Bob Marshall Wilderness Complex and to the west by the Swan Mountains and primarily comprises sedimentary rock with dense stands of coniferous forest that exhibit historical clear-cut logging and associated roads.

Of the 6,100 km of roads on the Flathead National Forest, 544 km have been decommissioned and an additional 612 km are slated for decommissioning (U.S. Forest Service, Flathead National Forest, unpublished database for road decommissioning projects). The effects that these roads have on aquatic habitat vary and are based on (1) watershed characteristics and geomorphology (e.g., slope and soil type, land use, road density and use); (2) proximity of the road to the stream (riparian buffers, number of road crossings); and (3) stream characteristics (the power of the stream to move or flush sediment from system [e.g. Duncan and Ward 1985; Luce et al. 2001]). Similarly, influences of road decommissioning will vary depending on the location and quantity of the decommissioned roads in the watershed as well as how and when they were decommissioned.

We chose 12 study streams with fairly similar watershed and stream size and gradient characteristics, which controlled for differences in stream power and watershed size while exhibiting differences in watershed road treatments (Table 1). Twin Creek had a significantly larger watershed area, but had characteristics similar to our other streams. Study watersheds generally had roads that paralleled the stream with a riparian buffer greater than 20 m. To minimize confounding effects, watersheds of study streams did not have recent (within 5 years) wildfires or timber sales within the watershed. Three watersheds had roads-in-use (Wheeler, Emery, and Quintonkon creeks), while three watersheds had entirely roadless watersheds (Riverside, Tin, and Twin creeks) to provide reference stream conditions. Of the six watersheds containing decommissioned roads, two streams had all roads within their watershed decommissioned (Slide Creek and Connor Creek) and the

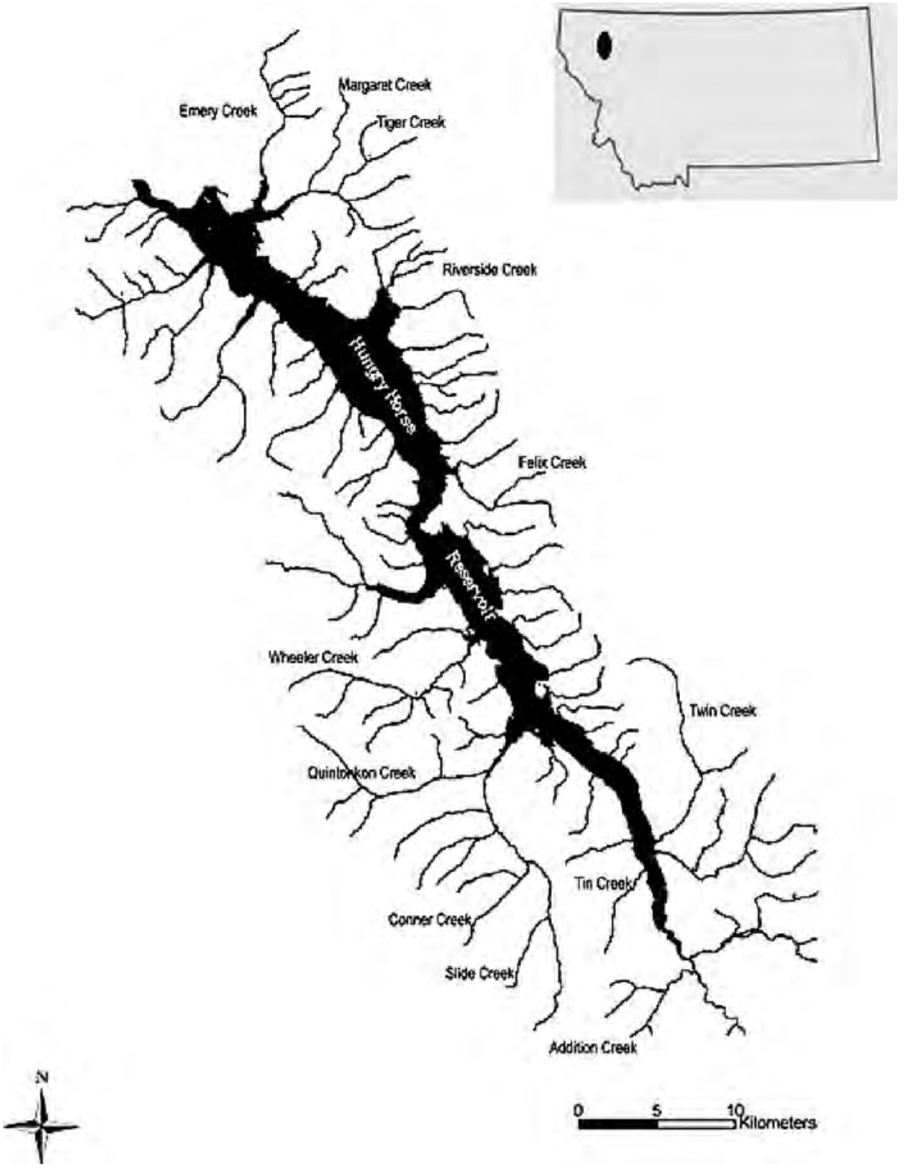


FIGURE 1.—Study area located in the Flathead National Forest (Hungry Horse and Spotted Bear Ranger Districts) in northwestern Montana. All of the study streams were tributaries to the South Fork of the Flathead River at or near Hungry Horse Reservoir.

remaining four watersheds contained a mix of road treatments (bermed with regrowth, as well as gated roads in administrative use; Table 1).

Methods

Basic road surveys were conducted to verify our categorization of roads within the different treatments. Watershed treatments were characterized as roadless, roads in use, or decommissioned. If they were decommissioned we qualitatively assessed the level of vegetative regrowth (sparse grass, dense grass, shrubs, or trees), and noted any signs of road activity (e.g., motorized vehicle tracks) for the primary road adjacent to the stream. We separated our decommissioned road treatments based on the level of revegetation of the primary road in the watershed. Conner, Slide, and Tiger creeks all had grass, bushes, and trees on the primary road and were classified as high

TABLE 1.—Stream and watershed habitat characteristics for 12 watersheds studied in the South Fork Flathead River basin.

Stream	Level of regrowth on decommissioned roads	Elevation (m)	Incline (%)	Total road density (km/km^2)	Road-in-use density (km/km^2)	Number of road crossings	Distance from Hungry Horse, Montana (km)	Watershed area (km^2)
Wheeler	Open road	1,364	3	0.61	0.24[a]	16	63	46.26
Emery	Open road	1,202	2	1.58	0.28	30	14	38.54
Quintonkon	Open road	1,223	2	0.69	0.25	15	70	55.45
Addition	Low	1,323	2	0.22	0.01[b]	4	93	38.87
Felix	High	1,139	2	1.51	0.00	4	46	19.91
Tiger	Low	1,234	2	0.13	0.00	0	21	17.46
Margaret	Low	1,295	5	0.67	0.00	3	19	10.42
Slide	High	1,347	2	0.33	0.00	0	84	12.90
Conner	High	1,299	2	0.53	0.07[c]	3	80	17.60
Riverside	Roadless	1,163	3	0.00	0.00	0	31	14.79
Tin	Roadless	1,184	2	0.02[d]	0.00	0	84	16.88
Twin	Roadless	1,113	2	0.00	0.00	0	79	116.92

[a] Seasonal closures.
[b] Gated during this study (summer 2004); decommissioned at the end of summer 2004.
[c] Bridge out at Sullivan Creek so no road in use in Conner watershed.
[d] Main road at base of watershed downstream from sampling.

regrowth watersheds. Other decommissioned watersheds (Addition, Margaret, and Felix) exhibiting only sparse grass were grouped together into a low regrowth category.

To quantify the influence that roads have on a watershed, we calculated a series of road-related variables for each of our watersheds. Both total road density (for all classes of roads) and the density of roads currently in use within each study watershed were calculated from U.S. Forest Service geographical information systems (GIS) road layers using the distance tool in ArcMap at a resolution of 1:24,000. Similarly, distance along roads between the stream access point to the closest town (Hungry Horse, Montana) was established as a surrogate measure of accessibility and hence traffic volume (Table 1). In addition, we noted any road crossings (e.g., bridge, culvert) in the field and used a Flathead National Forest map (scale: 1:126,720) to estimate the number of roads crossing streams within each watershed (Table 1).

Approximately 300 m of each stream was sampled both in the summer (June–July) and fall (September–November) of 2004, except at Wheeler Creek, which was only sampled in the fall. The lower half of each stream was divided into contiguous 100-m sections and three of these sections were randomly selected for sampling.

During summer sampling we performed habitat surveys (Overton et al. 1997). Proceeding upstream, we described each channel habitat unit (riffle, run, or pool) and measured its length (m), mean wetted width (m), middle depths of riffles (cm) and maximum depth of pools (cm). In each section we measured average incline and elevation, visually estimated bank stability, quantified large wood, and estimated canopy cover. Channel incline was assessed with a compass, elevation was obtained using a Garmin global positioning system (GPS), and canopy cover was estimated with a Moosehorn densitometer (80 readings along eight different cross-sectional transects per section). The stability of stream banks was rated on a scale from 1 to 4 as follows: 1 = banks were stable, less than 5% of the bank having signs of erosion or bank failure absent or minimal; 2 = banks were moderately stable, with infrequent, small areas (5–30% of bank in reach) indicative of erosion; 3 = banks were moderately unstable, 30–60% of the bank showing signs of erosion resulting in high erosion potential during floods; and 4 = banks were unstable, eroded areas being seen frequently along straight sections and bends (60–100% having erosional banks). We deployed a temperature logger (ibuttons, Maxim Dallas semiconductor) in each section to collect water temperature data every 90 min.

During fall sampling we measured pool habitat characteristics and performed substrate coring in study sections. Pool frequency and depth were analyzed for differences among the three treatment types using a Kruskal–Wallis test (Zar 1999). Ten substrate cores (McNeil core samples) per stream were collected in the lower two sections (five per section) to measure substrate composition and fine sediments. All cores were collected in flowing water, over cobble substrate, and at a pool–riffle break (as suggested by OPSW 1999). Cores were taken to a depth of 15 cm into the substrate. Oven-dried core samples were weighed after being shaken through sieves with mesh sizes of 75, 50, 25, 19, 12.5, 9.5, 6.3, 4.75, and 2.0 mm and 850, 425, and 63 μm. An average of 3.8 kg ± 0.058 (mean ± SE) of substrate was collected per core. Since fine

TABLE 2.—Characteristics of streams surveyed in the South Fork Flathead River basin (LWD = large woody debris, ND = no data).

Stream	Temperature (°C)	LWD/100 m Singles	LWD/100 m Aggregates	Bank stability[a]	Riffle area (%)	Average width (m)	Midstream depth (cm)	Pool frequency (per 100 m)	Maximum pool depth (cm)	Sediment <6.3 mm (%)
Wheeler	ND	6.8	1.9	1.0	85.9	8.9	35.3	1.2	89.5	23.88
Emery	7	23.1	8.0	1.0	89.1	4.4	29.7	4.7	67.3	34.22
Quintonkon	7	5.7	1.0	1.1	97.6	7.7	32.7	1.2	89.5	20.42
Addition	ND	16.8	4.2	1.1	83.0	6.7	52.7	6.1	79.7	22.02
Felix	9	11.4	3.0	1.6	97.9	5.7	19.3	3.0	71.7	20.64
Tiger	9	6.6	2.0	1.0	97.7	4.6	23.0	5.5	58.3	18.49
Margaret	8	15.7	4.0	1.0	97.9	3.8	22.3	6.1	59.3	20.78
Slide	8	12.1	3.9	1.3	94.9	5.0	27.7	3.0	77.7	14.81
Conner	10	3.0	1.6	1.1	96.2	5.4	29.0	3.7	54.3	14.45
Riverside	ND	8.9	5.0	1.0	58.1	4.9	38.8	7.4	66.3	21.36
Tin	8	7.8	1.5	1.1	97.3	4.8	33.7	4.0	61.7	13.36
Twin	10	0.0	0.0	1.1	83.2	9.3	31.7	3.0	77.7	18.53

[a] Scale = 1 to 4; see text for details.

material disturbed by coring typically remains in suspension within the corer and is often not included in the captured substrate, we improved our estimate of the fine particle component by agitating the remaining sediment within the core and extracting three 150-mL subsamples of water to measure suspended sediment. The height of the water within the corer was measured and converted to a volume based on a depth-to-volume curve produced in the laboratory specifically for this corer. These subsamples were returned to the laboratory where the sediment was settled and measured in Imhoff cones. The volume of fine sediment was then multiplied by the volume of water in the corer to determine the total fines. These wet volumes of fine sediment were then converted to a dry weight using a conversion factor developed by Shepard and Graham (1982) allowing us to add these measures of fine sediment to the fraction of our substrate composition data that was less than 63 μm in size.

Substrate composition was expressed as the percentage of substrate particles (SP) smaller than 6.3 mm. This is the size fractionation used to assess spawning habitat for both bull trout and westslope cutthroat trout (e.g., Shepard and Graham 1982; Weaver and Fraley 1991; 1993). We compared percent of substrate particles less than 6.3 mm among treatment types with a Kruskal–Wallis nonparametric analysis of variance (ANOVA) (Zar 1999). We examined correlations in our dataset associated with roads and watersheds. After eliminating highly correlated variables a step-wise multiple linear regression was used to evaluate which watershed characteristics (e.g., road crossings, watershed area) best predicted the percent of fine substrate. Finally, watersheds with decommissioned roads were analyzed using a stepwise multiple regression analysis to examine whether level of regrowth, number of road crossings, or watershed area explained a significant amount of variation in the percentage of substrate composed of fine sediment (Zar 1999).

Results

Stream Habitat Characteristics

Overall, stream sections were of similar size and gradient, and the habitat was dominated by riffles. Bank stability was high in all streams (Table 2).

Substrate Composition and Road Impacts

To investigate how roads affect the substrate composition of our study streams, we examined whether there was a correlation between the percentage of fine sediment (%SP < 6.3 mm) in the substrate and total road density, density of roads in use, distance from the closest town (Hungry Horse), and the number of road–stream crossings within the watershed. There was a significant positive relationship between percentage of fine sediment and road density (Pearson correlation = 0.36; $P = 0.038$, $n = 12$), roads in use (Pearson correlation = 0.43; $P = 0.021$, $n = 12$), and the number of road–stream crossings (Pearson correlation = 0.84; $P = 0.001$, $n = 12$, Figure 2). Furthermore, there was a negative trend but nonsignificant correlation (Pearson correlation = −0.573; $P = 0.051$, $n = 12$) between percentage of fine sediment in the substrate and potential road use (i.e., distance from Hungry Horse). These measures of watershed road characteristics were all significantly correlated with each other making it impossible to separate their potential effects. Given the extent of the riparian buffers (typically >20 m) in these watersheds, personal observations of erosion at road crossings during the road surveys and the high correlation of road–stream crossings with percentage of fine sediment, we used number of road–stream crossings for our analyses to detect potential effects of decommissioning roads.

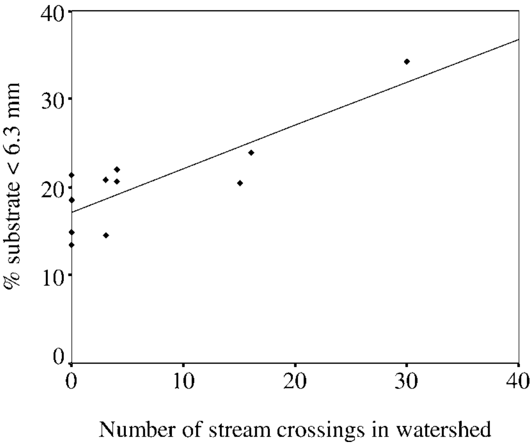


FIGURE 2.—Relationship between the percentage of substrate particles less than 6.3 mm in size and the number of stream crossings in the watershed ($r^2 = 0.70$, $P = 0.001$). Strong positive correlations were also found among total road density, the density of roads in use, and stream crossings.

Watershed Treatment Comparisons

There were no statistically significant differences in the number of pools per 100 m ($P = 0.981$) or maximum pool depth among our three treatment groups ($P = 0.207$; Table 2).

Watersheds with roads in use had the highest median percentage of substrate particles of less than 6.3 mm in stream cores and decommissioned and roadless watersheds exhibited similar percentages of fine sediment in stream cores, although the differences were not statistically significant (Kruskal–Wallis test: $\chi^2 = 3.15$, df = 2, $P = 0.20$; Figure 3a). Watersheds with decommissioned roads were tested for differences in percentage of fine sediment versus number of road crossings, watershed size, and amount of regrowth on roads. Percentage of fine sediment in stream substrate within the decommissioned watersheds was not significantly related to number of road crossings or watershed size. However, there was a significant effect of the level of regrowth with fine sediment (regrowth = 0.019, number of road crossings $P = 0.385$, area $P = 0.852$, final regression $F = 14.67$, $P = 0.02$, df = 5), whereby decommissioned roads with high levels of regrowth appeared to have a lower percentage of fine sediment in the stream substrate (Mann–Whitney test: $Z = -1.96$, $P = 0.05$; Figure 3b).

Discussion

Road building leads to increased sedimentation and a reduction in fish habitat quality (Gucinski et al. 2001; for reviews, see Meehan 1991; Trombulak and Frissell 2000) and areas without roads are often strongholds for native fish communities (Lee et al. 1997; Baxter et al. 1999). The percentage of substrate particles less than a given size for a specific species or guild is often considered the best indicator of fish habitat degradation from roads (Young et al. 1991). In this study, watersheds that had higher total road density, roads in use, and road–stream crossings exhibited higher percentages of fine sediment compared with those watersheds that had lower levels of road influence (Figures 2, 3a). These general trends tentatively support expectations about the relationship among roads, substrate composition, and potential for spawning success.

Other studies have found that as traffic increases, there are concomitant increases in sediment yields from roads (e.g., Reid and Dunne 1984). Using the distance along roads of each creek from the town of Hungry Horse as a surrogate measure of road use by vehicles, we found no significant relationship between increased percentage of fine sediment and increased potential traffic. Upon examination of our watersheds, we found that Emery Creek, which probably has the heaviest traffic volume given its relative accessibility (Table 1), exhibits the highest percent composition of fine sediment.

Having established a relationship between road density and crossings and fine sediment composition in streams (Figure 2), we examined whether road decommissioning is correlated with a lower percentage of fine sediment in stream substrate. We did not see significant differences among our three treatment groups. Watersheds with roads in use had higher levels of fine sediment in the substrate than either those without roads or those with decommissioned roads, but the high amount of fine sediment in Emery Creek had a large influence on these trends (Table 2).

Our lack of statistically significant results among treatments may stem from the combination of confounding factors and low power. For instance, in May 2004 (several weeks before sampling), our study area experienced a 14-year peak flood event with discharges approximately 50% higher than mean annual peak flow levels. This may have influenced our streams by flushing fine sediment from our study sites, thereby affecting our ability to detect differences in chronic sediment loading in these watersheds (U.S. Geological Survey, gauging station 12359800, South Fork Flathead River at Twin Creek near Hungry Horse).

There was a significant difference in the percentage of fine sediment in the substrate of streams with different levels of regrowth on decommissioned roads. Streams associated with watersheds containing a high amount of regrowth, whereby a mixture of trees, shrubs, and grasses had established themselves on the

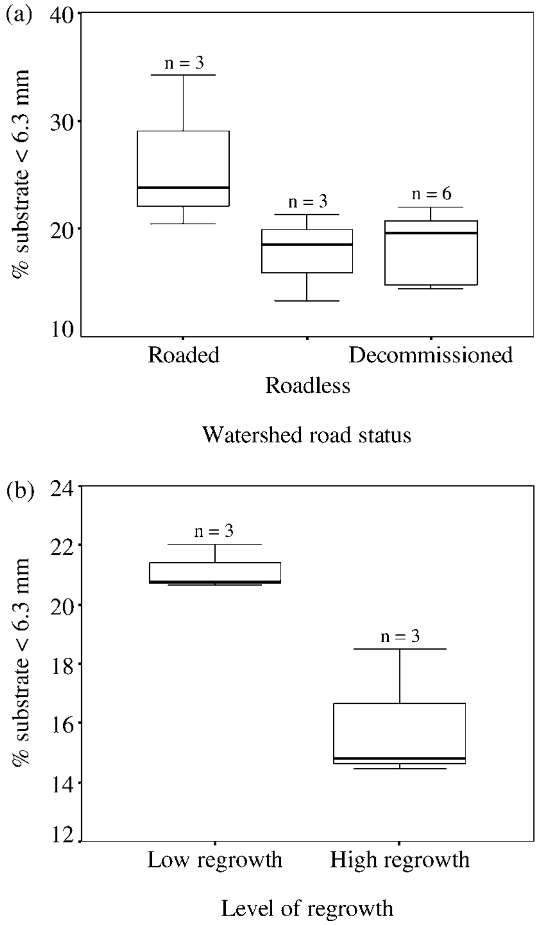


FIGURE 3.—Box plots showing **(a)** the percentage of fine substrate for each road treatment type ($\chi^2 = 3.15$, df = 2, $P = 0.20$) and **(b)** the percent of fine substrate with respect to the level of roadbed regrowth within decommissioned road treatments ($Z = -1.96$, $P = 0.05$). High regrowth refers to old roadbeds with a mixture of trees, shrubs, and grasses, while low regrowth refers to sparse grass. The heavy lines within the boxes represent the median values, the lower and upper boundaries of the boxes the 25th and 75th percentiles, and the whiskers the 10th and 90th percentiles.

old road, had lower percentages of fine sediment in the substrate than did those watersheds with only sparse grass (Figure 3b). Thus, as decommissioned roads become increasingly revegetated over time, the amount of fine sediment loading is reduced to the levels that existed before the roads were built.

The few studies in which road decommissioning has been shown to have large beneficial effects for fish habitat were conducted in areas with more erosive soils or higher susceptibility to mass wasting. The soils in the Flathead National Forest are not as erosive as some granitic soils where many of the most obvious road sedimentation problems exist (e.g., Clearwater National Forest, Megahan and Kidd 1972). However, large flood events and culvert blow-outs are not uncommon in this forest.

Our results suggest that road decommissioning that results in vegetative regrowth reduces fine sediment in streams, thereby conferring positive effects on stream habitat for bull and cutthroat trout in the Flathead National Forest. Other studies have demonstrated how upgrading passage barriers (e.g., perched culverts) can result in recolonization by juvenile bull trout (USFWS 2002). Bull trout populations also increased following full recontouring of the streams and culvert removals on the nearby Kootenai National Forest (Wegner 1999); a 48% decline in fine sediment and a 16% increase in bull trout redds was observed in the 5 years following decommissioning. Our study has attempted to elucidate differences in substrate composition associated with different road treatment types and levels of regrowth associated with decommissioning actions. Based on our results, we suggest that decommissioning roads that lead to high levels of revegetation probably reduces the amount of fine sediment in streams.

While road decommissioning appears to be an effective tool with which to mitigate many of the negative effects of roads on fish habitat, care must be taken when designing studies to demonstrate its effects. Given our estimated variance, detecting statistical significance would require large-effect sizes (~30–40% change in percentage of fine substrate), as well as large sample sizes ($n \geq 25$ streams). With the large amount of spatial variation in sedimentation that we observed among watersheds, even after controlling for watershed and stream characteristics, we recommend study designs in which streams serve as their own controls, that is, either replicated before–after or replicated before–after–control impact designs, to evaluate the effects of road decommissioning (Roni et al. 2005).

Acknowledgments

Funding provided by the Yellowstone to Yukon Conservation Science Grants Program. We thank J. Fox, E. Dallalio, and D. Bixby for data collection, R. Wahl, S. Amish, and three anonymous reviewers for review comments, as well as P. Van Eimeren and D. Mucklow from the Flathead National Forest for other support.

References

Bams, R. A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravels. Pages 71–87 *in* T. G.

Northcote, editor. Symposium on salmon and trout in streams. MacMillan, Vancouver.

Baxter, C. V., C. A. Frissell, and F. R. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. Transactions of the American Fisheries Society 128:854–867.

Duncan, S. H., and J. W. Ward. 1985. The influence of watershed geology and forest roads on the composition of salmon spawning gravel. Northwest Science 59:204–213.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642–655.

Everest, F. H., R. L. Beschta, J. D. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. *In* E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fisheries interactions. University of Washington, Contribution 57, Seattle.

Forman, R. T. T., and R. D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conservation Biology 14:36–46.

Fraley, J. J., and B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake River system, Montana. Northwest Science 63:133–143.

Furniss, M. J., T. D. Roelofs, and S. C. Yee. 1991. Road construction and maintenance. W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19, Bethesda, Maryland.

Gucinski, H., M. J. Furniss, R. R. Ziemer, and M. H. Brookes. 2001. Forest roads: a synthesis of scientific information. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Haskell, D. G. 2000. Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian Mountains. Conservation Biology 14:57–63.

Jones, J. A., F. J. Swanson, B. C. Wemple, and K. U. Snyder. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14:76–85.

Kolka, R., and M. Smidt. 2001. Revisiting forest road retirement. Water Resources Impact 3:15–16.

Lee, D. C., J. Sedell, B. Rieman, R. Thurow, and J. Williams. 1997. Broad-scale assessment of aquatic species and habitats. Pages 1057–1496 *in* T. M. Quigley and S. J. Arbelbinde, editors. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great basins, volume 3. U.S. Forest Service General Technical Report PNW-GTR-405.

Liknes, G. A., and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. Pages 53–60 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Luce, C. H. 1997. Effectiveness of road ripping in restoring infiltration capacity of forest roads. Restoration Ecology 5:265–275.

Luce, C. H., B. E. Rieman, J. B. Dunham, J. L. Clayton, J. G. King, and T. A. Black. 2001. Incorporating aquatic ecology into decisions on prioritization of road decommissioning. Water Resources Impact 3:8–14.

Madej, M. A. 2001. Erosion and sediment delivery following removal of forest roads. Earth Surface Processes and Landforms 26:175–190.

Meehan, W. R., editor. 1991. Influences of forest and rangeland management on salmonid fisheries and their habitats. American Fisheries Society, Bethesda, Maryland.

Megahan, W. F., and W. J. Kidd. 1972. Effects of logging and logging roads on erosion and sediment deposition from steep terrain. Journal of Forestry 70:136–141.

OPSW (Oregon Plan for Salmon and Watersheds). 1999. Water quality monitoring, technical guidebook, version 2.0. OPSW, Corvallis.

Overton, C. K., S. P. Wollrab, B. C. Roberts, and M. A. Radko. 1997. R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory procedures handbook. U.S. Forest Service General Technical Report INT-GTR 346.

Phillips, R. W., R. L. Lantz, E. W. Claire, and J. R. Morning. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104:462–466.

Reid, L. M., and T. Dunne. 1984. Sediment production from forest road surfaces. Water Resource Research 20:1753–1761.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River basin. North American Journal of Fisheries Management 17:1111–1125.

Roni, P., M. C. Liermann, C. Jordan, and E. A. Steel. 2005. Steps for designing a monitoring and evaluation program for aquatic restoration. Pages 13–34 *in* P. Roni, editor. Monitoring stream and watershed restoration. American Fisheries Society, Bethesda, Maryland.

Shepard, B. B., and P. J. Graham. 1982. Monitoring spawning gravel bed material used by bull trout on the Glacier View District, Flathead National Forest. Montana Fish, Wildlife and Parks, Completion Report, Kalispell.

Switalski, T. A., J. A. Bissonette, T. H. DeLuca, C. H. Luce, and M. A. Madej. 2004. Benefits and impacts of road removal. Frontiers in Ecology and the Environment 2:21–28.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

USFS (U.S. Forest Service). 2002. Report of the Forest Service: fiscal year 2001. USFS, Washington, D.C.

Weaver, T., and J. J. Fraley. 1991. Fisheries habitat and fish populations. Flathead Basin Forest Practices, Water Quality and Fisheries Cooperative Program. Flathead Basin Commission, Kalispell, Montana.

Weaver, T., and J. J. Fraley. 1993. A method to measure emergence success of westslope cutthroat trout fry from varying substrate compositions in a natural stream channel. North American Journal of Fisheries Management 13:817–822.

Weaver, T., and R. G. White. 1985. Coal Creek fisheries monitoring study III. Montana State Cooperative Fisheries Research Unit, Quarterly Progress Report, Bozeman.

Wegner, S. 1999. Monitoring of watershed restoration activities: Quartz Creek–Middle Kootenai bull trout recovery area. Pages 317–324 *in* D. S. Olsen and J. P. Potyondy, editors. Proceedings of the Bozeman Specialty Conference on Wildland Hydrology. American Water Resources Association, Middleburg, Virginia.

Wofford, J. E. B., R. E. Gresswell, and M. A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15:628–637.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. North American Journal of Fisheries Management 11:339–346.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey.

The Journal of Wildlife Management; DOI: 10.1002/jwmg.21258

Research Article

Security Areas for Elk During Archery and Rifle Hunting Seasons

DUSTIN H. RANGLACK,[1,2] *Fish and Wildlife Ecology and Management Program, Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA*

KELLY M. PROFFITT, *Montana Fish, Wildlife, and Parks, 1400 South 19th Street, Bozeman, MT 59718, USA*

JODIE E. CANFIELD, *Custer Gallatin National Forest, USDA Forest Service, 10 E Babcock Ave., Bozeman, MT 59771, USA*

JUSTIN A. GUDE, *Montana Fish, Wildlife, and Parks, 1420 East Sixth Ave., Helena, MT 59620, USA*

JAY ROTELLA, *Fish and Wildlife Ecology and Management Program, Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA*

ROBERT A. GARROTT, *Fish and Wildlife Ecology and Management Program, Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA*

ABSTRACT Fall elk (*Cervus canadensis*) habitat management on public lands provides security areas for reasonable elk survival and hunter opportunity. The management focus of maintaining or improving security areas, combined with conservative harvest regulations, may explain why some elk populations have increased in the western United States. However, in areas that include lands that restrict public hunter access, elk may alter their space use patterns during the hunting season by increasing use of areas that restrict public hunter access rather than using security areas on adjacent public lands. We used global positioning system location data from 325 adult female elk in 9 southwest Montana populations to determine resource selection during the archery and rifle hunting seasons. We found that during the archery season, in order of decreasing strength of selection, elk selected for areas that restricted access to public hunters, had greater time-integrated normalized difference vegetation index values, had higher canopy cover, were farther from motorized routes, and had lower hunter effort. During the rifle season, in order of decreasing strength of selection, elk selected for areas that restricted access to public hunters, were farther from motorized routes, had higher canopy cover, and had higher hunter effort. Interactions among several covariates revealed dependencies in elk resource selection patterns. Further, cross-population analyses revealed increased elk avoidance of motorized routes with increasing hunter effort during both the archery and rifle hunting seasons. We recommend managing for areas with ≥13% canopy cover that are ≥2,760 m from motorized routes, and identifying and managing for areas of high nutritional resources within these areas to create security areas on public lands during archery season. During the rifle season, we recommend managing for areas with ≥9% canopy cover that are ≥1,535 m from motorized routes, and are ≥20.23 km^2. Lastly, given increased elk avoidance of motorized routes with higher hunter effort, we recommend that to maintain elk on public lands, managers consider increasing the amount of security in areas that receive high hunter effort, or hunting seasons that limit hunter effort in areas of high motorized route densities. © 2017 The Wildlife Society

KEY WORDS elk, Hillis paradigm, hunting, Montana, NDVI, resource selection function, road effects, security areas.

In addition to their ecological impacts on vegetation and plant community structure (Hobbs 1996; Wolf et al. 2007; Marshall et al. 2013, 2014), elk (*Cervus canadensis*) provide important cultural and economic benefits to much of the western United States through tourism and hunting (Duffield and Holliman 1988). In many western states, the majority of elk hunting occurs on public lands, highlighting the need for wildlife managers and public land managers to cooperatively manage elk habitat. Traditional fall elk security area management on public land is based on managing motorized routes and hiding cover. This concept was first formalized by Hillis et al. (1991) based on work conducted during the rifle hunting season on elk that occupied relatively continuous conifer forests in western Montana. The objective of managing for security areas was to provide a reasonable level of male elk survival during the rifle hunting season while still allowing for hunter opportunity. Hillis et al. (1991) recommended to manage for contiguous cover blocks ≥1.01 km^2 that are ≥0.80 km from the nearest motorized

Received: 5 August 2016; Accepted: 15 February 2017

---

[1] *E-mail: ranglackdh@unk.edu*

[2] *Present Address: Department of Biology, University of Nebraska at Kearney, Kearney, NE 68849-1140, USA.*

route, though the requirements for block size and distance to the nearest motorized route were not considered to be an exact recipe to be followed in all situations. As such, a variety of security definitions, some including specific requirements for canopy cover, are commonly implemented in national forest management plans (Christensen et al. 1993). The relative importance of canopy cover for elk security areas has been questioned, especially in areas with less dense forest cover (Montana Department of Wildlife and Parks [MDFWP] and U.S. Department of Agriculture [USDA] Forest Service 2013), but has not been formally evaluated.

Extrapolations of traditional security area parameters to less densely forested habitats, mixed ownership regions, archery hunting seasons, and female elk survivorship may not be valid. In areas that include a matrix of publicly accessible and restricted access lands, elk may decrease their use of security areas (Hillis paradigm) on public lands and increase their use of areas that restrict public hunter access during the hunting season (Burcham et al. 1999; Conner et al. 2001; Hayes et al. 2002; Proffitt et al. 2010, 2013). Additionally, in many areas, hunting seasons are designed to decrease the number of elk, and as such are focused on increasing the harvest of adult female elk rather than solely on maintaining male elk survival. If female elk are not available to hunters in sufficient numbers because of a distribution shift from publicly accessible to restricted access lands, then harvest is not an effective tool to reduce adult female survival and overall elk population growth. Elk distribution shifts from publicly accessible to restricted access lands, whether the result of short-term changes in hunting pressure (Millspaugh et al. 2000, Proffitt et al. 2010) or long-term behavioral adaptations (Boyce 1991), is a major challenge to wildlife and land managers as they attempt to maintain elk populations at socially acceptable levels while also meeting public demand for hunting opportunities (Haggerty and Travis 2006).

The timing and degree of changes in elk distributions during hunting season are not consistent across populations; some populations show little to no change in distribution across publicly accessible and restricted access lands during the hunting season, or even increase use of publicly accessible areas during the hunting seasons. This may be the result of a functional response in resource selection (Mysterud and Ims 1998, Mabille et al. 2012), where the strength of selection for or against publicly accessible or restricted access lands is dependent on the availability of that resource. Each population's annual range comprises different proportions of publicly accessible lands with different levels of hunter pressure. Thus, differences in the strength of selection for various habitat attributes may be related to these differences in hunter access and hunter pressure. Additionally, the effects of the archery and rifle season on elk distributions vary across populations and likely correlate with different degrees of hunting pressure during each season. Some elk populations begin redistribution during the archery season (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2013), whereas others do not respond until the rifle season (Millspaugh et al. 2000, Johnson et al. 2004, Proffitt et al. 2013), if at all. Differences in hunter pressure during rifle and archery seasons and differences in topography and elk migratory behavior have been suggested to explain the differences among the selections made by different populations (Conner et al. 2001, Proffitt et al. 2013).

Although most research and management has focused on the impacts of rifle hunting on elk, archery hunting has been increasing in popularity, with a 98% increase in archery license sales in Montana since 1985 (Montana Fish, Wildlife and Parks, unpublished data). As such, understanding elk responses to archery hunting and incorporating potential archery hunting effects into elk management plans is important. Archery hunting can lead to reduced pregnancy rates and delayed conception in elk (Davidson et al. 2012). Nutritional condition of female elk during the late-summer and rut is also related to pregnancy rates and conception (Noyes et al. 2004, Cook et al. 2013). Human disturbance associated with archery hunting may shift elk distributions away from areas of high nutritional resources, potentially affecting elk population dynamics further than would be expected through archery hunting mortality alone.

We used fine-scale location data collected during 2005–2014 to assess female elk resource selection during the archery and rifle hunting seasons in 9 elk herds in southwestern Montana. We also examined potential functional responses in elk resource selection by comparing the standardized coefficient estimates from population-specific models along gradients of accessible:restricted access lands and mean hunter pressure to determine whether the relative availability of publicly accessible land or population-specific hunter pressure influence the direction or strength of elk resource selection during the hunting seasons. Finally, we evaluated the traditional paradigm of elk security areas (Hillis et al. 1991) against security area metrics derived from our top resource selection function models for archery and rifle hunting seasons.

STUDY AREA

The study area included the annual ranges of 9 elk populations in southwestern Montana (Fig. 1). Climate in these ranges is characterized by short, cool summers and long, cold winters. Vegetation types across these ranges included a mix of montane forest (e.g., aspen [*Populus tremuloides*], Douglas fir [*Pseudotsuga menziesii*], lodgepole pine [*Pinus contorta*]), open sage-grassland (e.g., big sagebrush [*Artemesia tridentata*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], Idaho fescue [*Festuca idahoensis*]), and upland grasslands, meadows, and unvegetated areas, but the relative proportions of these vegetation types varied among the populations. All elk ranges included a mix of public lands that are generally accessible to public hunters, primarily managed by the United States Forest Service or Bureau of Land Management, privately owned lands that are accessible to hunters through a State of Montana hunter access program, and privately owned lands with unknown and varying degrees of restrictions on public hunter access. Additionally, several of the herd ranges overlap with Yellowstone National Park, which is public land but no

Figure 1. Annual ranges of 9 elk population in southwest Montana, USA, 2005–2014.

hunting is allowed. Elevation, motorized route densities, and indices of nutritional resources varied among the populations' ranges (Table 1). Mule deer (*Odocoileus hemionus*), white tail deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces americanus*) also occupy the elk ranges. Wolves (*Canis lupus*), mountain lions (*Puma concolour*), American black bears (*Ursus americanus*), and coyotes (*Canis latrans*) are the elk predators in the system, and grizzly bears (*Ursus arctos*) are also found in the ranges in the eastern portion of the study area. Gude et al. (2006), White et al. (2012), and Proffitt et al. (2013, 2014) provide full descriptions of these areas.

METHODS

During 2005–2014, we captured and radio-collared adult female elk from 9 populations in southwestern Montana on their winter ranges using helicopter net-gunning or chemical immobilization (Table 2). Elk populations were selected for capture and radio-collaring as part of several different projects related to carnivore-elk interactions, elk brucellosis, or elk survival investigations. In all cases, collared elk were selected randomly from those present on the winter ranges. Collar functionality differed among populations and years, and all collars contained global positioning system (GPS) receivers that collected 12–48 locations/day for a minimum of 1 year. Because our goal in this project was to synthesize data collected across a large spatial scale, we pooled data from these 9 elk populations to create a regional elk location dataset; we also used the individual population datasets. All animals were handled according to approved Institutional Animal Care and Use Committee protocols.

We developed separate archery- and rifle-season resource selection functions using a used-available framework (Johnson 1980, Manly et al. 2007). Archery and rifle seasons for each year were defined by the Montana Fish, Wildlife, and Parks hunting season dates (Appendix S1, available online in Supporting Information). We treated locations collected from the GPS collars as the used sample. We randomly selected 4 used locations per individual per day to reduce spatial autocorrelation in the data (Hansteen et al. 1997), to ensure that sample sizes were equal for all individuals regardless of collar scheduling, and to avoid potential bias in habitat use that can result from systematic data selection (e.g., collecting locations at 0000, 0600, 1200, 1800). The collars were designed to drop-off after 1 year; however, for a small number of individuals, the drop-off feature failed. To maintain equal sampling effort for all individuals, we used only data from the first year each individual was collared. For 5 of the populations, there were a small number of individuals ($\leq$12/population) that had $\geq$1 day with <4 locations. In these cases, we used all available data for those days (<4 locations), thus underweighting those individuals in the models. We still included $\geq$92% of the possible locations for the period of interest for those individuals. We defined population-specific annual ranges by randomly selecting 1 location per day per individual to reduce spatial autocorrelation among the locations, and then building 99% kernel density estimator (KDE) contours using

Table 1. The mean and standard deviation (where applicable) of landscape attributes of 9 elk population annual ranges within southwestern Montana, USA, 2005–2014.. The values presented are based on the minimum spatial scale available for each of the covariates.

	Elevation (m)		Distance to motorized routes (m)		Canopy cover (%)		Time-integrated NDVI[a]		Publicly accessible	Hunter effort (days/km^2)	
Population	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	Proportion	$\bar{x}$	SD
Bitterroot East Fork	1,917	329	1,662	1,861	26.4	26	48.3	11	0.77	7.48	4.2
Bitterroot West Fork	1,907	274	1,999	2,204	35.8	23	45.1	8.8	0.96	1.9	0.2
Blacktail	2,200	264	1,831	1,635	14.9	22.6	51	13	0.82	4.85	2.53
Dome Mountain	2,430	282	6,369	5,417	26.2	24.1	53	10	0.19	1.97	4.16
Madison Valley	2,273	356	2,981	2,853	26	25.9	52.1	13	0.62	5.79	3.02
Paradise Valley	2,194	424	3,406	3,070	25	24.1	47.3	12	0.45	8.23	3.10
Pioneers	2,144	286	1,675	1,562	25.8	28.9	44.8	13	0.75	5.91	2.68
Sage Creek	2,177	226	2,408	2,226	10.6	19.7	50.4	13	0.81	4.15	1.37
Sapphires	1,452	341	884	990	25.2	25.6	40.2	12	0.56	5.83	1.27

[a] Normalized difference vegetation index.

Table 2. Global positioning system location data collection and the number of collared elk in 9 southwest Montana, USA, elk populations.

Population	Yr	No. individuals included in the analysis
Bitterroot East Fork	2011	23
	2012	18
	2013	16
Bitterroot West Fork	2011	9
	2012	15
	2013	18
Blacktail	2011	22
	2012	6
Dome Mountain	2007	11
	2008	27
Madison Valley	2005	17
	2006	24
Paradise Valley	2009	37
Pioneers	2013	28
Sage Creek	2012	16
	2013	3
Sapphires	2014	36

kernelUD in the adehabitat package in R, with the *ad hoc* smoothing method. We randomly generated available points at a 1:5 used:available ratio within the population-specific annual range, such that the available sample for each herd was drawn from within that herd's annual range (Northrup et al. 2013).

We evaluated 9 covariates (Table 3) describing elk resource selection based on a review of previous elk studies and current metrics used for elk habitat management (Hillis et al. 1991, Christensen et al. 1993, Proffitt et al. 2011, McCorquodale 2013, Ranglack et al. 2016). To represent roads and other motorized routes, we included distance to motorized routes (McCorquodale 2013). In this case, we included only routes that were open to public motorized use during the hunting season. We excluded all other routes (private, administrative, or closed routes) because we were focused only on those routes and areas that would be accessible to public hunters. Private (on private land and access controlled by private landowners), administrative (gated forest roads available only to agency personnel for infrequent administrative use), and closed routes (routes that are closed to motorized use for all users) are also excluded when classifying security areas (MDFWP and USDA Forest Service 2013). To represent general landscape characteristics, we included 4 landscape attributes: canopy cover, slope, elevation, and solar radiation. Hunting pressure was represented using 2 covariates: accessible for public hunting (hunter access) and hunter effort. Hunter access was a binary covariate contrasting lands that were freely accessible to public hunters with lands that may restrict public hunter access. For the purposes of this analysis, we considered public lands that permitted hunting and private lands enrolled in the State of Montana's Block Management hunter access program to be publicly accessible, and considered all other lands restricted, though there was likely some unknown level of hunter pressure on most of these lands. We estimated hunter effort annually per hunting district using the Montana Fish, Wildlife and Parks harvest survey program, and created an index of hunter pressure for each hunting district as hunter days/km^2, which we used for the archery and rifle seasons. During the archery season (Appendix S1), we included a remotely sensed metric of greenness derived from the normalized difference vegetation index (NDVI), time-integrated NDVI, to represent effects of nutritional resources on selection (Pettorelli et al. 2011). Time-integrated NDVI represents the net primary production during the growing season (Jonsson and Eklundh 2002, White et al. 2009), and is an important factor influencing summer elk resource selection in this area (Garroutte et al. 2016, Ranglack et al. 2016). During the rifle season (Appendix S1), we included snow water equivalent (SWE) as a covariate representing effects of snowpack on selection. We generated SWE values based on the maximum SWE value from the Snow Data Assimilation System (SNOWDAS; National Operational Hydrologic Remote Sensing Center 2004) for each pixel during each of 6 6-day periods during the rifle season (i.e., hunt period). These hunt periods were unique for each year. Full details on covariate development are included in Appendix S2, available online in Supporting Information.

Although resource selection analyses are typically conducted at the resolution of the available covariate data, animals may perceive and select resource attributes at different spatial scales (Anderson et al. 2005, DeVoe et al. 2015, Laforge et al. 2015); therefore, we considered each continuous covariate over 6 different spatial scales (30, 100, 250, 500, 750, 1,000 m) using a moving window average with a search radius equal to the spatial scale, unless the resolution of the original data did not allow for analysis at certain spatial

Table 3. The covariates included in analysis of female elk archery season and rifle season resource selection in southwest Montana, USA, 2005–2014, with the spatial scales and the functional forms (linear, pseudothreshold, quadratic) or data type (binary) that we evaluated for each covariate.

Covariate	Functional form(s)	Spatial scales (m)	Season(s)
Access	Binary	30	Both
Canopy cover	Pseudothreshold	30, 100, 250, 500, 750, 1,000	Both
Distance to motorized routes	Pseudothreshold	30	Both
Elevation	Quadratic	30, 100, 250, 500, 750, 1,000	Both
Hunter effort	Linear, pseudothreshold	Hunting unit	Both
Slope	Quadratic	30, 100, 250, 500, 750, 1,000	Both
Snow water equivalent	Linear, pseudothreshold	1,000	Rifle only
Solar radiation	Quadratic	30, 100, 250, 500, 750, 1,000	Both
Time-integrated NDVI[a]	Pseudothreshold	250, 500, 750, 1,000	Archery only

[a] Normalized difference vegetation index.

scales (Table 3). Examining spatial scales is becoming increasingly important as remote sensing technology advances, leading to increasingly fine data resolutions, which may exceed the ability of individual animals to detect differences from one pixel to the next. Additionally, because the relationship between selection and covariates might be nonlinear, we evaluated multiple functional forms (linear, quadratic, pseudothreshold) for each continuous covariate. We fit pseudothreshold functional forms using a natural log transformation (Franklin et al. 2000). We considered binary covariates only at the 30-m spatial scale because that was the scale of the original data. We evaluated spatial scale and functional forms for each covariate in an exploratory analysis, unless the most appropriate functional form could be identified *a priori* from existing literature (Table 3).

We standardized all continuous covariates by subtracting the mean and dividing by 2 times the standard deviation prior to analysis (Gelman 2008, Lele 2009). We used a multi-tiered approach to model selection (Franklin et al. 2000) to reduce the number of competing models (Burnham and Anderson 2002). We screened all continuous covariates for multi-collinearity using Pearson's correlation coefficients. We not included covariates that were collinear ($|r| \geq 0.7$) with one another in the same model. In tier 1, we examined all possible univariate models in an exploratory analysis to determine the most explanatory functional form(s) and spatial scale(s) for each covariate. We ranked models using corrected Akaike's Information Criterion (AIC_c) and advanced covariates from all the models within 5 AIC_c units of the top model to the next tier. In the next tier, we combined the top covariate forms and scales in all possible combinations to determine the overall best-supported model, according to AIC_c, for elk resource selection during the hunting seasons. We also included interactions between hunter access and distance to motorized routes, hunter access and canopy cover, distance to motorized routes and canopy cover, distance to motorized routes and time-integrated NDVI or SWE (archery or rifle), and distance to motorized routes and hunter effort. We removed uninformative covariates, if any, following recommendations made by Arnold (2010). We modeled resource selection separately for the archery and rifle seasons.

We pooled data from all herds and fit models using a conditional logistic regression model, conditioned on herd-year (unique for each population by yr combination) for the archery season to allow for the annually varying time-integrated NDVI values and herd-hunt period (unique for each population and hunt-period combination) for the rifle season to allow for the 6-day variation in SWE using cph in R version 3.2.2. We chose this modeling framework to ensure that the available points for each stratum were evaluated against the used points for that stratum, because there were time-varying covariates, a different set of instrumented individuals for each year, and different available choice sets for each population.

We then fit population-specific models using the same model structure as that found in the top pooled model to examine the functional response between the distance to motorized routes, canopy cover, hunter effort, and hunter access standardized coefficient estimates along gradients of accessible:restricted access lands and hunter pressure, because these varied among populations. We generalized least squares estimation using gls in the nlme package in R for the population-specific models. Because our dependent variables (standardized model coefficient estimates) were estimates with associated standard errors instead of measured values, we weighted each estimate by the inverse of the variance (Marin-Martinez and Sanchez-Meca 2009), such that estimates that were estimated with greater precision were given more weight than those that were estimated with less precision. We identified functional responses as significant if the 95% confidence intervals on the slope of the estimated regression lines did not overlap 0.

We then evaluated the relative support from the data for our resulting top models and models representing the traditional security area paradigm (Hillis et al. 1991, Christensen et al. 1993). To do so, we examined plots from our top models depicting how relative resource selection changed as canopy cover and distance to motorized routes increased across the range of available values for publicly accessible elk during each season while holding all other covariates at their means. From those, we identified the values of canopy cover and distance to motorized routes where relative resource selection begins to reach a pseudothreshold, which we arbitrarily defined as having a relative slope of 0.5 (slope = range of Y values/[2 × range of X values]). We considered these cutoff values to be analagous to the $\geq$40% canopy cover and $\geq$0.8-km distance to motorized route commonly used in the traditional security area paradigm (Hillis et al. 1991, Christensen et al. 1993). To test the influence of block size on elk selection of areas with canopy cover and distance from motorized routes (attributes considered indicative of security areas), we varied the block size of our security area definitions to include areas $\geq 0\,\text{km}^2$ (no size requirement), $\geq 1.01\,\text{km}^2$, $\geq 2.02\,\text{km}^2$, $\geq 4.05\,\text{km}^2$, $\geq 8.09\,\text{km}^2$, and $\geq 20.23\,\text{km}^2$. We then generated new binary rasters of elk security areas for each season using those cutoff values from our top models as the input (maps comparing the top archery and rifle security metrics with the traditional security area paradigm can be found in Appendix S3).

To evaluate the importance of the canopy cover component of traditional security metrics, we generated rasters representing traditional security areas with a range of canopy cover values ($\geq$0%, $\geq$10%, $\geq$20%, $\geq$30%, $\geq$40%, $\geq$50%, $\geq$60%, $\geq$70%), while holding the distance to route ($\geq$0.8 km) and size of the block ($\geq 1.01\,\text{km}^2$) constant and compared models with this range of traditional security covariates. This resulted in 8 traditional security area metrics and 6 security area metrics derived from our analyses for each season.

To compare traditional security areas with those identified in our analyses, we extracted values for used and available points from our new security rasters and the traditional paradigm rasters with varying canopy cover. We then fit our top model for each season, replacing the canopy cover and distance to motorized routes covariates with either the traditional security area paradigm with varying canopy cover or our new security area values. We compared these models using AIC_c to determine which combination of canopy cover, distance to motorized routes, and block size covariates was most supported by the data.

Lastly, to determine whether the proportion of security areas within a population home range influenced the extent to which the population redistributed from publicly accessible to restricted access lands through the course of the fall hunting season, we examined a potential relationship between elk redistribution and the proportion of the annual range qualified as a security area, using linear regression. We quantified redistribution as the difference between the proportion of used locations on publicly accessible lands in August and the proportion of used locations on publicly accessible lands during the rifle season for each population. The proportion of the population annual range defined as a security area was based only on the publicly accessible portion of the annual range, and was calculated based on the security area metrics from our top archery and rifle models, and using the traditional security area definition that included 40% canopy cover.

RESULTS

We used 57,282 archery season and 47,602 rifle season elk locations collected from 325 individual elk in our analyses. Of the used locations, 61.9% and 52.5% occurred on publicly accessible lands during the archery and rifle seasons, respectively. Mean elevation of used points was $2{,}104 \pm 463$ (SD) m and $2{,}005 \pm 420$ m during the archery and rifle seasons, respectively. Mean distance to motorized routes of used points was $2{,}586 \pm 2{,}982$ m and $2{,}058 \pm 2{,}109$ m during the archery and rifle seasons, respectively. Mean time-integrated NDVI of used points during the archery season was 52.6 ± 11.6. Mean SWE of used points during the rifle season was 27.7 ± 28.8 mm. The mean slope of the used points was 14.3 ± 9.4 degrees and 14.1 ± 8.9 degrees during the archery and rifle seasons, respectively. The mean canopy cover of the used points was $27.7 \pm 25.2\%$ and $19.6 \pm 23.2\%$ for the archery and rifle seasons, respectively.

Elk Resource Selection

Using the pooled regional dataset, the full model was the most supported model of elk resource selection during the archery hunting season, with the next best model having a $\Delta\mathrm{AIC}_c = 80.4$. In general, elk were more likely to use areas that restricted public access. Regardless of accessibility, elk were less likely to use hunting districts with higher hunter effort. Further, elk were more likely to use areas as distance to motorized routes, canopy cover, time-integrated NDVI, and solar radiation increased, though distance to motorized routes and canopy cover quickly reached a pseudothreshold at $\geq$2,760 m and $\geq$13%, respectively, for publicly accessible lands. Elk used moderate slopes as compared to flat or steeper slopes (Fig. 2 and Table 4). All interactions improved model fit. Model results indicated that elk were more likely to use areas with higher canopy cover at all distances from motorized routes and were more likely to use areas far from motorized routes at all levels of canopy cover. At high NDVI values, there was little difference in elk selection for areas near versus far from motorized routes, but at low NDVI values, elk were more likely to use areas far from motorized routes. Elk also were less likely to use areas with higher hunter effort if they were closer to motorized routes, but elk showed little response to increases in hunter effort far from motorized routes. Additionally, the difference in strength of selection for areas with high and low canopy cover were greater on publicly accessible lands than on lands that restricted access. This same pattern was also found for the difference in the strength of selection for areas near and far from motorized routes (Fig. 3 and Table 4, Appendix S4).

Using the pooled regional dataset, the full model was the most supported model of elk resource selection during the rifle hunting season, with the next best model having a $\Delta\mathrm{AIC}_c = 36.6$. Similar to the archery hunting season model, elk were more likely to use areas that restricted public access during the rifle season. Regardless of accessibility, elk were more likely to use areas as distance to motorized routes, canopy cover, hunter effort, and solar radiation increased, and less likely to use areas as elevation and SWE increased. Elk responses to distance to motorized routes, canopy cover, and hunter effort quickly reached pseudothresholds at $\geq$1,535 m, $\geq$9%, and $\geq$1.33 hunter days/km^2, respectively, for publicly accessible lands. Elk also were more likely to use moderate slopes (Fig. 4 and Table 4). All of the interactions improved model fit. Elk showed a stronger response to increases in SWE when far from motorized routes than when near motorized routes. Elk showed stronger selection for areas farther from motorized routes in areas with high hunter effort, whereas they showed little response to increases in hunter effort when near motorized routes. Similar to the archery season, the difference in strength of selection for areas with high and low canopy cover were greater on publicly accessible lands than on lands that restricted public access. However, contrary to the archery season results, the difference in the strength of selection for areas near and far from motorized routes was greater in areas that restricted access (Fig. 5 and Table 4, Appendix S4).

In our functional response analysis, we detected no changes in the strength of selection for areas that had higher canopy cover, restricted public access, or lower hunter effort with increases in the ratio of accessible:restricted access lands and hunter effort during the archery and rifle seasons (Table 5, Appendix S5). However, elk were significantly more likely to use areas farther from motorized routes as mean hunter effort in the annual range increased during the archery (Fig. 6a) and rifle seasons (Fig. 6b). This response was very similar during the rifle season (0.20 ± 0.09, estimate ± SE) and the archery season (0.19 ± 0.07).

Security Areas

Based on the top model from the archery season, we identified areas with $\geq$13% canopy cover (1,000-m spatial scale) and $\geq$2,760 m from a motorized route as security areas for elk during the archery season. The model including these 2 parameters, without a defined minimum block size ($\geq$0 km^2),

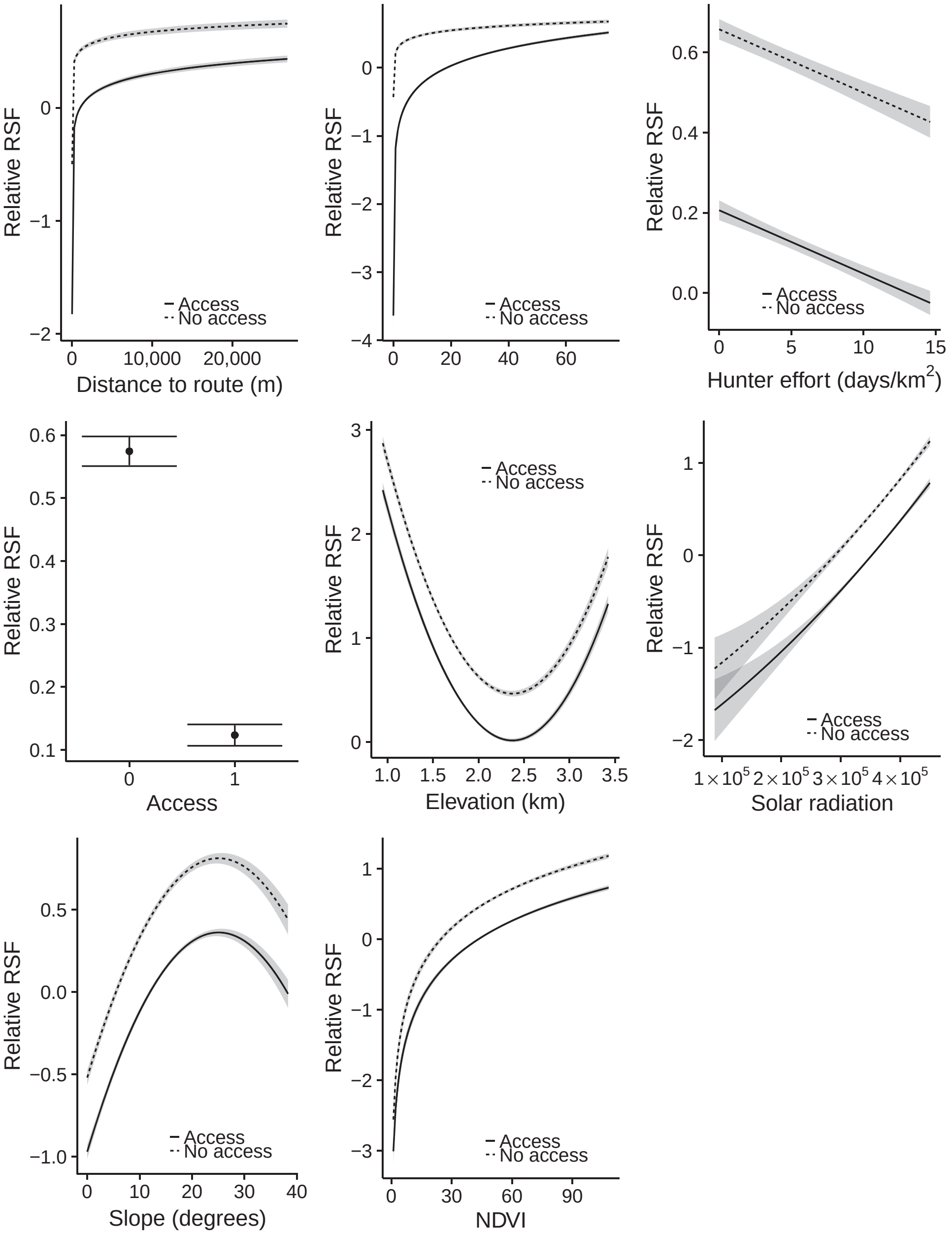


Figure 2. Plots of the main effects for the covariates included in the top archery season model of the resource selection function (RSF) for elk in southwest Montana, USA, 2005–2014, presented on the original, non-standardized scale. The plots present the coefficient estimate (lines) and 95% confidence interval (shaded) for areas that allow (access) or do not allow (no access) public hunter access across the available range for each covariate, with the other variables held at their mean value. The *y*-axis is analogous to the log-odds of selection. NDVI is time-integrated normalized difference vegetation index.

received the most support, with the next best model having a $\Delta\text{AIC}_c = 88.9$ (Table 6). All of the new security area metrics arising from our most supported archery season model were more strongly supported than all of the traditional security area metrics. Of the traditional security area metrics with a minimum block size of 1.01 km^2 $\geq$0.80 km from a motorized route, $\geq$10% canopy cover was the most supported (Table 6).

Based on the top model from the rifle season, we identified areas with $\geq$9% canopy cover (1,000-m spatial scale) and $\geq$1,535 m from a motorized route as security areas for elk during the rifle season. The model including these 2 parameters with a minimum block sizes of 20.23 km^2 received the most support, with the next best model having a $\Delta\text{AIC}_c = 24.7$ (Table 6). Similar to the archery season models, all of the new security area metrics derived from our most supported rifle season model were more strongly supported than all the traditional security area metrics. Of the traditional security area metrics with a minimum block size of 1.01 km^2 $\geq$0.80 km from a motorized route, $\geq$0% canopy cover was the most supported (Table 6). We did not detect any relationships between the amount of elk redistribution from accessible to restricted access lands and the proportion of the annual range in any of the security area metrics.

Table 4. The functional form, spatial scale, standardized coefficient estimates, and 95% confidence intervals for the top regional model of archery season and rifle season female elk resource selection in southwest Montana, USA, 2005–2014.

	Archery			Rifle		
Covariate	**Functional form and spatial scale**	**Coefficient estimate**	**CI**	**Functional form and spatial scale**	**Coefficient estimate**	**CI**
Access	Binary; 30 m	−0.75	(−0.78, −0.72)	Binary; 30 m	−0.93	(−0.96, −0.91)
Canopy cover	Pseudothreshold; 1,000 m	0.55	(0.51, 0.60)	Pseudothreshold; 1,000 m	0.41	(0.37, 0.44)
Distance to motorized routes	Pseudothreshold; 30 m	0.43	(0.40, 0.47)	Pseudothreshold; 30 m	0.73	(0.68, 0.78)
Elevation	Quadratic[a]; 30 m	−0.62 0.87	(−0.65, −0.59); (0.84, 0.90)	Quadratic; 1,000 m	−1.14 0.34	(−1.19, −1.09); (0.31, 0.38)
Hunter effort	Linear; Hunting unit	−0.32	(−0.35, −0.30)	Pseudothreshold; Hunting unit	0.19	(0.16, 0.21)
Slope	Quadratic; 1,000 m	0.70 −0.51	(0.67, 0.72); (−0.55, −0.47)	Quadratic; 1,000 m	1.11 −1.06	(1.07, 1.15); (−1.11, −1.02)
Snow water equivalent (SWE)				Linear; 1,000 m	−0.26	(−0.30, −0.23)
Solar radiation	Quadratic; 1,000 m	0.55 0.02	(0.53, 0.58); (0.00, 0.05)	Quadratic; 1,000 m	0.66 −0.34	(0.62, 0.71); (−0.37, −0.30)
Time-integrated NDVI[b]	Pseudothreshold; 250 m	0.63	(0.61, 0.66)			
Canopy cover × access		1.28	(1.20, 1.36)		0.39	(0.34, 0.45)
Distance to route × access		0.25	(0.21, 0.30)		−0.46	(−0.52, −0.39)
Distance to route × canopy cover		−0.42	(−0.51, −0.32)		−0.29	(−0.38, −0.20)
Distance to route × hunter effort		0.95	(0.91, 1.00)		1.15	(1.11, 1.19)
Distance to route × NDVI		−0.63	(−0.69, −0.58)			
Distance to route × SWE					−0.47	(−0.50, −0.43)

[a] The second value presented for quadratic covariates represents the squared term.
[b] Normalized difference vegetation index.

DISCUSSION

Overall, our results suggest that elk habitat management during hunting seasons should focus on hunter access, hunter effort, canopy cover, and motorized routes. These covariates all had important effects on elk resource selection during the archery and rifle seasons and are under some degree of management control. Additionally, nutritional resources are important influences of female elk resource selection during the archery hunting season and should be considered in elk hunting season habitat management strategies. Depending on population size objectives (increase or decrease elk population size) managers can attempt to manipulate each of these factors to make elk more or less vulnerable to harvest. However, managers should also consider that increases in hunter effort (particularly during the rifle season) or motorized routes may encourage elk to select for areas that restrict public hunter access and result in a redistribution of elk away from public lands. We also recommend that new security area metrics derived from our most supported models be considered (Table 6). Because these metrics are predictive of elk resource selection, they may encourage elk to remain on publicly accessible lands throughout the hunting seasons, enabling sufficient harvest to affect population growth rate and providing season-long hunter opportunities on public land.

Our modeling of female elk resource selection during the archery and rifle hunting seasons suggests that, in general, female elk have similar resource selection patterns in both seasons, particularly in relation to factors over which managers have some level of control (distance to motorized routes, canopy cover, and hunter access). Lands that restricted access to hunters were preferred to publicly accessible lands during both seasons. Thus, we recommend that managers work closely with private landowners to increase public accessibility to private lands if management goals are to reduce elk population size. Additionally, the results of our functional response analysis suggest that high hunter effort during the archery season increases elk avoidance of areas near motorized routes (Fig. 6a) in a similar manner to elk responses during the rifle season (Fig. 6b). We recommend managers consider wildlife related motorized travel closure dates that include archery and rifle season in areas of high hunter effort, or hunting seasons that limit hunter effort in areas of high motorized route densities to maintain elk distribution on publicly accessible lands.

The increase in elk selection for areas farther from motorized routes with increases in hunter effort (Fig. 6) helps to explain the documented shift in elk movements during archery hunting seasons that occur in some areas (Conner et al. 2001, Vieira et al. 2003). Contrary to Vieira et al. (2003), we found that hunter effort influenced elk resource selection during the archery season; elk generally avoided areas of high hunter effort, with this response being stronger in areas near motorized routes. In our study sites, this selection pattern also involves elk selecting for lands that restricted access, which had one of the strongest effects on elk resource selection during the archery season. Security for elk

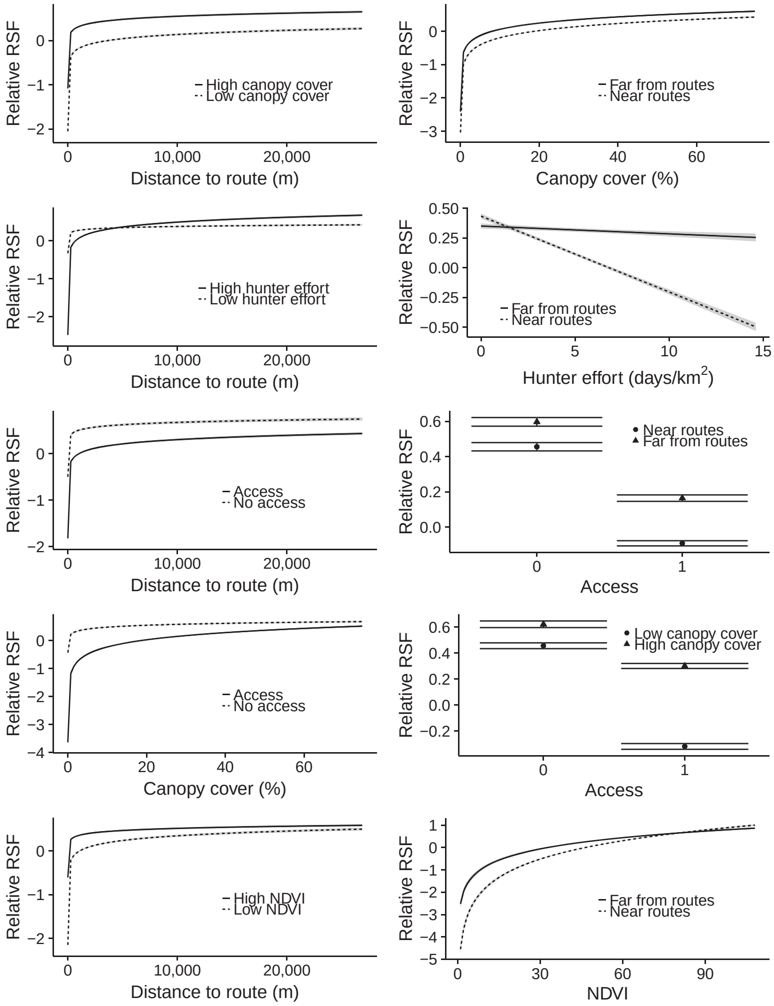


Figure 3. Plots of the interactions included in the top archery season model of the resource selection function (RSF) for elk in southwest Montana, USA, 2005–2014, presented on the original, non-standardized scale. Each row presents 1 interaction, with 1 interacting variable presented on the *x*-axis and the other presented using 2 lines on the plot, 1 for a low value (first quartile) and 1 for a high value (third quartile) of that covariate. The specific high and low values used are available in Appendix S4. The plots present the coefficient estimate (lines) and 95% confidence interval (shaded) across the available range for each covariate, with the other variables held at their mean value. The *y*-axis is analogous to the log-odds of selection. NDVI is time-integrated normalized difference vegetation index.

on publicly accessible lands has traditionally been regarded as areas away from motorized routes with high canopy cover that can maintain elk even during periods of hunting stress (Lyon 1979, 1983; Hillis et al. 1991). Hunter access had a stronger influence on elk resource selection in both hunting seasons than either distance to motorized routes or canopy cover (Table 4).

The influence of late-summer nutrition on ungulate population dynamics and resource selection has been documented (Cook et al. 2004, 2013; Monteith et al. 2014; Ranglack et al. 2016), but the potential effects of nutrition on archery season elk distributions have not been previously evaluated. Using data from these same study areas, Ranglack et al. (2016) reported that during July and August, female elk selected strongly for areas of high nutritional resources (as represented by time-integrated NDVI), but that motorized routes had a relatively small influence on selection. Using standardized coefficient estimates to compare summer and archery season effects in the same 9 elk herds, female elk avoidance of motorized routes nearly doubled during the archery season, whereas selection for areas with higher time-integrated NDVI values decreased by nearly half. Our results suggest that during the archery hunting season, female elk continue to seek out areas of high nutritional value, even when they are near motorized routes (Fig. 3), but this selection has been reduced, likely because of the increased avoidance of motorized routes or selection for the other covariates that we documented as influential. If elk attempt to select for areas of high nutritional value throughout the archery hunting season but are unable to do so because of hunting risk, archery hunter pressure may compromise female nutritional status at a critical time of year (Noyes et al. 2004, Davidson et al. 2012). This suggests that archery hunting has the potential to affect fall nutritional condition of female elk, and potentially pregnancy rates and body fat levels of elk entering the winter season. This topic needs more investigation and managers may need to consider including motorized route closures, earlier closure dates

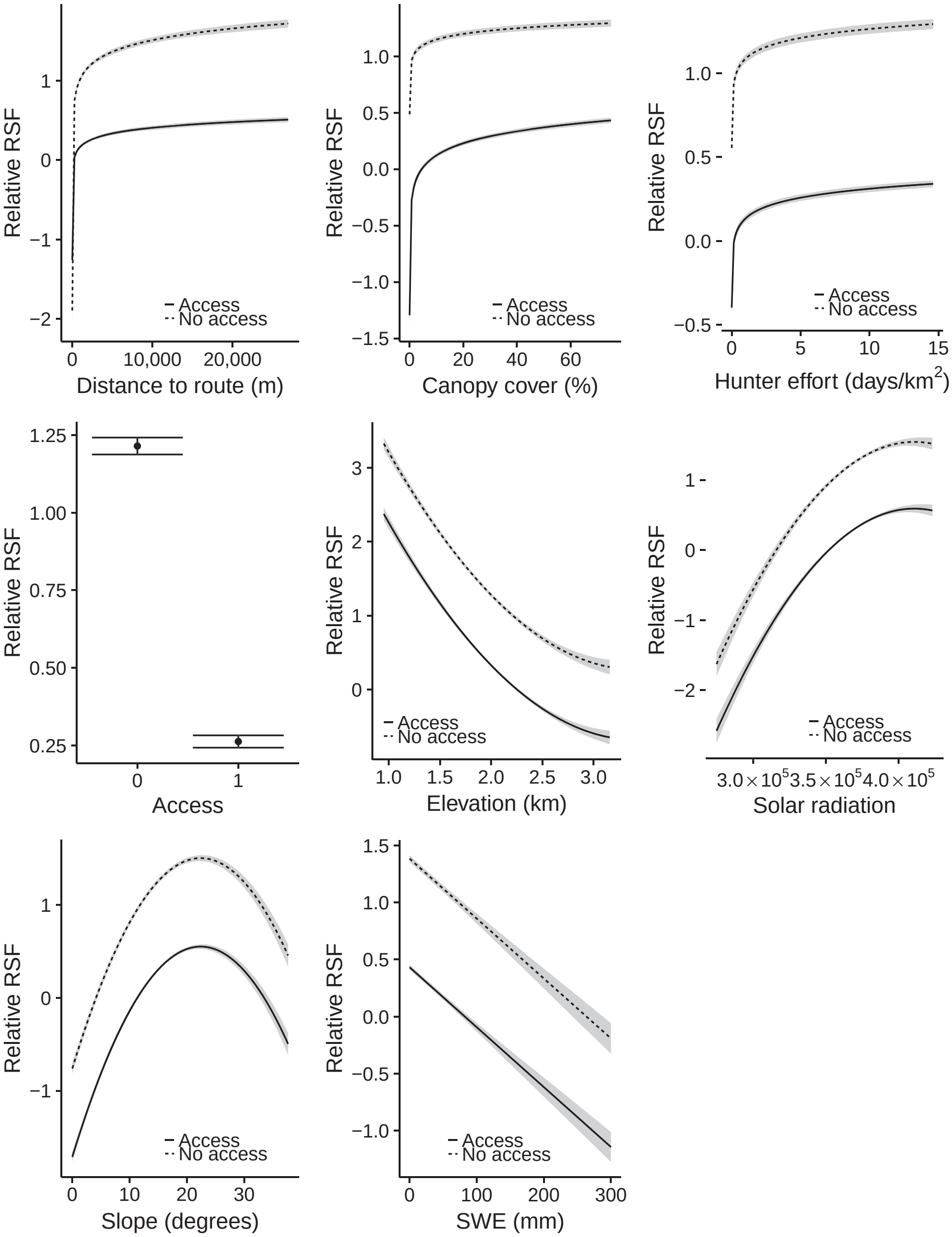


Figure 4. Plots of the main effects for the covariates included in the top rifle season model of the resource selection function (RSF) for elk in southwest Montana, USA, 2005–2014, presented on the original, non-standardized scale. The plots present the coefficient estimate (lines) and 95% confidence interval (shaded) for areas that allow (access) or do not allow (no access) public hunter access across the available range for each covariate, with the other variables held at their mean value. The *y*-axis is analogous to the log-odds of selection. SWE is snow water equivalent.

during travel planning, and limits on hunter numbers during the archery season in areas of high nutritional value for elk if maintaining elk access to nutritional resources is part of the management intention.

During the rifle season, elk avoided areas near motorized routes and the response was stronger than during the archery season, indicating that the impact of motorized routes on elk resource selection continues to increase from summer (Ranglack et al. 2016) to archery and rifle seasons. Although not unexpected given the vast literature on road effects on ungulates (McCorquodale 2013), these differences suggest that elk response to motorized routes varies seasonally and is strongly related to the risks associated with hunting seasons. Based on the thresholds we identified in our most supported models, during the archery season, we recommend managing for areas ≥2,760 m from the nearest motorized route; this distance decreases during the rifle season to ≥1,535 m. This indicates that although the overall influence of motorized routes on elk resource selection during the archery season is lower than during the rifle season, the spatial scale of effects during archery season is larger. This may be because archery hunters are more apt to hike farther away from motorized routes in pursuit of elk. In contrast, rifle hunters have a stronger but more limited area of influence around motorized routes. The impact of motorized routes on elk resource selection during the hunting seasons is further supported by

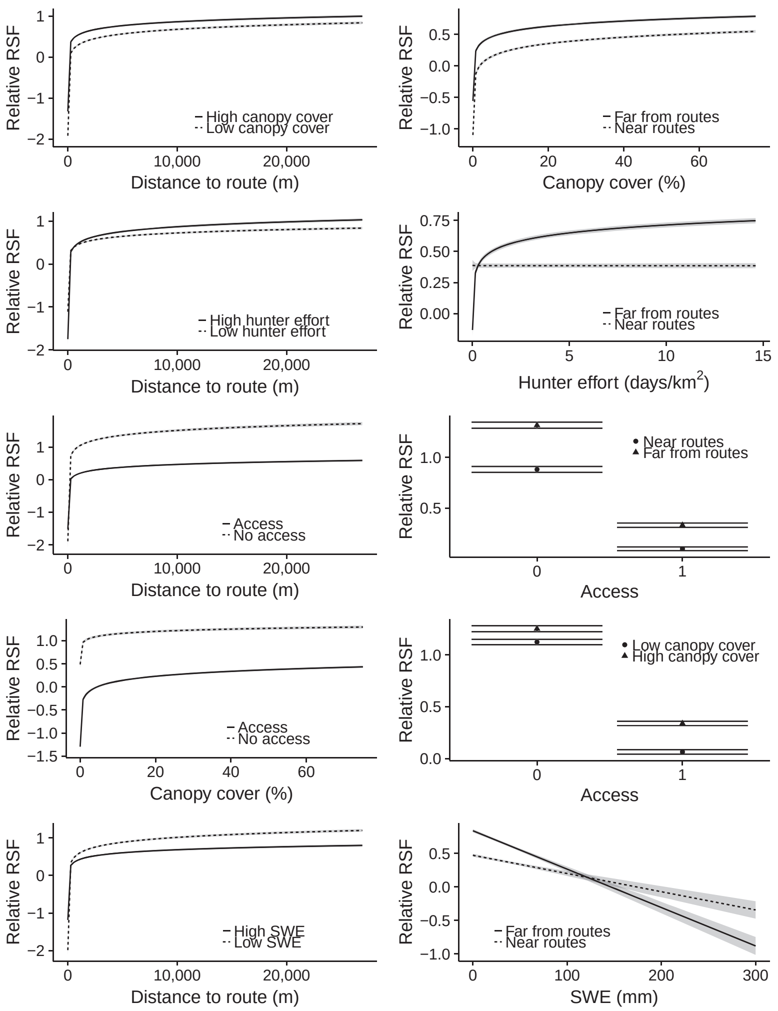


Figure 5. Plots of the interactions included in the top rifle season model of the resource selection function (RSF) for elk in southwest Montana, USA, 2005–2014, presented on the original, non-standardized scale. Each row presents 1 interaction, with 1 interacting variable presented on the *x*-axis and the other presented using 2 lines on the plot, 1 for a low value (first quartile) and 1 for a high value (third quartile) of that covariate. The specific high and low values used are available in Appendix S4. The plots present the coefficient estimate (lines) and 95% confidence interval (shaded) across the available range for each covariate, with the other variables held at their mean value. The *y*-axis is analogous to the log-odds of selection. SWE is snow water equivalent.

the functional response depicting increasing selection for areas farther from motorized routes with higher hunter effort (Fig. 6). Given the increasing popularity of archery hunting, the different impacts of archery and rifle hunters should be incorporated into management by extending motorized route closures such that they include the archery season (MDFWP and USDA Forest Service 2013). Additionally, because of the larger spatial influence of motorized routes during the archery season, some motorized routes may warrant closure during the archery season only and can be re-opened during the rifle hunting season.

Overall, we saw very similar patterns of resource selection during the archery and rifle hunting seasons, in terms of direction of selection for the different covariates but also for

Table 5. The estimated regression slope (and SE) examining potential functional responses between the standardized coefficient estimates from the population-specific models for hunter access, canopy cover, distance to motorized routes, and hunter effort along gradients of accessible:restricted access and mean hunter effort for elk population annual ranges, southwestern Montana, USA, 2005–2014. Values with confidence intervals that do not overlap 0 are indicated with an asterisk.

	Archery		**Rifle**	
Covariate	**Accessible:restricted access**	**Mean hunter effort**	**Accessible:restricted access**	**Mean hunter effort**
Hunter access	1.23 (1.06)	0.02 (0.10)	−0.02 (1.03)	−0.10 (0.10)
Canopy cover	0.79 (0.82)	0.11 (0.07)	0.42 (1.00)	0.11 (0.10)
Distance to motorized routes	1.06 (0.68)	0.19 (0.07)*	0.81 (0.75)	0.20 (0.09)*
Hunter effort	−1.09 (0.56)	−0.01 (0.08)	−0.06 (0.94)	0.06 (0.10)

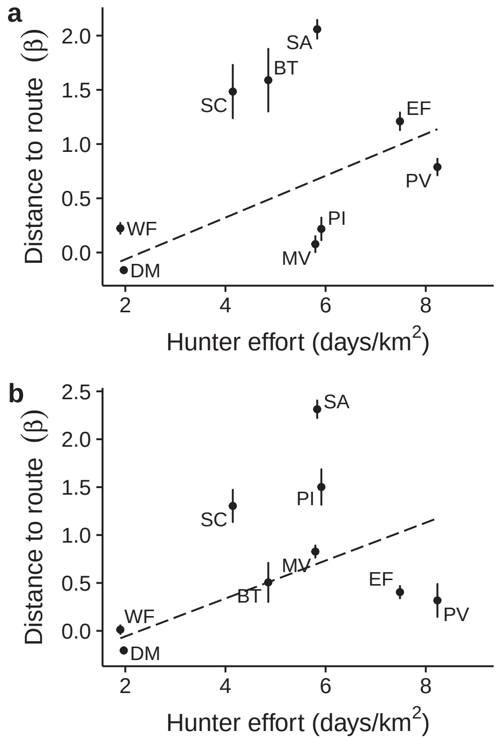


Figure 6. The relationship between the estimated effect of distance to motorized routes and mean hunter effort (days/km^2) for the archery (a) and rifle (b) seasons for resource selection by elk in southwest Montana, USA, 2005–2014. The standardized estimated coefficient from each population, and standard error, is presented with the results of the generalized least squares model designated by the dashed line. Populations are labeled as follows: BT = Blacktail, DM = Dome Mountain, EF = Bitterroot East Fork, MV = Madison Valley, PI = Pioneers, PV = Paradise Valley, SA = Sapphires, SC = Sage Creek, and WF = Bitterroot West Fork.

the spatial scale of each covariate that received the most support from the data. However, the direction of selection for hunter effort changed from the archery to rifle season (Table 4), possibly because of the impacts of snow during the rifle season. Snow accumulation is strongly associated with the ecology and behavior of animals in cold climates because snow can reduce access to forage patches (Craighead et al. 1973, Bruggeman 2006) and increase energy expenditure for thermoregulation, travel, and search for food (Parker et al. 1984, Telfer and Kelsall 1984). We found the influence of SWE on elk resource selection to be moderated by distance to motorized routes, with elk showing stronger responses to increases in SWE when far from motorized routes than when near motorized routes (Fig. 5). This indicates that when near routes, elk are balancing searching for areas of low SWE with other factors. During the archery season, when elk are not limited by snow and the effect of motorized routes is weaker, elk are more likely to use areas with lower hunter effort. However, during the rifle season, elk are more limited in the habitats that are available to them because of snow accumulation. Hunters may in turn respond to these more tightly defined elk resource selection patterns, making it appear that elk are more likely to be found in areas of high hunter effort when in reality hunter effort may be higher where elk are more likely to be present.

The traditional security paradigm of managing for blocks of unfragmented forest cover away from motorized routes (Lyon 1979, 1983; Hillis et al. 1991) has been widely accepted and is likely a factor contributing to increasing elk populations over the last 50 years (Lonner and Cada 1982, Hillis et al. 1991, Picton 1991, O'Gara and Dundas 2002). Our results suggest that similar security paradigms could be applied to southwestern Montana in efforts to encourage female elk to use public lands. During the archery season, our analysis suggests that areas with ≥13% canopy cover (1,000-m scale) that are ≥2,760 m from the nearest motorized route may be perceived by female elk as secure, regardless of block size. During the rifle season, areas with ≥9% canopy cover, that are ≥1,535 m from the nearest motorized route, with a block size of ≥20.23 km^2 may be perceived by female elk as secure. This, along with our analysis of the traditional

Table 6. Comparison of the traditional security habitat paradigm based on ≥0.80 km from a motorized route, ≥1.01-km^2 block size, and canopy cover varying from ≥0–70% in increments of 10% and security area definitions based on results of the top ranked model and 6 different minimum block sizes (≥0, 1.01, 2.02, 4.05, 8.09, and 20.23 km^2) for each elk hunting season, southwestern Montana, USA, 2005–2014. During the archery season, the top model defined secure areas based on ≥13% canopy cover (1,000-m spatial scale), ≥2,760 m from a motorized route. During the rifle season, the top model defined secure areas based on ≥9% canopy cover (1,000-m spatial scale), ≥1,535 m from a motorized route.

	Archery		Rifle	
Model rank	**Model**	**ΔAIC_c[a]**	**Model**	**ΔAIC_c**
1	Archery ≥0 km^2	0.0	Rifle ≥20.23 km^2	0.0
2	Archery ≥1.01 km^2	88.9	Rifle ≥0 km^2	24.7
3	Archery ≥2.02 km^2	94.0	Rifle ≥2.02 km^2	66.3
4	Archery ≥4.05 km^2	138.2	Rifle ≥1.01 km^2	90.4
5	Archery ≥8.09 km^2	167.0	Rifle ≥4.05 km^2	105.0
6	Archery ≥20.23 km^2	229.7	Rifle ≥8.09 km^2	151.6
7	Traditional ≥10% canopy	482.2	Traditional ≥0% canopy	266.3
8	Traditional ≥0% canopy	781.7	Traditional ≥10% canopy	1,327.1
9	Traditional ≥20% canopy	1,088.0	Traditional ≥20% canopy	1,699.7
10	Traditional ≥30% canopy	1,208.4	Traditional ≥30% canopy	1,767.2
11	Traditional ≥40% canopy	1,407.5	Traditional ≥40% canopy	1,988.1
12	Traditional ≥50% canopy	1,843.8	Traditional ≥50% canopy	2,491.7
13	Traditional ≥60% canopy	2,049.3	Traditional ≥70% canopy	3,214.8
14	Traditional ≥70% canopy	2,691.1	Traditional ≥60% canopy	3,229.7

[a] Corrected Akaike's Information Criterion.

paradigm with varying levels of canopy cover (Table 6), suggests that the often used 40% canopy cover threshold for security areas is too stringent, and that the influence of motorized routes is more important than canopy cover to female elk resource selection. Indeed, our models show that although important initially, the influence of canopy cover on elk resource selection reaches pseudothresholds at relatively low values for both hunting seasons. We found that for the archery season no minimum block size requirement was supported by our data, whereas the largest minimum block size we tested (20.23 km^2) was required during the rifle season. This pattern perhaps reflects the generally higher hunter pressure and harvest during the rifle season than the archery season, leading to a need for large security areas.

Although it may be beneficial to increase the proportion of security areas within population annual ranges, we found no relationship between the proportion of security areas within the annual range and the amount of redistribution that occurs in these elk populations. This highlights that even when security areas are available on publicly accessible lands, elk may still choose to redistribute to lands that restrict access. This may be due to learned behaviors that are passed from one generation to the next (Boyce 1991), refuge from hunting risk on lands that restrict access, or other unmeasured factors. In any case, this result highlights the importance of state and federal wildlife and land management agencies working collaboratively with private landowners.

MANAGEMENT IMPLICATIONS

We recommend that managers manage for areas with $\geq$13% canopy cover that are $\geq$2,760 m from a motorized route during the archery season to maintain elk distribution on publicly accessible lands during archery and rifle seasons. Special attention should also be given to areas of high nutritional resources during the archery season, as this is an important nutritional period that may affect elk population dynamics (Noyes et al. 2004, Davidson et al. 2012). During the rifle season, we recommend management for areas with $\geq$9% canopy cover that are $\geq$1,535 m from a motorized route, and are $\geq$20.23 km^2. However, elk may continue to use restricted access lands as a result of the strong hunting refuge they provide and learned behavior (MDFWP and USDA Forest Service 2013). Given the strength of selection for areas that restricted access to public hunters in both seasons, we recommend managers work closely with private landowners to increase public accessibility to private lands if management goals are to reduce elk population size, while considering the amount of hunter pressure and motorized routes in the elk populations they are managing. Lastly, given the functional response between distance to motorized routes and hunter effort, we recommend that managers consider wildlife-related travel closure dates to include both archery and rifle seasons in areas of high hunter pressure, or hunting seasons that limit hunter pressure in areas of high motorized route densities.

ACKNOWLEDGMENTS

This project was developed with assistance from Montana Fish, Wildlife and Parks staff (Q. Kujala, A. Grove, N. J. DeCesare) and United States Forest Service staff (E. Tomasik). We thank the many field biologists and aircraft pilots that captured and radio-collared elk during 2005–2014 including J. A. Cunningham, M. Duffy, J. L. Grigg, K. L. Hamlin, B. Jimenez, C. S. Jourdonnais, M. Hebblewhite, M. S. Ross, J. Shamhart, M. Shelton, and R. Swisher. The data used in this project were collected by a variety of biologists, faculty, and graduate students at Montana Fish, Wildlife and Parks, Montana State University, University of Montana, and MPG Ranch. C. J. Butler, M. T. Kohl, B. H. Lowry, P. J. Mahoney, and 2 anonymous reviewers provided valuable input in preparing this manuscript. This project was funded by Montana Fish, Wildlife and Parks and the United States Forest Service.

LITERATURE CITED

Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management 69:298–310.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Boyce, M. S. 1991. Migratory behavior and management of elk (*Cervus elaphus*). Applied Animal Behaviour Science 29:239–250.

Bruggeman, J. E. 2006. Spatio-temporal dynamics of the central bison herd in Yellowstone National Park. Dissertation, Montana State University, Bozeman, USA.

Burcham, M., W. D. Edge, and C. Les Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin 27:833–839.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science and Business Media, New York, New York, USA.

Christensen, A., L. Lyon, and J. Unsworth. 1993. Elk management in the Northern Region: considerations in forest plan updates or revisions. U.S. Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in Northwest Colorado. Journal of Wildlife Management 65:926–940.

Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of Northern Yellowstone elk. Journal of Mammalogy 85:714–722.

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. Mccorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1–45.

Craighead, J. J., F. C. Craighead, R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison Drainage Herd as determined by biotelemetry. Wildlife Monographs 33:3–50.

Davidson, G. A., B. K. Johnson, J. H. Noyes, B. L. Dick, and M. J. Wisdom. 2012. Effect of archer density on elk pregnancy rates and conception dates. Journal of Wildlife Management 76:1676–1685.

DeVoe, J. D., R. A. Garrott, J. J. Rotella, S. R. Challender, P. J. White, M. O'Reilly, and C. J. Butler. 2015. Summer range occupancy modeling of non-native mountain goats in the greater Yellowstone area. Ecosphere 6: art217.

Duffield, J., and J. Holliman. 1988. The net economic value of elk hunting in Montana. Montana Department of Fish, Wildlife and Parks, Helena, USA.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Garroutte, E., A. Hansen, and R. Lawrence. 2016. Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the Greater Yellowstone Ecosystem. Remote Sensing 8:404.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. Ecological Applications 16:285–298.

Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37:816–830.

Hansteen, T. L., H. P. Andreassen, and R. A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Management 61:280–290.

Hayes, S. G., D. J. Leptich, and P. Zager. 2002. Proximate factors affecting male elk hunting mortality in northern Idaho. Journal of Wildlife Management 66:491–499.

Hillis, J., M. Thompson, J. Canfield, L. Lyon, C. Marcum, P. Dolan, and D. McCleerey. 1991. Defining elk security: the Hillis paradigm. Pages 38–43 *in* A. Christensen, L. Lyon, and T. Lonner, editors. Proceedings of a Symposium on Elk Vulnerability. Montana State University, Bozeman, USA.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. Elk and mule deer responses to variation in hunting pressure. Transactions of the 69th North American Wildlife and Natural Resources Conference 69:625–640.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jonsson, P., and L. Eklundh. 2002. Seasonality extraction by function fitting to time-series of satellite sensor data. IEEE Transactions on Geoscience and Remote Sensing 40:1824–1832.

Laforge, M. P., E. Vander Wal, R. K. Brook, E. M. Bayne, and P. D. McLoughlin. 2015. Process-focussed, multi-grain resource selection functions. Ecological Modelling 305:10–21.

Lele, S. R. 2009. A new method for estimation of resource selection probability function. Journal of Wildlife Management 73:122–127.

Lonner, T. N., and J. D. Cada. 1982. Some effects of forest management on elk hunting opportunity. Pages 119–128 *in* T. L. Britt and D. P. Theobald, editors. Proceedings of the western states and provinces elk workshop. Arizona Game and Fish Department, Phoenix, USA.

Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry 77:658–660.

Lyon, L. J. 1983. Road density models describing habitat for elk. Journal of Forestry 81:592–596.

Mabille, G., C. Dussault, J. P. Ouellet, and C. Laurian. 2012. Linking trade-offs in habitat selection with the occurrence of functional responses for moose living in two nearby study areas. Oecologia 170:965–977.

Manly, B. F., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2007. Resource selection by animals: statistical design and analysis for field studies. Second edition. Springer Science & Business Media, New York, New York, USA.

Marin-Martinez, F., and J. Sanchez-Meca. 2009. Weighting by inverse variance or by sample size in random-effects meta-analysis. Educational and Psychological Measurement 70:56–73.

Marshall, K. N., D. J. Cooper, and N. T. Hobbs. 2014. Interactions among herbivory, climate, topography and plant age shape riparian willow dynamics in northern Yellowstone National Park, USA. Journal of Ecology 102:667–677.

Marshall, K. N., N. T. Hobbs, and D. J. Cooper. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proceedings of The Royal Society B 280:20122977.

McCorquodale, S. M. 2013. A brief review of the scientific literature on elk, roads, and traffic. Washington Department of Fish and Wildlife, Olympia, USA.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management 64:994–1003.

Montana Department of Wildlife and Parks [MDFWP] and U.S. Department of Agriculture [USDA] Forest Service. 2013. U.S. Forest Service and Montana Department of Wildlife and Parks collaborative overview and recommendations for elk habitat management on the Custer, Gallatin, Helena, and Lewis and Clark National Forests. MDFWP, Bozeman, Montana, USA.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1–62.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435–1441.

National Operational Hydrologic Remote Sensing Center. 2004. Snow Data Assimilation System (SNODAS) Data Products at NSIDC, 2005–2014. National Snow and Ice Data Center, Boulder, Colorado, USA.

Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456–1463.

Noyes, J. H., B. K. Johnson, B. L. Dick, and J. G. Kie. 2004. Influence of age of males and nutritional condition on short- and long-term reproductive success of elk. Transactions of the North American Wildlife and Natural Resources Conference 69:572–585.

O'Gara, B. W., and R. G. Dundas. 2002. Distribution: past and present. Pages 67–119 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Wildlife Management Institute, Washington, D.C., USA.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Picton, H. D. 1991. A brief history of elk: the hunt, research and management. Pages 10–15 *in* A. Christensen, L. Lyon, and T. N. Lonner, editors. Proceedings of a Symposium on Elk Vulnerability, Bozeman, Montana, USA.

Proffitt, K. M., J. A. Cunningham, K. L. Hamlin, and R. A. Garrott. 2014. Bottom-up and top-down influences on pregnancy rates and recruitment of northern Yellowstone elk. Journal of Wildlife Management 78:1383–1393.

Proffitt, K. M., J. L. Grigg, R. A. Garrott, K. L. Hamlin, J. Cunningham, J. A. Gude, and C. Jourdonnais. 2010. Changes in elk resource selection and distributions associated with a late-season elk hunt. Journal of Wildlife Management 74:210–218.

Proffitt, K. M., J. A. Gude, K. L. Hamlin, R. A. Garrott, J. A. Cunningham, and J. L. Grigg. 2011. Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. Journal of Applied Ecology 48:471–478.

Proffitt, K. M., J. A. Gude, K. L. Hamlin, and M. A. Messer. 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. Journal of Wildlife Management 77:514–524.

Ranglack, D. H., K. M. Proffitt, J. Canfield, J. A. Gude, J. J. Rotella, and R. A. Garrott. 2016. Evaluating elk summer resource selection and applications to summer range habitat management. Montana Department of Fish, Wildlife, and Parks, Helena, USA.

Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828–1834.

Vieira, M. E. P., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. Journal of Wildlife Management 67:717–728.

White, M. A., K. M. de Beurs, K. Didan, D. W. Inouye, A. D. Richardson, O. P. Jensen, J. O'keefe, G. Zhang, R. R. Nemani, W. J. D. van Leeuwen, J. F. Brown, A. De Wit, M. Schaepman, X. Lin, M. Dettinger, A. S. Bailey, J. Kimball, M. D. Schwartz, D. D. Baldocchi, J. T. Lee, and W. K. Lauenroth. 2009. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. Global Change Biology 15:2335–2359.

White, P. J., K. M. Proffitt, and T. O. Lemke. 2012. Changes in elk distribution and group sizes after wolf restoration. American Midland Naturalist 167:174–187.

Wolf, E. C., D. J. Cooper, and N. T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. Ecological Applications 17:1572–1587.

Associate Editor: Kathryn Schoenecker.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Wildlife Monographs 199:1–69; 2018; DOI: 10.1002/wmon.1033

Modeling Elk Nutrition and Habitat Use in Western Oregon and Washington

MARY M. ROWLAND,[1] *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
MICHAEL J. WISDOM, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RYAN M. NIELSON,[2] *Western EcoSystems Technology (WEST), Inc., 2121 Midpoint Drive, Suite 201, Fort Collins, CO 80525, USA*
JOHN G. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RACHEL C. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
BRUCE K. JOHNSON,[3] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
PRISCILLA K. COE,[3] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
JENNIFER M. HAFER, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
BRIDGETT J. NAYLOR, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
DAVID J. VALES, *Muckleshoot Indian Tribe, 39015 172nd Avenue SE, Auburn, WA 98092, USA*
ROBERT G. ANTHONY,[†] *Oregon State University, 1500 Southwest Jefferson Way, Corvallis, OR 97331, USA*
ERIC K. COLE, *U.S. Fish and Wildlife Service, National Elk Refuge, P.O. Box 510, Jackson, WY, 83001, USA*
CHRIS D. DANILSON,[4] *Washington Department of Fish and Wildlife, Region 4, 111 Sherman Street, La Conner, WA 98257, USA*
RONALD W. DAVIS,[5] *Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61820, USA*
FRANK GEYER, *Quileute Tribe, 401 Main Street, La Push, WA 98350, USA*
SCOTT HARRIS, *Washington Department of Fish and Wildlife, 48 Devonshire Road, Montesano, WA 98563, USA*
LARRY L. IRWIN,[3] *National Council for Air and Stream Improvement, P.O. Box 68, Stevensville, MT 59870, USA*
ROBERT MCCOY, *Makah Forestry, P. O. Box 116, Neah Bay, WA 98357, USA*
MICHAEL D. POPE, *Greenbelt Land Trust, P.O. Box 1721, Corvallis, OR 97339, USA*
KIM SAGER-FRADKIN, *Lower Elwha Klallam Tribe Natural Resources, 760 Stratton Road, Port Angeles, WA 98363, USA*
MARTIN VAVRA,[3] *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*

ABSTRACT Studies of habitat selection and use by wildlife, especially large herbivores, are foundational for understanding their ecology and management, especially if predictors of use represent habitat requirements that can be related to demography or fitness. Many ungulate species serve societal needs as game animals or subsistence foods, and also can affect native vegetation and agricultural crops because of their large body size, diet choices, and widespread distributions. Understanding nutritional resources and habitat use of large herbivores like elk (*Cervus canadensis*) can benefit their management across different land ownerships and management regimes. Distributions of elk in much of the western United States have shifted from public to private lands, leading to reduced hunting and viewing opportunities on the former and increased crop damage and other undesired effects on the latter. These shifts may be caused by increasing human disturbance (e.g., roads and traffic) and declines of early-seral vegetation, which provides abundant forage for elk and other wildlife on public lands. Managers can benefit from tools that predict how nutritional resources, other environmental characteristics, elk productivity and performance, and elk distributions respond to management actions. We present a large-scale effort to develop regional elk nutrition and habitat-use models for summer ranges spanning 11 million ha in western Oregon and Washington, USA (hereafter Westside). We chose summer because nutritional limitations on elk condition (e.g., body fat levels) and reproduction in this season are evident across much of the western United States. Our overarching hypothesis was that elk habitat use during summer is driven by a suite of interacting covariates related to energy balance: acquisition (e.g., nutritional resources, juxtaposition of cover and foraging areas), and loss (e.g., proximity to open roads, topography). We predicted that female elk consistently select areas of higher summer nutrition, resulting in better animal performance in more nutritionally rich landscapes. We also predicted that factors of human disturbance, vegetation, and topography would affect elk use of landscapes and available nutrition during summer, and specifically predicted that elk would avoid open roads and areas far from cover-forage edges because of their preference for foraging sites with secure patches of cover nearby. Our work had 2 primary objectives: 1) to develop and evaluate a nutrition model that estimates regional nutritional conditions for elk on summer ranges, using predictors that reflect elk nutritional ecology; and 2) to develop a summer habitat-use model that integrates

Received: 6 October 2015; Accepted: 28 May 2018

[1] *E-mail*: mrowland@fs.fed.us
[2] *Current affiliation: Eagle Environmental, Inc., 30 Fonda Rd., Sante Fe, NM 87508, USA.*
[3] *Retired.*
[4] *Current affiliation: Washington Department of Natural Resources, Northwest Region, 919 North Township Street, Sedro-Woolley, WA 98284, USA.*
[5] *Current affiliation: Natural Resource Conservation Management, Western Carolina University, Cullowhee, NC 28723, USA.*
[†] *Deceased.*

the nutrition model predictions with other covariates to estimate relative probability of use by elk, accounting for ecological processes that drive use. To meet our objectives, we used 25 previously collected data sets on elk nutrition, performance, and distributions from 12 study areas. We demonstrated the management utility of our regional-scale models via application in 2 landscapes in Washington.

The elk nutrition model predicts levels of digestible energy in elk diets (DDE; kcal DE/g of consumed forage) during summer. Model input data were from foraging experiments using captive female elk and field measurements of site characteristics at fine scales (~0.5 ha). The nutrition model included a set of equations that predicted forage biomass as a function of site characteristics and a second set that predicted DDE primarily as a function of forage biomass. We used the nutrition model to develop a DDE map across the Westside. We then evaluated performance of the model by comparing predicted DDE to nutritional resource selection by elk and to population-level estimates of autumn body fat and pregnancy rates of lactating elk. To model elk habitat use, we compiled 13 unique telemetry data sets from female elk ($n = 173$) in 7 study areas (data collected June–August 1991–2009). We used a generalized linear model with 5 of the data sets, coupled with ecologically relevant covariates characterizing nutrition, human disturbance, vegetation, and physical conditions, to estimate intensity of use with the negative binomial model. We evaluated model performance by mapping predicted habitat use with the regional model and comparing predictions with counts of elk locations using 8 independent telemetry data sets.

The nutrition model explained a reasonably high amount of variation in forage biomass ($r^2 = 0.46$–0.72) and included covariates of overstory canopy cover, proportion of hardwoods in the canopy, potential natural vegetation (PNV) zone, and study area. Dietary DE equations in the model explained about 50% of the variation in DDE ($r^2 = 0.39$–0.57) as a function of forage biomass by PNV zone and study area. Broad-scale application of the nutrition model in the Westside region illustrated the predominance of landscapes that failed to meet nutritional needs of lactating females (≤2.58 kcal/g) and their calves, especially at moderate elevations in closed-canopy forests in both the Coast Range and the southern Cascades. Areas providing DDE at (>2.58–2.75 kcal/g) or in excess (>2.75 kcal/g) of the basic requirement of lactating females were uncommon (<15% of area) or rare (<5% of area), respectively, and primarily occurred in early-seral communities, particularly at higher elevations. Wild elk avoided areas with DDE below basic requirement and selected for areas with DDE >2.60 kcal/g. Percentage of elk ranges providing DDE levels near or above basic requirement was highly correlated with pregnancy rates of lactating females. Autumn body fat levels were highly correlated with percentage of elk ranges providing DDE levels above basic requirement.

The regional model of elk habitat use with greatest support in the empirical data included 4 covariates: DDE, distance to nearest road open to motorized use by the public, distance to cover-forage edge, and slope. Elk preferred habitats that were relatively high in DDE, far from roads, close to cover-forage edges, and on gentle slopes. Based on standardized coefficients, changes in slope (−0.949) were most important in predicting habitat use, followed by DDE (0.656), distance to edge (−0.305), and distance to open road (0.300). Use ratios for the regional model indicated these changes in relative probability of use by elk: a 111.2% increase in use for each 0.1-unit increase in DDE; a 22.7% increase in use for each kilometer away from an open road; an 8.1% decrease in use for each 100-m increase in distance to edge; and a 5.3% decrease in use for each percent increase in slope. The regional model validated well overall, with high correlation between predicted use and observed values for the 4 Washington sites ($r_s \geq 0.96$) but lower correlation in southwestern Oregon sites ($r_s = 0.32$–0.87).

Our results demonstrated that nutrition data collected at fine scales with captive elk can be used to predict nutritional resources at large scales, and that these predictions directly relate to habitat use and performance of free-ranging elk across the Westside region. These results also highlight the importance of including summer nutrition in habitat evaluation and landscape planning for Westside elk. The models can inform management strategies to achieve objectives for elk across land ownerships. The regional model provides a useful tool to understand and document spatially explicit habitat requirements and distributions of elk in current or future landscapes. The 2 examples of management application demonstrated how effects of management on elk nutrition and habitat use can be evaluated at landscape scales, and in turn how animal performance and distribution are affected. Results further illustrated the importance of managing for nutrition in combination with other covariates (i.e., roads, slope, cover-forage edges) that affect elk use of nutritional resources to achieve desired distributions of elk. Our meta-analysis approach to habitat modeling provides a useful framework for research and management of wildlife species with coarse-scale habitat requirements by identifying commonalities in habitat-use patterns that are robust across multiple modeling areas and a large geographic range. Use of such methods in future modeling, including application in monitoring programs and adaptive management, will continue to advance ecological knowledge and management of wildlife species like elk.

KEY WORDS animal performance, *Cervus candensis*, elk, habitat-use model, land management, meta-analysis, nutritional ecology, Pacific Northwest.

Modelando la Nutrición de Alce y el Uso del Hábitat en el Oeste de Oregon y Washington

RESUMEN Los estudios de selección y uso de hábitats por la vida silvestre, especialmente herbívoros grandes, son fundamentales para comprender su ecología y gestión, especialmente si los predictores de uso representan requisitos de hábitat que pueden estar relacionados con la demografía o aptitud física. Muchas especies de ungulados sirven a las necesidades de la sociedad como animales de caza o alimento sustancial, y también pueden afectar la vegetación nativa y los cultivos agrícolas debido a sus grande opciones de dieta de tamaño corporal y su amplia distribucion. El entendimiento de los recursos nutricionales y el uso de hábitat de grandes herbívoros como el alce (*Cervus canadensis*) puede beneficiar su gestión en diferentes propiedades de la tierra y regímenes de gestión. Distribuciones de alce en gran parte del oeste de los Estados Unidos han cambiado de tierras públicas a privadas, conduciendo a oportunidades a la caza y observación reducidas en la primera y el aumento del daño a los cultivos y otros efectos no deseados en este último. Estos cambios pueden ser causados por el aumento de la perturbación humana (por ejemplo, carreteras y tráfico) y la disminución de la vegetación serals-tempranas, que proporcionan abundante forraje para los alces y otros animales salvajes en las tierras públicas. Los gerentes pueden beneficiarse de técnicas que predicen cómo los recursos nutricionales, otras características ambientales, la productividad y el rendimiento de los alces y las distribuciones de alces responden a las acciones de la administración. Presentamos un esfuerzo a gran escala para desarrollar modelos regional de nutrición de alces y uso de hábitats para las zonas de distribución de verano que abarcan 11 millones de hectáreas en el oeste de Oregon y Washington, EE. UU. (en lo sucesivo Westside). Elegimos verano porque limitaciones nutricionales a condición del alce (por ejemplo, niveles de grasa corporal) y la reproducción en esta temporada son evidentes en gran parte de los Estados Unidos. Nuestra hipótesis general era que el uso de hábitat de alces durante el verano está impulsado por un conjunto de covariables que interactuan relacionadas con el equilibrio energético: adquisición (por ejemplo, recursos nutricionales, yuxtaposición de áreas de cobertura y áreas de forrajeo) y pérdida (por ejemplo, proximidad a caminos abiertos, topografía). Predijimos que las alces hembra seleccionan consistentemente áreas de mayor nutrición de verano, lo que resulta en un mejor rendimiento animal en paisajes más ricos nutricionalmente. También predijimos que los factores de perturbación humana, vegetación y topografía afectarían el uso de alces de los paisajes y la nutrición disponible durante el verano, y predijimos específicamente que el alce evitaría caminos abiertos y áreas lejos de los bordes de forraje debido a su preferencia por los sitios de forrajeo con parches seguros de cobertura cerca. Nuestro trabajo tuvo dos objetivos principales: 1) desarrollar y evaluar un modelo de nutrición que estima las condiciones nutricionales regionales para el alce en las zonas de distribución de verano, utilizando predictores que reflejan la ecología nutricional de los alces; y 2) desarrollar un modelo de verano de uso del hábitat que integre las predicciones del modelo de nutrición con otras covariables para estimar la probabilidad relativa de uso de alces, teniendo en cuenta los procesos ecológicos que impulsan el uso. Para cumplir nuestros objetivos, utilizamos 25 conjuntos de datos recopilados previamente sobre nutrición, rendimiento y distribuciones de alces de 12 áreas de estudio. Demostramos la utilidad de gestión de nuestros modelos a escala regional a través de la aplicación en 2 paisajes en Washington.

El modelo de nutrición de alces predice niveles de energía digestible en las dietas de alces (DDE; kcal DE/g de forraje consumido) durante el verano. Los datos de entrada del modelo provenían de experimentos de forrajeo utilizando alces femeninos cautivos y mediciones de campo de las características del sitio a escalas finas ($\sim$ 0.5 ha). El modelo de nutrición incluyó un conjunto de ecuaciones que predijeron la biomasa del forraje como una función de las características del sitio y un segundo conjunto que predijo DDE principalmente como una función de la biomasa del forraje. Usamos el modelo de nutrición para desarrollar un mapa DDE a través del Westside. Luego evaluamos el desempeño del modelo comparando DDE predicho con la selección de recursos nutricionales por alces y con las estimaciones a nivel poblacional de la grasa corporal otoñal y las tasas de embarazo de alces lactantes. Para modelar el uso del hábitat de alces, compilamos 13 conjuntos únicos de datos de telemetría de alces hembra ($n = 173$) en 7 áreas de estudio (datos recogidos en Junio – Agosto de 1991 – 2009). Utilizamos un modelo lineal generalizado con 5 de los conjuntos de datos, junto con covariables ecológicamente relevantes que caracterizan la nutrición, la perturbación humana, la vegetación y las condiciones físicas, para estimar la intensidad de uso con el modelo binomial negativo. Evaluamos el rendimiento del modelo mapeando el uso previsto del hábitat con el modelo regional y comparando las predicciones con los recuentos de las ubicaciones de los alces utilizando 8 conjuntos independientes de datos de telemetría.

El modelo de nutrición explicó una cantidad razonablemente alta de variación en la biomasa de forraje ($r^2 = 0.46$–0.72) e incluyó covariables de la cubierta del dosel, la proporción de maderas duras en el dosel, la zona de vegetación natural potencial (PNV) y el área de estudio. Dietética DE ecuaciones en el modelo explican aproximadamente el 50% de la variación en DDE ($r^2 = 0.39$–0.57) como una función de la biomasa de forraje por zona PNV y área de estudio. Aplicación a gran escala del modelo de la nutrición en la región Westside ilustró el predominio de los paisajes que no cumplió con las necesidades nutricionales de hembras lactantes ($\leq$2.58 kcal/g) y sus terneros, especialmente en elevaciones moderadas en los bosques de dosel cerrado tanto en el Coast Range y el sur de Cascades. Áreas que proporcionan DDE al (>2.58–2.75 kcal/g) o en exceso (>2.75 kcal/g) del requisito básico de hembras lactantes eran poco frecuentes (<15% de área) o raras (<5% de área), respectivamente, y ocurrió principalmente en las comunidades serales tempranas, particularmente en las elevaciones más altas. Alces salvajes evitadas áreas con DDE por debajo del requisito básico y se seleccionó para áreas con DDE >2.6 0 kcal/g. El porcentaje de rangos de alces que proporcionan niveles de DDE cercanos o superiores a los requisitos básicos estuvo altamente correlacionado con las tasas de embarazo de las hembras lactantes. Los niveles de grasa corporal en otoño estuvieron altamente correlacionados con el porcentaje de rangos de alces que proporcionan niveles de DDE por encima del requisito básico.

El modelo regional de uso de hábitat de alces con mayor apoyo en los datos empíricos incluyó 4 covariables: DDE, distancia a la carretera más cercana abierta al uso motorizado por el público, distancia al borde cubierta-forraje y pendiente. Alce prefirió hábitats que eran relativamente altos en DDE, lejos de las carreteras, cerca de los bordes del forraje de cobertura y en pendientes suaves. Basado en los coeficientes estandarizados, los cambios en la pendiente (−0.949) fueron los más importantes para predecir el uso del hábitat, seguidos por DDE (0.656), distancia al borde (−0.305) y distancia al camino abierto (0.300). Las relaciones utilizadas para los modelos regionales indicaron estos cambios en la relativa probabilidad de uso por alce: un aumento del 111.2% en el uso para cada 0.1-unidad de aumento en DDE; un aumento del 22.7% en el uso por cada kilómetro de distancia de una carretera abierta; una disminución 8.1% en el uso de cada 100-m aumento de la distancia hasta el borde; y una disminución del 5.3% en el uso para cada incremento porcentual en la pendiente. El modelo regional se validó bien en general, con una alta correlación entre el uso previsto y los valores observados para los 4 sitios de Washington ($r_s \geq 0.96$) pero una correlación más baja en los sitios del suroeste de Oregón ($r_s = 0.32$–0.87).

Nuestros resultados demuestran que datos de nutrición recopilados en escalas finas recogida en escalas finas con alces en cautividad puede ser utilizado para predecir los recursos nutricionales a grandes escalas, y que estas predicciones se relacionan directamente con el uso del hábitat y el rendimiento de los alces que pasan libremente en toda la región Westside. Estos resultados también destacan la importancia de incluir la nutrición de verano en la evaluación del hábitat y la planificación del paisaje para alces en el Westside. Los modelos pueden informar estrategias de gestión para alcanzar objetivos para alces en todas las propiedades de la tierra. El modelo regional proporciona una técnica útil para comprender y documentar espacialmente requisitos explícitos de hábitat y distribuciones de alces en paisajes actuales o futuros. Los 2 ejemplos de aplicación de gestión demostraron cómo los efectos del gestión sobre la nutrición de alces y el uso del hábitat pueden evaluar a escala de paisaje y, a su vez, cómo se afectan el rendimiento y la distribución del animal. Los resultados ilustran además la importancia de la gestión de la nutrición en combinación con otras covariables (es decir; carreteras, pendiente, la cobertura de los bordes del forraje) que afectan el uso de los recursos nutricionales de alces para lograr la distribución deseadas de alces. Nuestro enfoque de metanálisis para el modelado de hábitats proporciona un marco útil para la investigación y el gestión de especies silvestres con requisitos de hábitats de escala gruesa al identificando elementos comunes en los patrones de uso del hábitat que son sólidos en múltiples áreas de modelado y un amplio rango geográfico. El uso de tales métodos en modelos futuros, incluida la aplicación en programas de monitoreo y gestión adaptativo, continuará avanzando el conocimiento ecológico y el gestión de especies silvestres como el alce.

Modélisation de L'alimentation du Wapiti et de son Utilisation de L'habitat dans L'ouest des États de l'Oregon et de Washington

RÉSUMÉ Les études sur la sélection et l'utilisation d'un habitat par un animal sauvage, en particulier les grands herbivores, sont cruciales pour comprendre son écologie et sa gestion, surtout si les prédicteurs de l'utilisation de l'habitat représentent des besoins qui peuvent être reliés à la démographie ou à l'état de santé de l'animal. De nombreux ongulés comblent des besoins sociétaux en tant que gibier ou nourriture de subsistance, et peuvent aussi avoir un effet négatif sur la végétation indigène et les cultures agricoles en raison de leur grande taille, de leurs choix alimentaires et de leur aire de répartition étendue. Comprendre le type de ressources nutritionnelles disponibles aux grands herbivores tels que le wapiti (*Cervus canadensis*) et l'utilisation de leur habitat peut faciliter leur gestion sous des régimes de gestion différents et sur des terres boisées ayant des propriétaires différents. Dans la plupart des régions de l'ouest des États-Unis, l'aire de répartition du wapiti a migré des terres publics vers des terres privées, ce qui a réduit les possibilités de chasse et d'observations sur les terres publics et accru les dommages aux récoltes et d'autres effets indésirables sur les terres privées. Il est possible que ce déplacement soit le résultat de perturbations humaines accrues (p. ex. chemins et trafic) et du déclin de la végétation dans les forêts aux premiers stades de

succession écologique qui offrent un fourrage abondant aux wapitis et autres animaux sauvages sur les terres publiques. Les outils qui prédisent la réponse des ressources nutritionnelles et d'autres caractéristiques environnementales ainsi que la productivité et la performance du wapiti et sa répartition suite à l'implantation de mesures de gestion peuvent aider les gestionnaires. Nous présentons un travail réalisé à grande échelle qui avait pour but de développer des modèles régionaux sur l'alimentation du wapiti et son utilisation de l'habitat dans des aires de répartition estivale s'étendant sur 11 millions d'hectares dans l'ouest des états de l'Oregon et de Washington des États-Unis (région ci-après appelée Westside). Nous avons choisi la saison estivale parce que les contraintes nutritionnelles sur la condition et la reproduction du wapiti (p. ex. le pourcentage de réserves lipidiques) durant cette saison sont apparentes dans la plupart des régions de l'ouest des États-Unis. Notre hypothèse fondamentale était la suivante: l'utilisation de l'habitat par le wapiti durant l'été est régie par une série de covariables interdépendantes reliées au bilan énergétique, soit les gains (p. ex. ressources nutritionnelles, juxtaposition des sites pour s'alimenter et s'abriter) et les pertes (p. ex. proximité de chemins ouverts, topographie). Nous avons prédit que la femelle wapiti choisit toujours des sites plus nutritifs en été, ce qui donne un animal plus performant dans les paysages plus riches en nutriments. Nous avons aussi prédit que les facteurs de perturbations humaines, la végétation et la topographie auraient une influence sur la nourriture disponible durant l'été et sur l'utilisation des paysages par le wapiti, et prédit particulièrement que le wapiti éviterait les chemins ouverts et les sites d'alimentation loin de la frontière limitrophe entre la zone d'alimentation et la zone d'abri en raison de sa préférence pour des sites d'alimentation où il y a des endroits à proximité pour s'abriter de façon sécuritaire. Nos travaux avaient 2 objectifs principaux: 1) développer et évaluer un modèle sur l'alimentation qui permettrait d'estimer les conditions nutritionnelles régionales dans les aires de répartition estivale du wapiti à l'aide de prédicteurs qui tiendraient compte de l'écologie nutritionnelle du wapiti; et 2) développer un modèle sur l'utilisation de l'habitat en été qui intègre les projections issues du modèle sur l'alimentation avec d'autres covariables pour estimer la probabilité d'utilisation d'un habitat par le wapiti en tenant compte des processus écologiques qui déterminent l'utilisation d'un habitat. Pour atteindre nos objectifs, nous avons utilisé 25 ensembles de données déjà recueillis sur l'alimentation, la performance et la répartition du wapiti dans 12 sites d'étude. Nous avons démontré l'utilité de nos modèles régionaux à des fins de gestion en les appliquant dans 2 paysages de l'état de Washington.

Le modèle sur l'alimentation du wapiti a calculé l'énergie digestible des aliments du wapiti (EDA; kcal ED/g de fourrage ingéré) durant l'été. Les données d'entrée dans le modèle provenaient d'expériences sur la quête alimentaire effectuées avec des femelles wapitis en captivité et de mesures de terrain sur les caractéristiques des sites à petites échelles (~0,5 ha). Le modèle sur l'alimentation contenait une première série d'équations qui calculaient la quantité de biomasse fourragère en fonction des caractéristiques d'un site et une deuxième série qui calculaient l'EDA en fonction principalement de la biomasse fourragère. Nous nous sommes servis du modèle sur l'alimentation pour dresser une carte de l'EDA dans toute la région du Westside. Nous avons ensuite évalué la performance du modèle en comparant les projections faites par le modèle sur l'EDA au choix des ressources nutritionnelles faits par les wapitis et à des estimations faites sur le taux de gestation des femelles en lactation et sur leurs réserves lipidiques à l'automne, et ce, à l'échelle des populations. Pour modéliser l'utilisation de l'habitat du wapiti, nous avons compilé 13 ensembles de données télémétriques sur la femelle wapiti ($n = 173$) dans 7 sites d'étude (données recueillies entre 1991 et 2009 durant les mois de juin, juillet et août). Nous avons utilisé un modèle linéaire généralisé avec 5 des ensembles de données qui ont été combinés à des covariables écologiquement pertinentes sur l'alimentation, les perturbations humaines, la végétation et les conditions physiques afin d'estimer l'intensité d'utilisation de l'habitat à l'aide du modèle binomial négatif. Nous avons évalué la performance du modèle en cartographiant l'utilisation prévue de l'habitat à l'aide du modèle régional et en comparant les projections au nombre de sites utilisés par le wapiti à l'aide de 8 ensembles indépendants de données télémétriques.

Le modèle sur l'alimentation a expliqué un assez grand nombre de variations dans la biomasse fourragère ($r^2 = 0{,}46–0{,}72$) et contenait des covariables sur le couvert forestier de l'étage dominant, la proportion de feuillus dans le couvert forestier, la zone de végétation naturelle potentielle (VNP) et le site d'étude. Les équations sur l'énergie digestible des aliments (EDA) dans le modèle a expliqué environ 50% des variations de l'EDA ($r^2 = 0{,}39–0{,}57$) en fonction de la biomasse fourragère par zone de VNP et site d'étude. Une application à grande échelle du modèle sur l'alimentation dans la région du Westside a fait ressortir une quantité importante de paysages qui ne réussissaient pas à combler les besoins nutritionnels des femelles en lactation ($\leq$2,58 kcal/g) et leurs faons, en particulier dans des forêts à couvert fermé à des altitudes modérées à la fois dans la chaîne côtière et dans le sud des monts Cascades. Les sites qui fournissaient une EDA égale aux (>2,58–2,75 kcal/g) ou supérieure aux (>2.75 kcal/g) besoins de base des femelles en lactation étaient peu courants (<15% du site) ou rares (<5% du site), respectivement, et se trouvaient principalement dans des forêts aux premiers stades de succession écologique, particulièrement à des altitudes plus élevées. Les wapitis sauvages évitaient les sites qui fournissaient une EDA sous les besoins de base et choisissaient des sites qui fournissaient une EDA >2,60 kcal/g. Le pourcentage des aires de répartition des wapitis qui fournissaient une EDA à peu près égale ou supérieure à leurs besoins de base était fortement corrélé aux taux de gestation des femelles en lactation. Les réserves lipidiques des wapitis en automne étaient fortement corrélées au pourcentage de leurs aires de répartition qui fournissaient une EDA supérieure à leurs besoins de base.

Le modèle régional sur l'utilisation de l'habitat par le wapiti qui corroborait le plus les données empiriques contenaient 4 covariables: EDA, distance au chemin ouvert le plus proche où circulent des véhicules motorisés, distance de la frontière limitrophe entre la zone d'alimentation et la zone d'abri et pente. Les wapitis ont préféré les habitats qui fournissaient une EDA relativement élevée et qui étaient loin des chemins, près de la frontière limitrophe entre la zone d'alimentation et la zone d'abri, et situés sur des pentes douces. Basés sur des coefficients normalisés, les changements dans la pente (−0,949) prédisaient le mieux l'utilisation de l'habitat, suivis de l'EDA (0,656), de la distance à la frontière limitrophe (−0,305) et de la distance à un chemin ouvert (0,300). Les ratios d'utilisation dans le modèle régional ont fait ressortir les changements suivants dans la probabilité relative que le wapiti utilise l'habitat: une augmentation de 111,2% dans l'utilisation de l'habitat par 0,1 unité d'augmentation de l'EDA, une augmentation de 22,7% dans l'utilisation de l'habitat par kilomètre additionnel entre le site d'alimentation et un chemin ouvert, une diminution de 8,1% dans l'utilisation de l'habitat par 100 m d'augmentation de la distance à la frontière limitrophe et une diminution de 5,3% dans l'utilisation de l'habitat par 1% d'augmentation dans la pente. Dans l'ensemble, le modèle régional a effectué une bonne validation, établissant une forte corrélation entre l'utilisation projetée et les valeurs observées pour les 4 sites de l'état de Washington ($r_s \geq 0,96$), mais une plus faible corrélation pour les sites situés dans le sud-ouest de l'état de l'Oregon ($r_s = 0,32$–$0,87$).

Nos résultats démontrent qu'il est possible d'utiliser des données sur l'alimentation recueillies à de petites échelles avec des wapitis en captivité pour prédire les ressources nutritionnelles à de grandes échelles et que ces projections sont directement reliées à la performance des wapitis en liberté et à leur utilisation de l'habitat dans l'ensemble de la région du Westside. Ces résultats montrent aussi l'importance d'inclure l'alimentation estivale dans l'évaluation de l'habitat et la planification du paysage pour le wapiti de la région du Westside. Les modèles peuvent être une source d'information pour établir les stratégies de gestion nécessaires pour atteindre les objectifs relativement aux wapitis qui se trouvent sur des terres boisées privées. Le modèle régional est un outil utile pour comprendre et documenter de façon spatialement explicite les besoins de l'habitat et la répartition des wapitis dans des paysages existants ou futurs. Les 2 exemples d'application sur le plan de la gestion ont démontré de quelle façon il était possible d'évaluer les effets de la gestion sur l'alimentation du wapiti et son utilisation de l'habitat à l'échelle des paysages et, par ricochet, les effets sur la performance et la répartition de l'animal. Les résultats illustrent également l'importance d'une gestion en fonction de l'alimentation combinée à d'autres covariables (c.-à-d. les chemins, la pente, la frontière limitrophe entre la zone d'alimentation et la zone d'abri) qui ont une influence sur l'utilisation des ressources nutritionnelles par le wapiti, et ce, afin d'obtenir la répartition désirée pour cet animal. Notre approche méta-analytique dans la modélisation de l'habitat fournit un cadre utile de recherche et de gestion des espèces fauniques qui intègre des besoins en habitat à une échelle grossière, en identifiant des éléments communs dans les profils d'utilisation de l'habitat qui sont robustes dans de multiples sites modélisés et dans une large aire géographique. L'utilisation de telles méthodes dans de futurs travaux de modélisation, notamment dans les programmes de surveillance et de gestion adaptative, continuera à faire avancer les connaissances en matière d'écologie et de gestion des espèces fauniques comme le wapiti.

Contents

Modeling to Evaluate Elk Habitat: Contemporary Approaches for Western Oregon and Washington

MICHAEL J. WISDOM, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
MARY M. ROWLAND, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RYAN M. NIELSON,[1] *Western EcoSystems Technology (WEST), Inc., 2121 Midpoint Drive, Suite 201, Fort Collins, CO 80525, USA*
JOHN G. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
BRUCE K. JOHNSON,[2] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
PRISCILLA K. COE,[2] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RACHEL C. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
DAVID J. VALES, *Muckleshoot Indian Tribe, 39015 172nd Avenue SE, Auburn, WA 98092, USA*
MARTIN VAVRA,[2] *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*

INTRODUCTION

Elk (*Cervus canadensis*) are among the most charismatic and popular wildlife species in North America. Their widespread distribution on public lands provides hunting and viewing opportunities that rival those for many species (Toweill and Thomas 2002). The economic contributions of elk hunting and viewing are substantial, with multi-million dollar benefits to rural towns throughout the western United States (Bunnell et al. 2002). The social contributions of elk to rural communities are equally strong, with elk hunting established as one of the most traditional activities associated with rural lifestyles (Bunnell et al. 2002). Native Americans throughout the central and western United States also considered elk an essential item in traditional tribal diets and integral to tribal culture and survival (McCabe 2002).

Despite the popularity of elk, the species also is one of the most controversial. The potential for elk and cattle to compete for food and space has been a topic of heated debate for over a century (Wisdom and Thomas 1996, Heydlauff et al. 2006). Herbivory by elk also has a strong but often ignored effect on vegetation development (Hobbs 1996, Wisdom et al. 2006, Averett et al. 2017). Poor nutrition and extensive road access on public lands can cause elk populations to shift distribution to adjacent private lands, diminishing public hunting and viewing opportunities (Wisdom and Cook 2000, Conner et al. 2001, Proffitt et al. 2010). In turn, when elk populations re-distribute seasonally or year-round to private lands, they can damage agricultural crops and commercial tree regeneration, and compete with domestic livestock for forage (Lyon and Christensen 2002, Heydlauff et al. 2006). Some private landowners design management specifically to entice elk populations to spend more time on private lands for lease hunting, thereby reducing opportunities for viewing and hunting on public lands (Toweill and Thomas 2002).

Issues of elk distribution are intimately linked with how landscapes are managed among land ownerships and management jurisdictions (Wisdom and Cook 2000, Lyon and Christensen 2002, Cleveland et al. 2012, Proffitt et al. 2013). To address these issues, accurate prediction of how elk use and respond to changes in habitat conditions within and across these large landscapes is essential. We addressed this need with the development of regional nutrition and habitat-use models for application on summer ranges in western Oregon and Washington (hereafter, Westside region), an area of 11.8 million ha between the crest of the Cascade Range and the Pacific Ocean in these 2 states (Fig. 1).

Our work was motivated by recommendations of the Sporting Conservation Council (SCC), a federal advisory committee that advised the Secretaries of Agriculture and Interior of the United States Government in the 2000s under the Federal Advisory Committee Act of 1972 (Public Law 92-46, 6 Oct 1972). In a letter sent to the Secretaries on 4 December 2007, the SCC formally endorsed development of new elk habitat models for the Westside region to address urgent land management needs of federal agencies (Sporting Conservation Council 2007). The SCC addressed 2 key management needs in their dialogue with federal managers: 1) new models to accurately predict elk distributions within and across land ownerships in response to forest management and human disturbances at landscape scales; and 2) new models that reflect contemporary scientific paradigms and methods.

Deficiencies in past habitat modeling approaches for elk motivated the rationale and direction of the SCC. Elk habitat models first developed in the late 1970s and 1980s (Brunt and Ray 1986; Thomas et al. 1979, 1988; Leege 1984; Lyon et al. 1985; Wisdom et al. 1986) provided practical methods to evaluate and manage habitat at landscape scales based on key variables that affect or account for elk use of landscapes. The models, however, were based on small-scale, observational studies with little or no spatial replication; did not accurately quantify the effects of multiple, interacting covariates; were not spatially explicit or were difficult to incorporate spatially; typically ignored elk nutrition; and often failed to clearly quantify the response variable, instead relying on a qualitative rating of habitats difficult to interpret. Most importantly, model predictions were not validated with independent data.

One of the 1980s models was developed to evaluate elk distributions and landscapes in the Westside region (referred to as the 1986 model; Wisdom et al. 1986). The 1986 model had 4 covariates: forage quality, open road density, cover quality, and size and spacing of cover and forage areas. The model was

---

[1] *Current affiliation: Eagle Environmental, Inc., 30 Fonda Rd., Sante Fe, NM 87508, USA.*
[2] *Retired.*

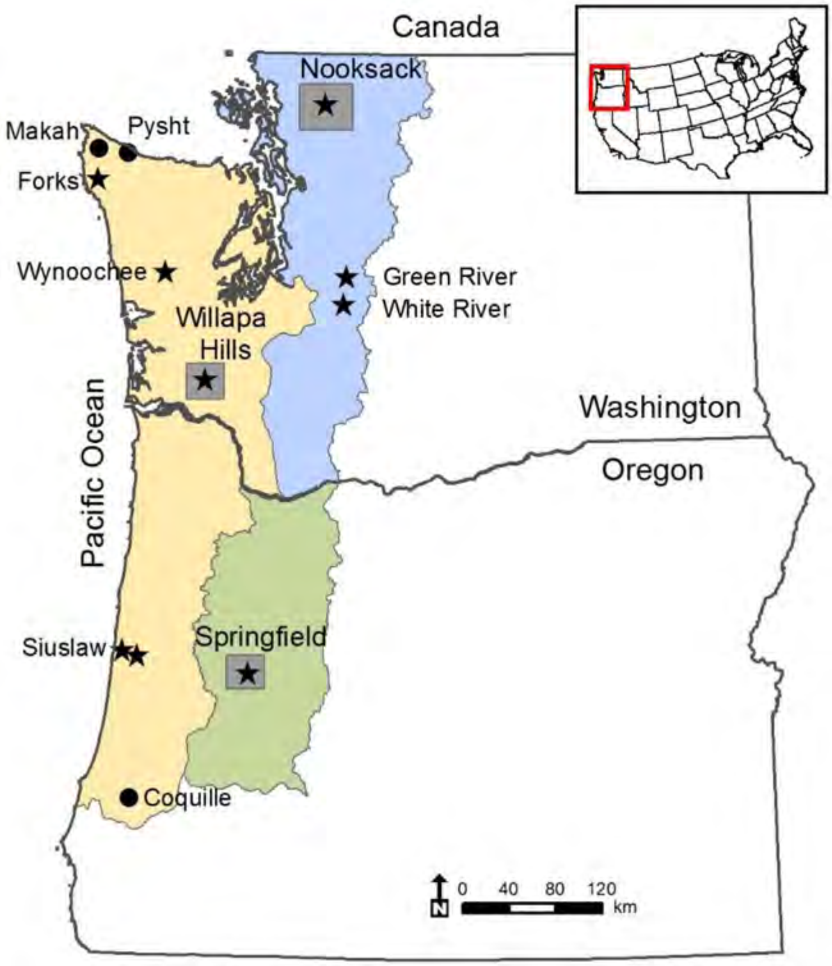


Figure 1. Location and distribution of 12 study areas in western Oregon and western Washington, USA (Westside region) where data were collected (1988–2009) to develop or validate elk nutrition and habitat-use models. Three study areas used to develop independent prediction equations for dietary digestible energy (DDE) and forage biomass using captive elk are denoted by shaded squares; color shading indicates the respective regions to which those equations apply: Nooksack, Willapa Hills, and Springfield. Study areas used for comparisons of predicted DDE levels with pregnancy rates and autumn body fat of wild elk are denoted by stars. Study areas used only for habitat use modeling are denoted by circles.

intended for use within and across land ownerships at watershed or larger landscape scales, similar to our current modeling (Rowland et al. 2018). Despite these similarities, the 1986 model had deficiencies like those of other elk habitat models of the 1970s and 1980s. Most importantly, the 1986 model was never validated with independent data, an essential requirement identified for its use (Wisdom et al. 1986).

Here we describe hypotheses, objectives, rationale, and a conceptual framework for our approach to nutrition and habitat-use modeling in the Westside region. We first describe the Westside region, status of elk populations, and current management issues as context to introduce our modeling approaches; we then provide details of modeling methods, results, and interpretations (Cook et al. 2018, Rowland et al. 2018, Wisdom et al. 2018*b*).

WESTSIDE MODELING REGION AND ELK

The Westside region is bounded to the East by the crest of the Cascade Range, to the West by the Pacific Ocean, to the North by the Canadian border, and to the South by the Coquille and Umpqua Rivers in southwest Oregon (Fig. 1). The region is dominated by coniferous, temperate rainforests and is considered one of the most productive ecosystems on earth (Franklin and Dyrness 1988). The region's environment has similar climate, geology, and vegetation types but follows a north–south gradient of higher to lower precipitation and associated changes in productivity (Appendix A, available online in Supporting Information; Franklin and Dyrness 1988). High amounts of precipitation (>200 cm annually) occur primarily during fall-spring in coastal and high-elevation forests (Franklin and Dyrness 1988). Vast forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heteropyhlla*), and western redcedar (*Thuja plicata*) dominate landscapes at lower and mid-elevations, and forests of Pacific silver fir (*Abies amabilis*) and mountain hemlock (*T. mertensiana*) dominate at higher elevations. Alpine communities are prevalent in the high montane areas of the Cascade Range and Olympic Mountains.

Forested lands are common above valley floors, and agricultural lands and urban areas dominate valley bottoms. Over 7 million people occupy urban areas, but rural areas are sparsely populated. Land ownerships include national forests or other federal lands (36%), private forests (44%), state lands (8%), agricultural areas

(8%), and urban areas or other lands (4%). Forested lands provide a variety of goods and services with emphasis on timber production in private forests (Adams and Latta 2007).

Elk populations in the region vary in size and distribution by geographic area and management regimes on different land ownerships (Washington Department of Fish and Wildlife 2002*a*, *b*, *c*, 2004, 2008, 2013; Oregon Department of Fish and Wildlife 2003; McCorquodale et al. 2012). Current populations are a mix of Roosevelt (*C. c. roosevelti*) and Rocky Mountain elk (*C. c. nelsoni*) subspecies, resulting from multiple translocations of Rocky Mountain elk into the native range of Roosevelt elk that encompasses the Westside region (Toweill and Thomas 2002; Washington Department of Fish and Wildlife 2002*a*, *b*, *c*, 2004, 2008, 2013). Populations are mostly stable but substantially lower in some state management units compared to the latter half of the 20th century, whereas a few are increasing (Appendix A; Washington Department of Fish and Wildlife 2002*a*, *b*, *c*, 2004, 2008, 2013; Oregon Department of Fish and Wildlife 2003). The only other wild ungulate that is common to the Westside region is black-tailed deer (*Odocoileus hemionus columbianus*), which largely co-occur with elk (Witmer et al. 1985). Common predators of elk in the Westside region include black bears (*Ursus americanus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). Gray wolves (*Canis lupus*) have been functionally extirpated from the region for many decades, including the time periods of data collection used in our modeling.

Although elk remain widely distributed in the region, early-seral vegetation has declined substantially during the past 25 years (Spies et al. 2007, Swanson et al. 2011). Because of mild temperatures and high precipitation, forest succession is rapid in the Westside region, and early-seral vegetation is quickly replaced by dense overstory canopies 10–20 years after timber harvest or stand-replacement fires (Hall et al. 1985). Up to 35% of forested landscapes in the Westside region burned at 25-year intervals or longer since at least the 1400s, helping to maintain a mosaic of early-seral vegetation communities (Weisburg and Swanson 2003). The size and frequency of disturbances required to establish these communities has declined sevenfold in the past 25–50 years (Weisburg and Swanson 2003).

Recent declines in early-seral vegetation have been concentrated on federal lands in response to a major reduction in timber harvest (Thomas et al. 2005, Adams and Latta 2007) in the early 1990s, based on direction established in the Northwest Forest Plan (U.S. Department of Agriculture [USDA] Forest Service and U.S. Department of the Interior [USDI] Bureau of Land Management 1994*a*, *b*). Timber harvest on many private lands increased over the same period (Adams and Latta 2007), resulting in a greater percentage of private land area in early-seral vegetation (Cook et al. 2018). However, the duration of early-seral vegetation has been truncated substantially by intensive conifer regeneration practices (Swanson et al. 2011, 2014).

Because early-seral forest vegetation provides highly nutritious forage for elk in the region (Witmer et al. 1985, Jenkins and Starkey 1996, Cook et al. 2016), the uneven distribution of early-seral vegetation on public versus private lands has raised concerns about maintaining elk numbers on public lands for hunting and viewing (USDA Forest Service 2001*a*, *b*; Washington Department of Fish and Wildlife 2002*a*). The widespread loss of early-seral vegetation is considered central to the current nutritional challenges for elk in the Westside region, and the absence of early-seral vegetation on public forests has resulted in nutritionally depauperate conditions (Cook et al. 2013, 2016). Thus the main management issue for Westside elk is not population size *per se*, but the disproportionately low numbers of elk on public forest lands (USDA Forest Service 2001*a*, *b*; Washington Department of Fish and Wildlife 2002*a*).

In addition, roads open to motorized traffic and trail-based summer recreational uses are common on public lands in the Westside region, and private lands often are closed to public access. On summer range, shifts in elk distribution away from open roads (Rowland et al. 2000, 2005; Wisdom et al. 2005*b*; Frair et al. 2008; Montgomery et al. 2012), and trail-based recreational uses are common on public forests (Wisdom et al. 2005*a*). Consequently, the potential for elk in the Westside region to shift distributions to private lands, in response to reduced nutrition and increased road and trail access on public lands, served as context for our modeling.

Study Areas and Data Sets for Regional Inference

Boundaries of the Westside region encompassed 12 study areas that we used for modeling elk nutrition and habitat use (Fig. 1; Table 1). Study areas included geographic and environmental variation in vegetation types, elevational and climatic gradients, forest structural conditions, and land ownerships (Fig. 1; Appendix A; Hall et al. 1985; Franklin and Dyrness 1988; Cook et al. 2016, 2018; Rowland et al. 2018). Consequently, the region's boundaries represent a logical, targeted inference space for modeling and applications.

We used 25 data sets from the 12 study areas for analyses (Fig. 1; Table 1). We defined a data set as a specific type of empirical data (nutrition, animal performance, or habitat use) collected within a given study area and time period that we used to develop or validate nutrition or habitat-use models (Table 1; Appendix A). We defined a study area as a distinct geographic area within which ≥ 1 data sets were collected. We defined validation as the evaluation of model predictions with independent observations of those predictions, or evaluation of hypothesized relationships of model predictions with animal performance or habitat use. Model validation therefore is any independent evaluation of *a priori* expectations of model performance, an inclusive approach that follows definitions and guidance of Power (1993), Rykiel (1996), and Johnson (2002).

Of the 25 data sets used for modeling, 3 were composed of nutrition data (e.g., estimates of elk nutritional resources during summer) collected from grazing trials of captive elk that served as the foundation for development of nutrition models (Table 1; Cook et al. 2016, 2018). Nine additional data sets were composed of estimates of animal performance (pregnancy rates and body fat estimates from lactating female elk; Cook et al. 2013) used for validation of nutrition models (Cook et al. 2018). Thirteen other data sets were composed of animal telemetry locations used to develop or validate habitat-use models (Table 1).

Table 1. Study areas, data sets and years of data collection, type of data collected, and use of data sets in elk nutrition and habitat-use modeling in western Oregon and Washington, USA.

Study area	Data set[a]	Data type	Modeling use
Coquille	Coquille North 1991–1992	Habitat use	Habitat-use model validation
	Coquille North 1993–1994	Habitat use	Habitat-use model validation
	Coquille South 1991–1992	Habitat use	Habitat-use model validation
	Coquille South 1993–1994	Habitat use	Habitat-use model validation
Forks	Forks 2000–2003	Animal performance	Nutrition model validation
	Quileute 2006–2008	Habitat use	Habitat-use model validation
Green River	Green River 1998–2006	Animal performance	Nutrition model validation
	Green-Cedar 2008	Habitat use	Habitat-use model development
	Green-Cedar 2006–2007, 2009	Habitat use	Habitat-use model validation
Makah	Makah 2000–2003	Habitat use	Habitat-use model validation
Nooksack	Nooksack 2002	Nutrition	Nutrition model development
	Nooksack 2000–2002	Animal performance	Nutrition model validation
	Nooksack 2008–2009	Habitat use	Habitat-use model validation
Pysht	Pysht 2009	Habitat use	Habitat-use model development
Siuslaw 1	Siuslaw 1 1988–1989	Animal performance	Nutrition model validation
Siuslaw 2	Siuslaw 2 1988–1989	Animal performance	Nutrition model validation
Springfield	Springfield 2000	Nutrition	Nutrition model development
	Springfield 2000–2002	Animal performance	Nutrition model validation
White River	White River 1998–2007	Animal performance	Nutrition model validation
	White River 2004	Habitat use	Habitat-use model development
	White River 2005	Habitat use	Habitat-use model development
	White River 2007	Habitat use	Habitat-use model development
Willapa Hills	Willapa Hills 2001	Nutrition	Nutrition model development
	Willapa Hills 2000–2002	Animal performance	Nutrition model validation
Wynoochee	Wynoochee 2003–2005	Animal performance	Nutrition model validation

[a] Data sets for habitat-use modeling were assigned to modeling or validation areas by Rowland et al. (2018).

CONTEMPORARY HABITAT MODELING FOR THE WESTSIDE REGION

Hypotheses, Objectives, and Rationale

Recent advances in data collection technologies and analytical methods for habitat modeling provided a significant opportunity to address the deficiencies associated with the 1986 model. During the mid-2000s, new data on elk nutrition, habitat use, and animal performance were collected across a variety of study sites in the region (Fig. 1; Table 1; Appendices A, B, available online in Supporting Information; Cook et al. 2013, 2018; Rowland et al. 2018). These data were not collected under any overarching design or unifying theme, but their availability across multiple study areas and conditions provided an opportunity to initiate a meaningful new round of model development and validation (Table 1). For our modeling, we define habitat as the resources and conditions present in an area that produce occupancy, including survival and reproduction needed for persistence of an organism (adapted from Hall et al. [1997]). This definition relates habitat to the environmental requirements of a species, not just vegetation.

Our goal was to replace the 1986 model using these new data in contemporary landscape models of nutrition and habitat use that could accurately account for elk distributions during summer across the Westside region. We focused on summer (Jun–Aug) because nutritional resources in most forest successional stages in the Westside region do not meet the maintenance requirements of lactating female elk during this period (Cook et al. 2016). Consequently, conditions on many summer ranges pose substantial constraints on animal condition, pregnancy rates, and lactation status in the region (Cook et al. 2013).

The overarching hypothesis driving our work was that elk habitat use during summer is driven by a collection of interacting covariates that influence energy balance: acquisition (e.g., nutritional resources), and expenditure (e.g., travel on steep slopes). We predicted that female elk consistently select areas of higher summer nutrition, resulting in better animal performance in more nutritionally rich landscapes. We also predicted that non-nutritional factors of human disturbance, vegetation, and topography further affect summer elk use of landscapes and available nutrition. Because the ecological mechanisms that drive these hypotheses operate across space and time, we further predicted that the same or similar nutrition and habitat-use models would perform well across the environmental conditions of the Westside region and years of data collection.

We had 2 major objectives to support our goal: 1) to develop and evaluate a nutrition model that could accurately estimate region-wide nutritional conditions for elk on summer ranges, based on predictors that reflect the ecological processes of animal nutrition; and 2) to develop and validate a summer habitat-use model that integrates the nutrition model predictions with other covariates to estimate relative probability of use by elk. For the second objective, we used a combination of covariates that most accurately predict and account for ecological processes of elk habitat use in the region (Fig. 2). Our objectives relied on analyses conducted at the population scale (Cook et al. 2018, Rowland et al. 2018), which combined attributes of second- and third-order selection defined by Johnson (1980). This combined order of selection provided population-level estimates of nutrition and habitat use across the range of the species in the Westside region (Wisdom et al. 2018*b*).

We identified 2 requirements to meet objectives. First, the models should be designed to gain new knowledge of the ecological

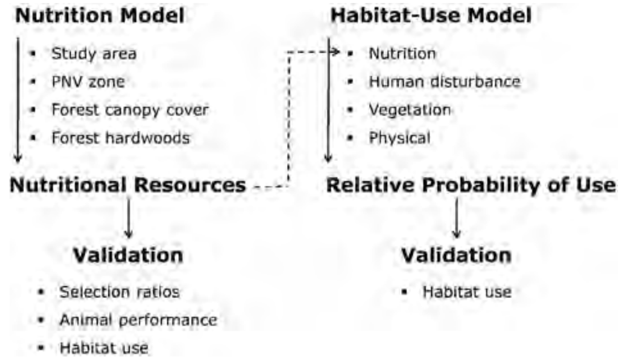


Figure 2. Conceptual structure of elk nutrition and habitat use models developed and validated for the Westside region, western Oregon and western Washington, USA. Types of covariates considered during model development and types of data used for validation of each model are shown below each model or type of validation. Three zones of potential natural vegetation (PNV) occurred in the Westside region: western hemlock at lower elevations, Pacific silver fir at moderate elevations, and mountain hemlock at higher elevations.

processes that serve as drivers of elk nutrition and habitat use. The literature on habitat use contains many models that provide useful predictions but not always with understanding of how model covariates represent underlying ecological processes that drive animal use in a robust manner across time and space (Morrison 2001, 2012). Second, these types of process-driven covariates, referred to as mechanistic covariates, should be foundational to modeling to ensure robust management applications. We define a mechanistic covariate as one that explicitly represents a species' habitat requirements and that can be manipulated by managers in a cause-effect manner to change nutrition or habitat use. Mechanistic covariates should have a documented or highly plausible connection to the ecological processes of energy acquisition or energy loss that underlie the species' ecology, nutrition, and habitat choices (Rowland et al. 2018).

Modeling Structure and Approach

We established a modeling structure (Fig. 2) to address our hypotheses, predictions, and objectives with use of the 25 data sets. The structure follows the philosophy and guidance of Levins (1966), who emphasized process-driven models sufficient to meet objectives with minimal parameters. This approach follows the principle of parsimony, where the balance between models with strongest empirical support and lowest number of parameters is identified (Burnham and Anderson 2002).

The nutrition model was designed as a stand-alone tool to estimate and map nutritional resources based on elk diet quality. These resources varied empirically by potential vegetation type, structural condition, and topography on Westside summer ranges (Cook et al. 2016, 2018). We assumed that fine-scale nutrition data collected from captive elk in the Westside region (Cook et al. 2016), rescaled to regional nutrition models, would reflect the nutritional levels and landscape-selection patterns of wild elk, and would correlate well with population performance metrics of pregnancy rates and body fat. Predictions from the nutrition model are intended for spatial application at scales of the local or regional landscape, or can be obtained using the model in a tabular format for planning scenarios (Rowland et. al 2013, Cook et al. 2018, Wisdom et al. 2018*b*).

The habitat-use model estimates the relative probability of animal use (Nielson and Sawyer 2013) on the same summer ranges and landscape scales in which nutrition is estimated (Rowland et al. 2018). We used elk telemetry locations to model the intensity of use in relation to habitat characteristics (Nielson and Sawyer 2013), which is considered an analysis of habitat use. Note that this definition is somewhat different than an analysis of habitat selection (Manly et al. 2002). By modeling habitat use along a continuum, more information is gained about the relationships between habitat characteristics and probability of use by the animal (Rowland et al. 2018). We modeled habitat use by considering covariates in 4 categories: nutrition (the response variables from the nutrition model), human disturbance, vegetation, and physical conditions that best explain use by elk (Fig. 2; Rowland et al. 2018).

Neither model predicts carrying capacity (Hett et al. 1978, Hobbs et al. 1982, Hobbs and Swift 1985, Beck et al. 2006), but both are necessary components of carrying-capacity models. Nutrition is the foundation for estimation of carrying capacity (Caughley 1979, Hobbs et al. 1982), and factors of human disturbance can reduce carrying capacity (Beck et al. 2006). In addition, neither the nutrition nor the habitat-use model was designed to predict population characteristics like density, recruitment, survival, or growth rate because these characteristics can be greatly influenced by additional factors such as predation and hunting (Sinclair and Krebs 2002, Johnson et al. 2013, Clark 2014). The habitat-use model was designed to predict elk distribution (relative probability of elk use) within local and regional landscapes, however, and these predictions represent the relative abundance of elk at those scales (Rowland et al. 2018).

Both models evaluate summer conditions for elk populations assumed to be hunted later in the year, either on the same summer ranges or on different fall ranges. Populations that live year-round near or within urban areas where hunting is prohibited behave differently than wild, hunted elk herds (Thompson and Henderson 1998, Starr 2013). Our objectives did not include modeling habitat use by unhunted elk in these special situations.

Our modeling approach used different types of validation (see definition provided earlier). For nutrition modeling, we did not evaluate predicted versus observed nutrition because independent data were not available to do so (i.e., we did not have direct observations of elk diet quality from captive elk in additional study areas that could be withheld for validation). Instead, we evaluated model performance based on *a priori* hypotheses of how nutrition model predictions related to selection ratios, measures of population performance, and habitat use (Cook et al. 2018, Rowland et al. 2018). These more-inclusive types of evaluation and validation have been advocated and used in ecological modeling per Rykiel (1996). For habitat-use modeling, predictions were validated in the more traditional sense, using independent observations of habitat use from data sets and study areas withheld from model development (Rowland et al. 2018). Cook et al. (2018) and Rowland et al. (2018) provide detailed rationale, methods, results, and interpretations of our modeling structure and approach for nutrition and habitat use, respectively. Wisdom et al. (2018*b*) then describe key implications for research and modeling of wildlife, provide example applications for elk, and discuss management challenges.

Development and Evaluation of a Landscape Nutrition Model for Elk in Western Oregon and Washington

JOHN G. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RACHEL C. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RONALD W. DAVIS,[1] *Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61820, USA*
MARY M. ROWLAND, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RYAN M. NIELSON,[2] *Western EcoSystems Technology (WEST), Inc., 2121 Midpoint Drive, Suite 201, Fort Collins, CO 80525, USA*
MICHAEL J. WISDOM, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
JENNIFER M. HAFER, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
LARRY L. IRWIN,[3] *National Council for Air and Stream Improvement, P.O. Box 68, Stevensville, MT 59870, USA*

INTRODUCTION

Nutrition influences productivity of ungulates by affecting many aspects of animal performance, including nutritional condition (defined as the state of body components [principally fat and lean mass] controlled by nutrition, which influences an animal's future fitness [Harder and Kirkpatrick 1994]), ovulation, timing of breeding and subsequent parturition, juvenile growth, primiparity, and susceptibility to a variety of causes of mortality (Verme and Ullrey 1984; Cook et al. 2004, 2013). Although nutritional limitations of ungulates in winter are commonly recognized (Wallmo et al. 1977, Houston 1982, Coughenour and Singer 1996), world-wide documentation of limiting effects of nutrition in summer and early autumn is increasing (Hjeljord and Histol 1999, Dale et al. 2008, Cook et al. 2013, Hurley et al. 2014, Rolandsen et al. 2017). Such also is the case in the temperate rainforests in western Oregon and Washington (hereafter, the Westside region), where depressed pregnancy rates and low autumn body fat levels of elk are well-documented (Trainer 1971, Smith 1980, Harper 1987, Stussy 1993, Cook et al. 2013). Nevertheless, substantial variation in nutritional condition and pregnancy rates of elk populations exists across the region (Cook et al. 2013), at least in part as a function of vegetation disturbance, succession, and ecological context (Merrill 1987, 1994; Hutchins 2006; Cook et al. 2016).

Because nutrition has quantifiable, cause-and-effect influences on nutritional condition, reproduction, and survival in ungulates, nutritional ecology offers a quantitative basis for scaling-up key relations between individual animals and their habitats to populations (Fryxell 1991, Parker et al. 1999). It also offers value for landscape assessments and resource planning on behalf of large ungulates. Many approaches have been used to quantify nutritional resources for ungulates, including 1) surveys of forage quantity and, sometimes, forage quality for carrying capacity models (Hanley et al. 2012); 2) complex, spatially explicit simulation models intended to predict distribution and performance of ungulates (e.g., Coughenour and Singer 1996, Moen et al. 1997); and 3) a variety of proxy variables assumed to represent nutritional influences (e.g., Thomas et al. 1988, Johnson et al. 2001, Garroutte et al. 2016). Whatever modeling approach is used, considerable uncertainty exists regarding the relevance and rigor of measures used to represent nutritional resources (Babin et al. 2011). For example, proxy variables and even some standard metrics of forage quality and quantity have rarely been validated as measures of nutritional resources (Searle et al. 2007, Cook et al. 2016). Also, appropriate approaches remain unclear for translating nutritional responses of herbivores to vegetation at fine scales to estimate individual animal performance and population dynamics at broad scales, especially in spatially and temporally heterogeneous environments (Owen-Smith 2002, Hobbs 2003). Particularly for management and planning applications, nutrition models should reflect influences of disturbance, succession, and ecological context and integrate these with routine land management and landscape planning protocols (Haufler 1994).

We used foraging ecology data collected using captive elk in western Oregon and Washington, USA (Cook et al. 2016) to develop a nutrition model designed for landscapes in summer and early autumn that can be linked with a spatially explicit habitat-use model (Rowland et al. 2018) for practical management applications (Wisdom et al. 2018*b*). In the temperate rainforests of western Oregon and Washington, nutritional value of plant communities, as indexed by digestible energy (DE) content of forage consumed by elk, is strongly driven by forest succession, disturbance, and ecological site conditions (plant phenology, climate, soils, composition and abundance of plant species; Merrill 1994, Merrill et al. 1995, Cook et al. 2016). Thus, we strove to develop our nutrition model to reflect these influences in landscapes ranging from relatively dry, low-elevation forests to wet and cold forests near timberline. Incorporating successional influences also should facilitate predictions of changes in nutritional resources over time and identify management options for modifying the nutritional environment across landscapes (Haufler 1994). Cook et al. (2016) developed regression equations to predict dietary digestible energy (DDE)—the content of digestible energy (kcal/g) in elk diets—as a function of the types of forage available to foraging elk, and used these

---

[1] *Current affiliation: Natural Resource Conservation Management, Western Carolina University, Cullowhee, NC 28723, USA.*

[2] *Current affiliation: Eagle Environmental, Inc., 30 Fonda Rd., Sante Fe, NM 87508, USA.*

[3] *Retired.*

equations to describe successional trajectories of DDE from newly harvested stands to late seral stages for each of the major vegetation zones of the region. However, they did not provide equations to estimate biomass of the forage classes that are required as input data to predict DDE. We adopted these DDE equations in our nutrition model, developed equations to predict these forage-class amounts based on environmental data (e.g., overstory canopy cover, ecological site potential) that were readily available in geographic information systems (GIS), and combined them into an overall nutrition model. Although Cook et al. (2016) explored various currencies for their prediction equations (e.g., energy, protein, intake rates of energy and protein), they concluded that DDE was the most valuable for describing nutritional value of plant communities and identifying nutritional limitations; it also was the most predictable nutritional metric for elk in the Westside.

Past work has established that elk performance, as measured by indices of nutritional condition and pregnancy rates, is relatively low in many elk populations (Trainer 1971, Harper 1987, Cook et al. 2013), and that nutritional value of many vegetation types provide inadequate nutrition for lactating elk and their calves during summer (Cook et al. 2016). However, direct links between fine-scale measures of nutritional value of vegetation types and broad-scale measures of performance (population-level pregnancy rates and nutritional condition) largely remain untested. Elk may compensate for poor nutritional resources by strongly selecting for those vegetation types that offer adequate nutrition and avoiding those that do not (Moen et al. 1997). In addition, other environmental influences such as herbivore density or harassment by predators or humans may be responsible for relatively poor performance in some populations. Hence, our overarching hypothesis was that elk preferentially seek those vegetation types that provide relatively high nutrition to compensate for inadequate nutritional resources, but compensation may be incomplete and elk performance reduced on elk ranges with strongly depauperate nutritional resources. We had the following predictions: 1) vast areas of our study region are dominated by nutritional resources that are inadequate ($<\sim 2.6$ kcal/g of DDE/g) to support high pregnancy rates and relatively high body fat levels; accordingly, elk will significantly select for areas that provide relatively high levels of DDE (e.g., $>\sim 2.6$ kcal/g where low DDE levels predominate); 2) population-level pregnancy rates and autumn body fat levels of lactating elk will vary with estimated DDE expressed as percentages of elk ranges offering differing levels of DDE; and 3) relatively high levels of body fat (i.e., $\geq 12\%$) are more likely to occur on elk ranges that offer a higher proportion of good nutrition (≥ 2.75 kcal/g) than ranges that do not but nevertheless are able to support high pregnancy rates (Cook et al. 2004). Our references to differing levels of DDE and their relevance to elk reflect findings of Cook et al. (2004) (Table 2).

We had 5 primary objectives for the nutrition model: 1) to use the model to construct spatially explicit nutritional resource maps that predict DDE across ecological gradients and forest succession using a GIS; 2) to assess the nutrition model developed with fine-scale data of vegetation characteristics by evaluating relationships between predicted DDE and nutritional resource use by elk, autumn body fat levels, and pregnancy rates for elk populations at broad scales; 3) to explicitly test our predictions that elk would select for areas offering relatively high DDE and that pregnancy rates and autumn body fat levels would vary with predicted levels of DDE across landscapes; 4) to summarize current nutritional resources for Westside elk and thus illustrate differences among ecological provinces and landowners; and 5) to integrate the nutritional resources map with other environmental variables to develop a habitat-use model for the study region (Rowland et al. 2018).

Table 2. Classes of dietary digestible energy (DDE) used to summarize nutrition modeling results for elk (modified from Cook et al. 2004). Basic requirements of lactating female elk during summer are met at the high-marginal class.

Class	Description	DDE (kcal/g)
1	Poor	<2.40
2	Low-marginal	2.40–2.58
3	High-marginal	>2.58–2.75
4	Low-good	>2.75–2.83
5	High-good	>2.83–2.90
6	Excellent	>2.90

STUDY AREAS

We acquired data to develop our nutrition model from 3 study areas located in the temperate rainforests of western Oregon and Washington, USA (Fig. 1; Table 1; see Cook et al. 2016 for additional details). The Nooksack area was located in the Cascade foothills and mountains south of Mt. Baker, Washington, the Willapa Hills area was located in the Coast Range of southwest Washington, and the Springfield study area was in the foothills of the central Oregon Cascades (Appendix A). At Nooksack, topography was relatively steep, with broad, glaciated valley bottoms and elevations ranging from 100 m to 1,400 m. Topography was gently rolling to steep at Willapa Hills and Springfield and elevation ranged from 100 m to 700 m, with occasional mountain peaks to 1,000 m. Annual precipitation varied from 100 cm to 300 cm, depending on elevation and latitude (Daly et al. 1994).

Three primary forest zones, based on potential natural vegetation (PNV) categories (Franklin and Dyrness 1988, Henderson et al. 1992), predominated across the 3 study areas: the western hemlock zone (WHZ) at lower elevations, the Pacific silver fir zone (SFZ) at moderate elevations, and the mountain hemlock zone (MHZ) at higher elevations. Alpine areas were present at Nooksack, but we did not acquire data from this type. The higher elevation forest zones—SFZ and particularly the MHZ—were well represented only in the Nooksack study area. In general, diversity of understory vegetation increased with elevation across the WHZ, SFZ, and MHZ and declined as plant succession advanced (Franklin and Dyrness 1988, Cook et al. 2016).

For evaluating the nutrition model, we used data on pregnancy rate and autumn body fat from lactating female elk in 7 wild populations described by Cook et al. (2013) and 2 populations described by Stussy (1993) (Fig. 1; Table 3). These included the Forks, Wynoochee, and Willapa Hills populations in the Coast Range of western Washington; the Nooksack, Green River, and the White River populations in the Cascades of western Washington; a population near Springfield in the Cascades of western Oregon; and 2 adjacent populations (Stussy 1993) in the

Coast Range of west-central Oregon. Data from elk in the Mount St. Helens population in southwest Washington were presented by Cook et al. (2013) but not used herein for statistical analyses for 2 reasons. First, the autumn fat data were collected during an October drive-trapping operation within a very small sub-portion of the population's range that was still highly affected by the eruption of Mount St. Helens (Cook et al. 2013). Second, the pregnancy data were collected during spring and thus could not be partitioned by lactation status as they were for the other populations (i.e., females with a calf at heel commonly cease lactating before spring).

In general, elk in the Coast Range largely occurred within the WHZ, and those in the Cascade Range were in the WHZ at low to moderate elevations and in the SFZ and MHZ at higher elevations. However, elk at Springfield had little access to the higher elevation PNV zones. Elk were considered to be the Roosevelt subspecies for all populations in the Coast Range and the Rocky Mountain subspecies in the Cascades (Cook et al. 2013). Elk were predominately non-migratory, although some elk populations of the Washington Cascades migrated to higher elevation ranges. Study area descriptions were presented by Cook et al. (2013) and Stussy (1993), and Appendix A contains additional descriptions of the Nooksack, Green River, White River, and Forks areas.

METHODS

Background

Cook et al. (2016) used 25 captive adult, lactating Rocky Mountain elk and their calves to investigate foraging dynamics in the 3 study areas of Nooksack, Willapa Hills, and Springfield. In addition, they measured overstory and understory vegetation characteristics in ~1-ha macroplots at these 3 study areas, with 1 field season (late Jun–Oct 2000–2002) devoted to each. Foraging behavior was sampled in macroplot pens (electrified enclosures), with 4 elk and their calves per pen and 3–4 pens operated simultaneously. Bite-count methods (Collins and Urness 1983, Wickstrom et al. 1984, Parker et al. 1999) were used to estimate key dietary metrics for elk, including patterns of selection among forage species, and intake rates of dry matter, DDE, and dietary digestible protein content, with intake rates of these nutrients expressed per minute and per 24-hour period. Digestible energy and protein were determined using detergent fiber assays coupled with assays of tannin astringency (Robbins et al. 1987*a*, *b*). Overstory and understory vegetation sampling was conducted along 5 parallel transects. Understory vegetation included current year's dry-matter biomass of each vascular plant species clipped in 2, 2-m^2 circular plots per transect ($n = 10$ clip plots/macroplot). Measures of overstory characteristics included canopy cover (CC) determined using a moosehorn ocular sighting tube (Bunnell and Vales 1990, Cook et al. 1995), stand height, mean diameter at breast height, and basal area using a variety of standard forest mensuration techniques, and composition of tree species along the transects. Evidence of thinning and PNV type (Franklin and Dyrness 1988, Henderson et al. 1992) was recorded, and stand age was acquired from landowner records. At each study area, Cook et al. (2016) sampled approximately 30 macroplots using the captive elk and an additional ~90 macroplots where only vegetation characteristics were measured.

The equations developed by Cook et al. (2016) to predict DDE were generally a function of the biomass (kg/ha) of palatable and relatively nutritious food in the plant community. They partitioned plant biomass into 3 selection categories: those that elk significantly selected (selected biomass; SB), those significantly avoided (avoided biomass), and those consumed in proportion to availability (neutral biomass; NB). Avoided biomass, mainly shade-tolerant evergreen shrubs, conifers, and evergreen ferns, composed 80% to 95% of the understory vegetation biomass in mid- and late-seral stages, particularly in

Table 3. Characteristics of elk populations in western Oregon and Washington, USA, used for elk nutrition model evaluation. Data are from prime-age (2–14 yr), lactating elk only unless otherwise noted. Body fat and pregnancy data were from Cook et al. (2013) and Stussy (1993), the latter for the 2 Siuslaw populations.

Population	Years sampled	n[a]	Autumn body fat (%)[b]	Pregnancy (%)[c]	Study area method[d]	Number of elk locations	Study area size (ha)
Forks, WA[e]	2000–2003	31	6.0	61	MCP + 500	400	27,847
Green River, WA	1998–2006	58	10.0	91	Study area		39,072
Nooksack, WA	2000–2002	21	12.5	95	MCP + 500	556	49,061
Springfield, OR	2000–2002	23	10.2	73[f]	MCP + 500	444	14,699
Siuslaw 1, OR	1988–1989	13	3.2	21	Study area		17,743
Siuslaw 2, OR	1988–1989	13	3.7	46	Study area		25,096
White River, WA	1998–2007	72	11.0	95	Study area		58,060
Willapa Hills, WA	2000–2002	22	6.2	78	MCP + 500	621	18,759
Wynoochee, WA	2003–2005	40	6.0	67	MCP + 500	1,719	76,444

[a] Number of unique elk captured at each study area (most elk were captured and sampled at least twice/yr for 2 yr). Relocations from these elk also were used to calculate home range boundaries except for the Siuslaw, Green, and White River study areas.

[b] Estimated from scaled LIVINDEX using ultrasonography of rump fat and a body condition score (Cook et al. 2001, 2010). For elk in the Siuslaw populations, body fat was estimated using the trimmed kidney fat index (Riney 1955) and converted to estimates of percent body fat using equations presented in Cook et al. (2001) for elk ranging from 4–12 years old (considered prime age in this study).

[c] Determined via ultrasound and palpation with the negatives confirmed with Pregnancy-Specific Protein B (Noyes et al. 1997). For the Siuslaw populations, pregnancy was determined by examination of uteri from uncollared hunter-harvested elk (Stussy 1993).

[d] MCP + 500 = minimum convex polygon around elk relocations plus 500-m buffer. Study area boundaries for the Siuslaw populations were provided by R. Stussy (Oregon Department of Fish and Wildlife, personal communication; Stussy 1993) and by D. Vales (Muckleshoot Indian Tribe, personal communication) for the White and Green River populations.

[e] Population overlaps with the Quileute telemetry data set.

[f] Pregnancy rates are from spring captures based on those females known to be lactating the previous autumn ($n = 15$) because the autumn captures were too early to detect pregnancy.

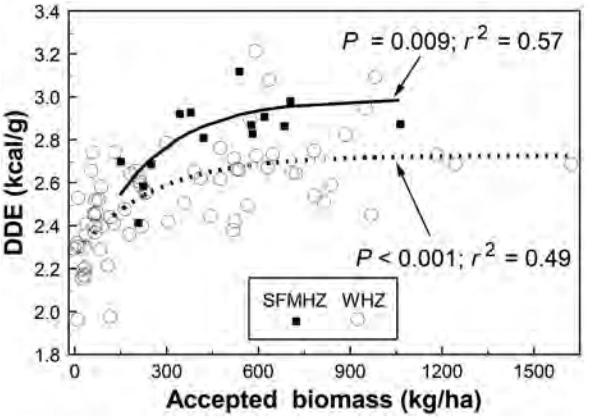


Figure 3. Non-linear relations of digestible energy (DDE) in elk diets and accepted biomass (biomass of neutral and selected species combined) by potential natural vegetation zones at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA, 2000–2002 (adapted from Cook et al. [2016]). Potential vegetation zones are WHZ = western hemlock zone; SFMHZ = Pacific silver fir and mountain hemlock zones combined. The equation for the WHZ was $\text{DDE} = 0.47 \times (5.755 – e^{(-0.0041(\text{AB}))})$ and for the SFMHZ, $\text{DDE} = 0.92 \times (3.218 - e^{(-0.0052(\text{AB}))})$, where AB = accepted biomass in kg/ha.

the WHZ. In general, as abundance of the palatable, nutritious plants declined, elk increased consumption of the unpalatable forage. Because the unpalatable forage offered lower DE, this change in dietary composition substantially reduced DDE. When SB and NB were combined into a category referred to as accepted biomass (AB), DDE was asymptotically correlated with biomass of AB, with some differences evident among PNV zones (Fig. 3). This relationship forms the general basis of our nutrition model. Instantaneous intake rates of forage and DE generally failed to decline with biomass of AB, except at very low levels of AB, because elk increased consumption of avoided species, most of which provided significantly larger bite mass and thus relatively high intake rates of dry matter. In many cases, DDE levels were low enough to affect animal performance, despite relatively high instantaneous intake rates. Thus, DDE was a considerably more sensitive indicator of the nutritional value of plant communities to elk than was instantaneous intake rate of DE (Cook et al. 2016).

Data Analysis

Cook et al. (2016) developed equations to predict DDE as a function of forage biomass (with AB, NB, and SB as covariates) for the 3 study areas and PNV zones in which they sampled vegetation and elk diets (Fig. 4; Table 4). We expanded on that work by developing equations to predict biomass of AB, NB, and SB using covariates reflecting site characteristics (e.g., PNV zone, overstory canopy cover) and study area (Fig. 4). Cook et al. (2016) found no evidence that biomass of avoided species provided additional value in predicting DDE, and thus we did not develop equations for this forage biomass class. Finally, Cook et al. (2016) found no significant influences of season on DDE, and thus we used all data collected from late June to early November for nutrition model development, although we restricted the Westside habitat-use model to June–August because of hunting seasons (Rowland et al. 2018).

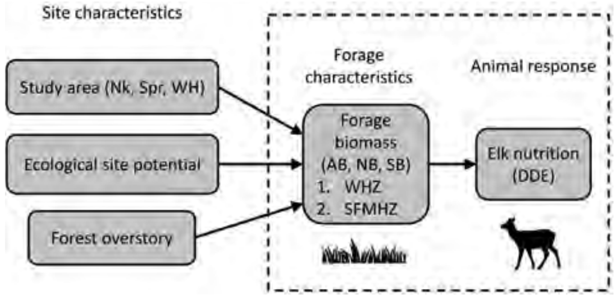


Figure 4. Illustration of basic components of the elk nutrition model for western Oregon and Washington, USA. The modeling process consisted of 2 basic steps to develop equations for 1) predicting biomass of forage based on forest overstory characteristics (e.g., overstory canopy cover, proportion of trees that are hardwood species) and ecological site potential as described for local potential natural vegetation (PNV) zones, and 2) predicting elk nutrition (dietary digestible energy [DDE]) based on forage biomass characteristics in 2 primary PNV zones of the region: western hemlock (WHZ) and Pacific silver fir-mountain hemlock (SFMHZ). Field data for both steps were collected by Cook et al. (2016), 2000–2002, at Nooksack, Washington (Nk), Springfield, Oregon (Spr), and Willapa Hills, Washington (WH) study areas. Equations to predict DDE based on biomass of 3 forage classes (AB = accepted biomass; NB = neutral biomass; and SB = selected biomass) within the 2 PNV zones were developed by Cook et al. (2016) from data collected using captive elk at the 3 study areas. Equations to predict forage biomass from selected site and forest overstory characteristics were developed herein. The final nutrition model combined both sets of equations into an overall model used to predict DDE across the Westside region.

To integrate analyses and summaries that we present here with DDE-elk performance relationships described by Cook et al. (2004:55), we modified their original 4 classes to create 6 DDE classes: <2.40, 2.40–2.58, >2.58–2.75, >2.75–2.83, >2.83–2.90, and >2.90 kcal/g (Table 2). Specifically, we halved the original good (2.75–2.90) and marginal (2.40–2.75) DDE classes to define the nutritional landscape of the Westside region more precisely. We defined basic DDE requirement as that level required for lactating elk to hold constant body fat levels over summer (~2.65–2.70 kcal/g of DDE; Cook et al. 2004) while raising a calf. Herein, we broadened this class by assuming that this basic requirement ranges from about 2.58 kcal to 2.75 kcal of DE/g of ingested food. However, this basic requirement inadequately provides for levels of autumn body fat of lactating elk, calf, and yearling growth rates, and early timing of breeding of which elk are capable if nutrition is excellent during summer (DDE >2.9 kcal/g; Table 2; Cook et al. 2004). We included analyses of DDE levels that not only satisfied the basic requirement but also those that exceeded the basic requirement.

Model development.—We developed equations to predict SB, NB, and AB based on overstory and other site characteristics using stepwise regression with backward elimination. In prior work, Cook et al. (2016) investigated a large number of potential overstory and site covariates, including their interactions; here, we reduced these into a more practical subset. Our first variable reduction step primarily reflected *a priori* expectations of importance but also reflected the reliability and coverage of data available in GIS for our entire mapping region. In light of this, we included 2 forest overstory variables (CC and proportion of overstory trees composed of hardwood species, the latter included because development of understory vegetation may be greater in hardwood forests than in conifer forests [Hanley et al. 2006]), PNV zone (to account for biophysical effects on

Table 4. Equations to predict dietary digestible energy (DDE) for elk based on biomass (kg/ha) of 3 forage classes by potential natural vegetation zones (Pacific silver fir and mountain hemlock zones [SFMHZ] and western hemlock zone [WHZ]) and 3 study areas (Nooksack [Nk], Willapa Hills [WH], and Springfield [Spr]) in western Oregon and Washington, USA (from Cook et al. [2016]).

Equation[a]	n	R^2	R^2_{adj}	$S_{y.x}$[b]	P
SFMHZ habitats, all seasons, all study areas					
$DDE = 2.44 + 0.000889(NB) + 0.00308(SB) - 0.00000546(SB \times NB)$	14	0.56	0.43	0.134	0.036
WHZ habitats, all seasons, by study area					
$DDE_{Nk} = 2.362 + 0.00108(NB) + 0.000504(SB) - 0.00000361(SB \times NB)$	19	0.49	0.39	0.223	0.015
$DDE_{WH} = 2.278 + 0.00062(NB) + 0.00120(SB) - 0.00000172(SB \times NB)$	26	0.52	0.46	0.177	0.001
$DDE_{Spr} = 2.300 + 0.00108(NB) + 0.00129(SB) - 0.00000418(SB \times NB)$	28	0.62	0.57	0.115	<0.001

[a] Forage class codes (variable names) are NB = biomass (kg/ha) of neutral plant species (those plants that elk neither significantly avoided or selected), SB = biomass (kg/ha) of selected plant species (those plant species that elk significantly selected), and AB = biomass (kg/ha) of accepted species (SB and NB combined).

[b] Standard error of the estimate.

vegetation composition, development, and plant chemistry [Franklin and Dyrness 1988, Henderson et al. 1992]), and study area.

We initially used the approach described by Stage (1976) to incorporate effects of slope and aspect on understory vegetation into our analyses. We found early in our analyses, however, that including slope and aspect in the regression equations resulted in a twofold overestimation of biomass on the steeper slopes of our study region. The fundamental problem was that most of the data were collected on flat and moderate slopes, and extrapolating results to the steeper slopes of the study area resulted in unrealistic estimates of forage biomass. Thus, we excluded slope and aspect from development of our final forage biomass prediction models.

We developed separate prediction models for each PNV zone because differences in vegetation and nutritional responses were greater among zones than among study areas (Cook et al. 2016). We also modeled differences within PNV zones among study areas using indicator variables. However, the MHZ and SFZ were well-represented in our sample only at Nooksack. Therefore, we pooled data across study areas for these 2 types, as was done for the DDE equations (Cook et al. 2016), and excluded indicator variables representing study areas for the MHZ and SFZ. Finally, because Cook et al. (2016) found no differences in DDE between the SFZ and MHZ, we pooled data, as they did, in these 2 high-elevation zones (hereafter referred to as SFMHZ).

Because forage abundance typically was nonlinearly related to CC (Cook et al. 2016), we used CurveExpert (CurveExpert 1.37; Daniel Hyams, Hixson, TN, USA) to identify functions to describe the nonlinear relations for our initial forage biomass-CC univariate analyses. This program provides multiple equations between response variables and covariates (1 covariate per run) and ranks each based on $S_{y \cdot x}$ (the standard error of the estimate). We selected the best formulations based on lowest $S_{y \cdot x}$, and then reran these using PROC NLIN (Gauss-Newton method, SAS Institute 1988) to identify their statistical significance. If nonlinear versions were significant ($P < 0.05$) and provided lower $S_{y \cdot x}$ than linear versions, we considered the relationship to be nonlinear. However, we used nonlinear equation types (e.g., quadratic, logarithmic) that could be readily combined with other variables (proportion hardwoods, PNV) in stepwise multiple regression analyses for those CC-forage biomass relationships that were found to be nonlinear.

Using each biomass variable (SB, NB, AB) as dependent variables in separate analyses, we used stepwise regression with backward elimination (PROC REG, SAS Institute 1988) to select a final model, based on a full model containing predictor variables for CC, hardwood proportion, PNV, and study area. We included the 2-way interactions between study area and CC but did not evaluate the interaction between proportion hardwoods and study area because stands with appreciable levels of hardwoods only occurred at Nooksack. We set the significance level for a variable to remain in the model at $P = 0.15$ for the stepwise analyses. We elected to use normal linear models for this analysis, preferring to avoid transformations of the response variables and thus retain data in their original units for simplicity and ease of application by users. We nevertheless evaluated residuals from the final models to identify 1) heteroscedasticity; 2) patterns in residuals that might flag inappropriate models; 3) non-normal distribution of residuals; and 4) deviation from 0 of residual means (Zar 2010). Our primary intent for using the residuals was an initial check that our modeling assumptions were met and provided reliable estimates of forage biomass.

We considered 10 independent variables in the stepwise regression analyses. Four of these were overstory canopy variables: percent CC and percent CC^2, where both were included to represent the nonlinear effect of CC, proportion hardwoods, and the interaction of CC and proportion hardwoods (the latter only applied in the WHZ because hardwood trees were largely absent from samples in the SFMHZ). We included 2 indicator variables representing the main effects of study area ($STAR_{WH}$, $STAR_{Spr}$, where $STAR_{WH}$ = study area for Willapa Hills, $STAR_{Spr}$ = study area for Springfield, and Nooksack was the reference study area). We also included the interaction of the indicator variables with CC and CC^2 (a total of 4 variables: $STAR_{WH} \times CC$, $STAR_{Spr} \times CC$, $STAR_{WH} \times CC^2$, $STAR_{Spr} \times CC^2$).

As an additional check for consistent errors of our forage biomass prediction equations, we plotted predicted and observed biomass estimates for SB, NB, and AB for our entire data set in relation to stand age, and then fit a linear model to the predicted and observed values to estimate the slope coefficient of each relationship (slopes significantly different from 1.0 would indicate consistent errors in our prediction equations). To check for errors in our entire suite of DDE and biomass prediction equations, we compared observed versus 2 sets of predicted values of DDE for 1) early-successional stages and closed-canopy forests within study areas in the WHZ, 2) early-successional and closed-canopy forests across study areas in the SFMHZ, and 3) thinned and unthinned forest in WHZ with stand age limited to 20–60 years. We generated the first set of predicted DDE values from estimates of AB, NB, and

SB actually measured in each macroplot, and the second set of DDE values from predicted AB, NB, and SB for each macroplot. We calculated a paired *t*-test for each predicted-observed pair to identify errors from predicting biomass of our understory plant groups versus using actual data for each PNV-study area-thinning group.

Nutritional resource mapping.—To predict forage biomass and DDE levels for each 30-m × 30-m pixel across the Westside, we combined the DDE and associated AB, NB, and SB prediction equations into a GIS-based model (ModelBuilder, ArcGIS 9.3 and 10.0, Environmental Systems Research Institute, Inc., Redlands, CA, USA). We derived estimates for the forage biomass covariates from existing GIS layers (Appendix B, Table B2, available online in Supporting Information). Values of CC and hardwood proportion were from the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) project (http://www.fsl.orst.edu/lemma/main.php?project=nwfp&id=studyAreas, accessed 20 Feb 2014; Appendix B). We used a digital elevation map (http://ned.usgs.gov) to calculate slope and aspect and obtained PNV data from the United States Forest Service (USFS; http://ecoshare.info/products/gis-data/, accessed 20 Feb 2014; Appendix B).

We used equations developed at Willapa Hills for prediction throughout the Coast Range including the Olympic Mountains west of Puget Sound and the Klamath Mountains at the extreme southwest portion of our study region (Fig. 1), those developed at Nooksack for areas in the northern Cascades, and those developed at Springfield for the western Cascades from the Washington-Oregon border to our southern boundary (Fig. 1). For agricultural areas, we used a constant DDE value of 2.83 kcal/g (National Research Council 1984), assuming that crops in this high-rainfall region would provide high-quality forage in most cases (crop types were variable, but pasture and hay lands, cereal grains, and orchards were common). We selected this DDE constant without specific knowledge of what crops were actually planted in a given year and locale, and thus it should be considered a rough estimate. However, agricultural areas were uncommon for most elk habitat-use modeling areas on the Westside and composed only 8% of the Westside region (Wisdom et al. 2018*a*). We did not derive predictions of DDE for areas we assumed to be non-habitat for elk (e.g., suburban and urban areas, snow fields; Appendix B, Table B3).

We applied our DDE and forage biomass prediction equations developed from data collected in the WHZ and SFMHZ, without modification, in PNV zones for which we had no empirical data based on similarities of plant species composition between unsampled and sampled PNV types (Table 5). We chose appropriate crosswalks (i.e., assignment of unsampled zones to the 2 sampled ones) using vegetation descriptions from Franklin and Dyrness (1988) and Henderson et al. (1992). In general, we predicted forage biomass and DDE for unsampled PNV zones at low to moderate elevations using equations for the WHZ, and predicted biomass and DDE for unsampled PNV zones at relatively high elevations using equations for the SFMHZ.

Nutrition model evaluation.—We evaluated the performance of the nutrition model using 3 response variables of wild elk in relation to predicted DDE levels: 1) resource selection; 2) levels of autumn body fat of prime-aged (2–14 years of age) lactating elk; and 3) pregnancy rates of prime-aged lactating elk. Thus, our approach involved evaluating relationships between DDE predictions from the nutrition model developed at fine scales and higher-order responses of wild elk at broad scales. For the first, we calculated selection ratios (use/availability) for several categories (i.e., bins) of DDE, where a ratio >1 indicates selection and <1 indicates avoidance (Manly et al. 2002). We conducted this analysis simply to illustrate selection for different levels of DDE, without accounting for influences of other environmental covariates. Analyses of habitat use, in which nutritional resources and other covariates were combined in a multivariable framework, are presented by Rowland et al. (2018). For the 5 model development areas where location data were available from elk with global positioning system (GPS) collars (Table 1), we used 279,339 elk locations and a roughly equal sample of systematic points (284,110 points) in the same areas to calculate proportions used, proportions available, and selection ratios for each of 8 DDE bins. We divided the bins into

Table 5. Crosswalks, or assignments, of unsampled potential natural vegetation (PNV) zones in the Westside region, western Oregon, and Washington, USA, to the 2 sampled zones (crosswalked zones; i.e., WHZ, SFMHZ) used to predict elk nutritional conditions sampled in western Oregon and Washington, arranged in decreasing order from most to least abundant.

Original PNV zone	Crosswalked zone[a]	Area (ha)	% region
Western hemlock	WHZ	6,581,853	56.14
Pacific silver fir	SFMHZ	1,541,776	13.15
Douglas-fir	WHZ	1,077,866	9.19
Sitka spruce	WHZ	820,183	7.00
Mountain hemlock	SFMHZ	710,532	6.06
Grand fir	WHZ	332,700	2.84
Parkland	SFMHZ	315,591	2.69
Alpine	SFMHZ	87,805	0.75
White fir		81,385	0.69
Oregon white oak		74,567	0.64
Steppe	WHZ	57,244	0.49
Subalpine fir	SFMHZ	38,712	0.33
Grassland	WHZ	2,044	0.02
Ponderosa pine		1,290	0.01
Jeffrey pine		10	0.00

[a] WHZ = western hemlock zone, SFMHZ = Pacific silver fir and mountain hemlock zones (combined). Empty cells are PNV zones masked from analysis owing to their dissimilarity to the 2 primary modeling zones.

increments that ensured all bins included at least ~5% of the landscape. We used bins of 0.05 kcal/g and truncated at DDE <2.45 kcal/g at the lower extent and >2.75 kcal/g at the upper extent. Equal-sized binning is a standard practice when calculating selection ratios or conducting analyses of predicted versus observed data for validation (e.g., Manly et al. 2002). This analysis was not a formal test of statistical significance; instead, we estimated selection ratios to identify the extent to which elk were associated with various levels of nutritional resources indexed by DDE. We calculated 90% confidence intervals (CIs) for the selection ratios by bootstrapping individual elk with $n = 2{,}000$ iterations and identified CI endpoints using the percentile method (Manly 2006).

We used population-level estimates of body fat in autumn and pregnancy rates from 9 populations described by Cook et al. (2013) and Stussy (1993) to evaluate the relation between these 2 performance measures and percentage area by DDE class in each elk range (Fig. 1). All body fat and pregnancy estimates were for elk that raised a calf the previous summer based on presence of milk in the udder (Cook et al. 2013) because performance (body fat and ovulation dynamics) is considerably more sensitive to nutrition in summer and early autumn in lactating versus non-lactating elk (Cook et al. 2004, 2013).

Cook et al. (2013) estimated body fat using an arithmetic combination of ultrasound measures of thickness of the subcutaneous rump fat layer and a body condition score (scaledLIVINDEX; Cook et al. 2010) collected during at least 2 autumns (1998–2005) for each population. Stussy (1993) measured kidney fat index (Riney 1955) in 1988 and 1989 from hunter-harvested elk; we converted kidney fat to percent body fat using equations from Cook et al. (2001). The body fat estimates were obtained in November and early December with 3 exceptions: those at Springfield were sampled in early October (Cook et al. 2013), and those of Stussy (1993) for the 2 Siuslaw populations were obtained mostly in January (late Dec–Feb). Because body fat declines over winter and probably over autumn in these areas (Kohlmann 1999, Cook et al. 2013), we attempted to account for this decline using a conservative estimate of change of −0.5 percentage point/month in the Coast Range and −0.9 percentage point/month in the Cascade Range (Cook et al. 2013; i.e., −1 for Springfield and +1 for both Siuslaw populations) to be consistent with an average late-November sampling date for the other populations. Cook et al. (2013) determined pregnancy using rectal entry with ultrasound and confirmed non-pregnancy with pregnancy-specific Protein B of serum (Noyes et al. 1997), whereas Stussy (1993) inspected uteri of harvested elk to determine pregnancy. Research involving animal capture and handling was conducted in accordance with approved animal welfare protocol for the Starkey Experimental Forest and Range (#92-F0004; Wisdom et al. 1993) as reported in Cook et al. (2013, 2016).

To develop DDE estimates for each population using data from Cook et al. (2013), we defined population range boundaries with minimum convex polygons (MCPs) plus a 500-m buffer around the MCP boundary of elk locations from very high frequency (VHF) collars for many of the populations (Table 3; most elk sampled for body fat and pregnancy carried collars). R. Stussy (Oregon Department of Fish and Wildlife, personal communication) provided population boundaries of sampled elk for both Siuslaw populations and D. Vales (Muckleshoot Indian Tribe, personal communication) provided boundaries for the Green River and White River populations (Table 3).

We calculated percentage of area within the population boundaries for 5 DDE classes that relate to performance measures of elk: >2.58–2.75, >2.75–2.90, >2.58, >2.75, and ≥2.90 kcal/g.

We then used logistic regression with a binomial link function (Hosmer et al. 2013) to predict pregnancy rates for the 9 elk populations, with the percentage of each population's range in each DDE class as the predictor. We computed r^2 values for logistic regression as described by McFadden (1974), and used 1 regression for each class to identify which level of DDE, if any, was related to pregnancy rate. We used the number of elk sampled in each population as an offset term to account for differences in sample size (Ramsey and Schafer 2012). We used linear regression on autumn body fat levels of each population with percent of area by DDE category to determine if any categories were related to body fat. We expected that areas with higher percentages of relatively good nutrition (DDE >2.75 kcal/g) would best predict body fat levels, whereas areas with somewhat lower nutrition (DDE >2.58–2.75 kcal/g) would best predict pregnancy rates (Cook et al. 2004).

We created a nutritional resource map for the entire Westside region, grouping DDE in 6 categories (Table 2), to provide an overview of the current (~2006) status of nutritional resources for elk and to compare nutritional resources among land owners. Based on this map, we calculated the percentage of area in each of the 6 DDE classes for the Westside region and for 7 ecological provinces as defined by Franklin and Dyrness (1988). We also calculated the amount (ha) and percentage of area by the 6 DDE classes for individual landowners, separated by PNV zones, and total area (ha) providing DDE >2.58 kcal/g to illustrate contributions by landowner. Landowners included the Bureau of Indian Affairs, Bureau of Land Management (BLM), USFS, National Park Service (NPS), states (primarily Washington Department of Natural Resources and Oregon Department of Lands), other government entities (counties, towns, and other miscellaneous), and private corporations (primarily forest management companies such as Weyerhaeuser Company, Plum Creek Timber Company, and Hancock Timber Resources Group). We excluded agricultural lands from these regional summaries.

We compared ambient temperature and precipitation levels during the summers for which vegetation and DDE data were collected (Cook et al. 2016) to 30-year averages (1981–2010) to evaluate potential deviations of our DDE and forage biomass data from long-term patterns. We determined temperature and precipitation levels for May–July and August–October for each study plot where captive elk were deployed during the year the plot was sampled and calculated the 30-year averages for these sites. We generated climate data with the ClimateWNA v4.62 software package (http://tinyurl.com/ClimateWNA) based on methodology described by Hamann et al. (2013).

RESULTS

Data from 346 macroplots from Cook et al. (2016) were available for model development: 276 macroplots in the WHZ, roughly equally distributed among the Nooksack, Willapa Hills, and Springfield study areas; 33, 8, and 7 in the SFZ at the 3 areas, respectively; and 22 in the MHZ, all at Nooksack. We used captive elk in 32, 28, and 30 of the macroplots at the 3 study areas, respectively.

Model Development

Of the predictor variables examined, CC exhibited a strong relation with biomass of our 3 forage classes (AB, NB, and SB) in the WHZ at all study areas. For AB, the relation was nonlinear and was best fit overall with an exponential equation, with relatively high biomass levels occurring in early-seral stages with low overstory CC and low biomass levels under moderate and very high levels of CC (Fig. 5A). Modeling the nonlinear relationships using a quadratic function (CC and CC^2) provided similar fit, and thus we opted to use a quadratic function to provide a simpler formulation for modeling the nonlinear relations in the subsequent stepwise regression. At very high levels of CC, several macroplots supported AB levels substantially in excess of that typically found in such stands. Nearly all of these were hardwood stands (inset of Fig. 5A). The general pattern for NB was nearly identical to that of AB; however, the relation between SB and CC was linear (Fig. 5B), with higher levels of SB in early-seral stands.

For our stepwise regression for data from the WHZ, analyses for both AB and NB included CC and CC^2, proportion hardwoods, and interactions of study area × CC and CC^2, with adjusted $R^2 \geq 0.65$ (Table 6). All independent variables included in both models were significant ($P < 0.002$). The regression equation for SB provided similar, though more variable results (adjusted $R^2 = 0.46$), except that the relation between SB and CC was linear rather than nonlinear (Table 6). Equations for all 3 forage classes reflected declining forage biomass as overstory CC

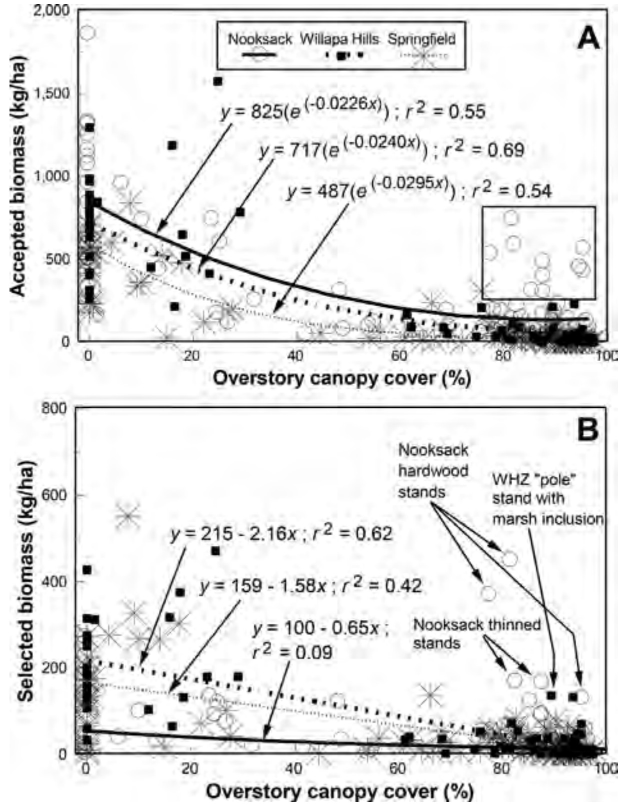


Figure 5. Relations of overstory canopy cover and biomass of accepted (A) and selected (B) plant species in the western hemlock zone (WHZ) at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA 2000–2002 (relations between neutral biomass and canopy cover were virtually identical to those for accepted biomass and canopy cover; thus, only results for accepted biomass are displayed). Of the 10 anomalous points included in the square in the lower right corner in panel A, 8 were in hardwood stands, 1 in a thinned stand, and 1 in an untreated coniferous forest. Equations were significant at $P < 0.005$.

Table 6. Equations to predict biomass (kg/ha) of 3 forage classes for elk based on stand and forest overstory conditions by potential natural vegetation zones (Pacific silver fir and mountain hemlock zones [SFMHZ] and western hemlock zone [WHZ]) and 3 study areas (Nooksack [Nk], Willapa Hills [WH], and Springfield [Spr]) in western Oregon and Washington, USA.

Equation[a]	*n*	R^2	R^2_{adj}	$S_{y.x}$[b]	*P*
SFMHZ, all seasons, all study areas					
$AB = 657.6 - 11.28(CC) + 0.0458(CC^2) + 553.06(HW)$	70	0.71	0.70	187.51	<0.001
$NB = 527.8 - 6.09(CC) + 590.49(HW)$	70	0.73	0.72	151.39	<0.001
$SB = 1/((0.00833 + 0.00062(CC))$	70	0.30	na[c]	68.45	<0.001
WHZ, all seasons, by study area					
$AB_{Nk} = 707.3 - 13.93(CC) + 0.0731(CC^2) + 383.2(HW)$	276[d]	0.69	0.68	187.06	<0.001
$AB_{WH} = 707.3 - 6.28(CC) - 0.0154(CC^2) + 383.2(HW)$					
$AB_{Spr} = 490.5 - 11.70(CC) + 0.0731(CC^2) + 383.2(HW)$					
$NB_{Nk} = 671.8 - 16.91(CC) + 0.1092(CC^2) + 268.1(HW)$	276[d]	0.66	0.65	158.76	<0.001
$NB_{WH} = 477.4 - 3.90(CC) - 0.0151(CC^2) + 268.1(HW)$					
$NB_{Spr} = 308.5 - 7.59(CC) + 0.0473(CC^2) + 268.1(HW)$					
$SB_{Nk} = 80.1 - 0.66(CC) + 99.83(HW)$	276[d]	0.47	0.46	70.48	<0.001
$SB_{WH} = 212.6 - 2.20(CC) + 99.83(HW)$					
$SB_{Spr} = 166.2 - 1.68(CC) + 99.83(HW)$					

[a] Forage class codes (variable names) are NB = biomass (kg/ha) of neutral plant species (those plants that elk neither significantly avoided nor selected), SB = biomass (kg/ha) of selected plant species (those plant species that elk significantly selected), and AB = biomass (kg/ha) of accepted species (SB and NB combined). Predictor variable codes are CC = overstory canopy cover (%); HW = proportion of stems in dominant canopy layer that are hardwood tree species (red and other alders [*Alnus* spp.], bigleaf maple [*Acer macrophyllum*], and paper birch [*Betula papyrifera*]).

[b] Standard error of the estimate.

[c] na = not applicable.

[d] Separate equations developed from one regression analysis using indicator variables with interactions to provide separate coefficients, among study areas, for the intercept and both CC variables.

increased and modestly higher biomass in stands dominated by hardwood trees despite relatively high overstory canopy cover.

Equations produced slightly negative estimates (i.e., less than 0) of AB and NB at overstory CC $\geq$91% and at CC $\geq$95% for SB at Willapa Hills. Thus, we set any predicted value of forage biomass <0 to 0 to eliminate negative predicted values.

In the SFMHZ, canopy cover again was the primary covariate for all 3 biomass classes. For AB and SB, the relation was nonlinear, but for NB, the relation was linear (Fig. 6A–C). The stepwise regression for AB included CC, CC^2, and hardwood proportion (Table 6) and accounted for 70% of the variation in AB. The stepwise regression for NB included CC ($P < 0.001$) and proportion hardwoods ($P = 0.002$) and accounted for 72% of the variation in NB (Table 6). The CC^2 term ($P = 0.262$) provided no improvement in either the $S_{y \cdot x}$ or adjusted R^2. For SB in the SFMHZ, proportion hardwood was not significant ($P = 0.86$), and thus, our options for SB included only 2 equation types, the multiple regression formulation with CC and CC^2 and the nonlinear reciprocal equation originally identified using CurveExpert. Because of the lower $S_{y \cdot x}$, we selected the reciprocal equation for prediction (Table 6).

Residuals from the prediction models, when plotted with overstory CC, generally indicated only modest heteroscedastic variances of each forage class across the range of CC, reflecting declining variance as CC increased (Figs. 5 and 6). We suspect that the greater variance at low CC reflected influences of factors that we did not include in the analysis, including site treatments just after logging, influences of vegetation communities that existed before logging (i.e., legacy influences), planting versus natural regeneration of conifers, time since logging, and other related factors. Overall, however, we observed no systematic patterns in the residuals (Appendix C, available online in Supporting Information), plots of residuals generally exhibited a normal distribution, and means of the residuals were $\sim$0, together suggesting the equations were robust. In addition, plots of observed and predicted values of our forage biomass types, though variable, illustrated good overall congruence across our data, and suggested that the equations were, in aggregate, unbiased (Fig. 7). Finally, estimates of DDE calculated directly from AB, NB, and SB field estimates in each macroplot using the DDE equations, and estimates of DDE calculated for each macroplot using predicted values of AB, NB, and SB, were consistently similar to observed DDE across high- and low-elevation forest zones, early-seral stages and closed-canopy forests among the study areas, and in thinned and unthinned stands (Fig. 8). We found no differences using paired t-tests between observed DDE and each estimate of predicted DDE by seral stage, PNV zone, nor study area ($P > 0.05$).

Based on the final model and vegetation data collected at each macroplot, predictions of DDE varied among PNV zones and defined a nutritional-succession sequence that illustrated substantial differences by seral stage and PNV zone (Fig. 9). These patterns illustrate the considerable nutritional value of early-seral communities, particularly those on moister soils and at higher elevations (Cook et al. 2016).

Westside Nutritional Resources for Elk

We identified 15 PNV types within our study area (Table 5). Of these, we considered 11 sufficiently similar to those sampled by Cook et al. (2016) for direct application of our DDE and forage biomass equations (Table 5). This group included 4 PNV types that were permanently sparsely or non-forested: alpine, parkland, steppe, and grasslands. We used equations for SFMHZ for alpine and parkland types, and used equations for the WHZ for the steppe and grassland PNVs. The forest zones that we deemed too different for using our DDE and biomass equations were generally restricted to the extreme southern portion of our study area and were rare. The sampled PNVs, unsampled but crosswalked PNVs, and unsampled PNVs that we deemed too different for using our DDE and biomass equations composed 75%, 23%, and $<$2% of our study area, respectively (Table 5).

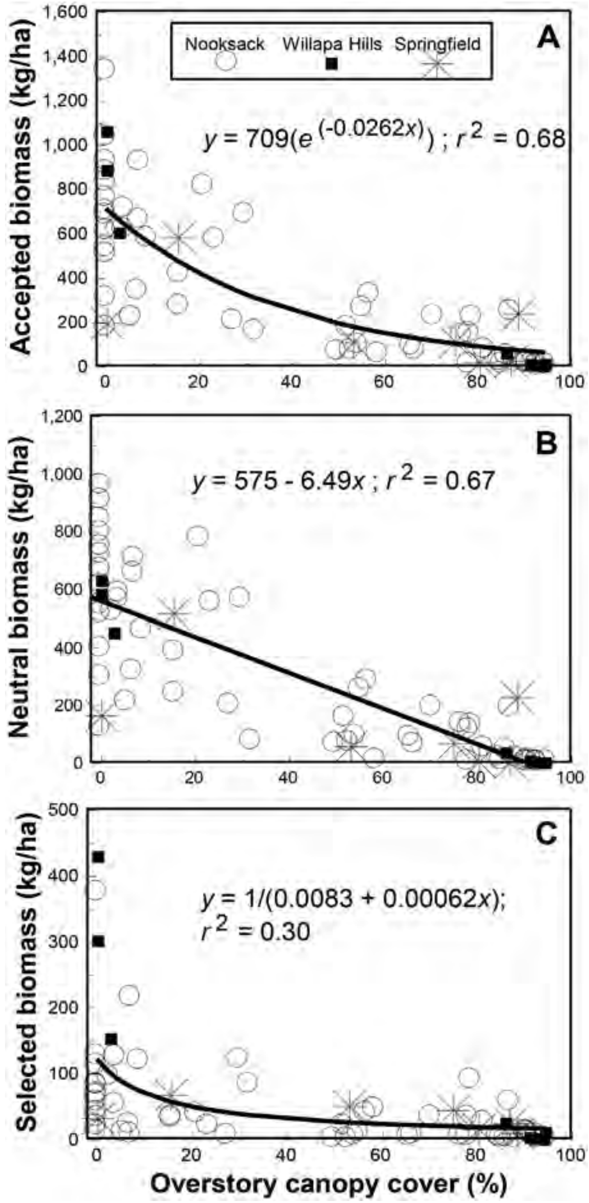


Figure 6. Relations of overstory canopy cover and biomass of accepted (A), neutral (B), and selected (C) plant species in Pacific silver fir and mountain hemlock potential natural vegetation zones at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA, 2000–2002. Equations were significant at $P < 0.001$.

Our Westside map of nutritional resources depicted vast landscapes of poor and below-requirement levels of DDE

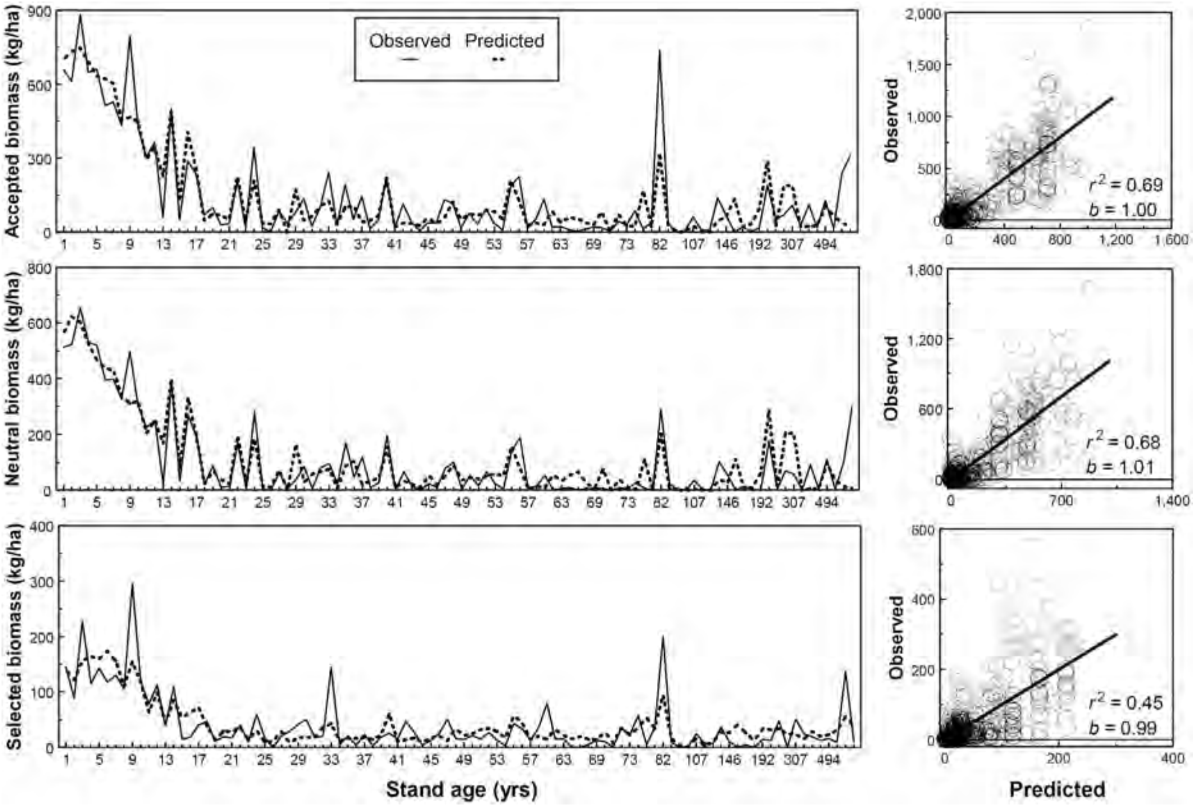


Figure 7. Observed and predicted values of accepted, neutral, and selected biomass of elk forage by stand age (left column). Cook et al. (2016) made predictions across the entire data set ($n = 349$) for vegetation sampling conducted at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA, 2000–2002. We also present coefficients of determination (r^2) and slope coefficients (b) for predicted versus observed values of 3 classes of forage biomass (right column).

(≤2.58 kcal/g) throughout most of the region in 2006 (Fig. 10). In general, high DDE levels that met or exceeded requirement occurred only in high elevation, montane areas, most prominently in the Olympic Mountains and Cascades of Washington.

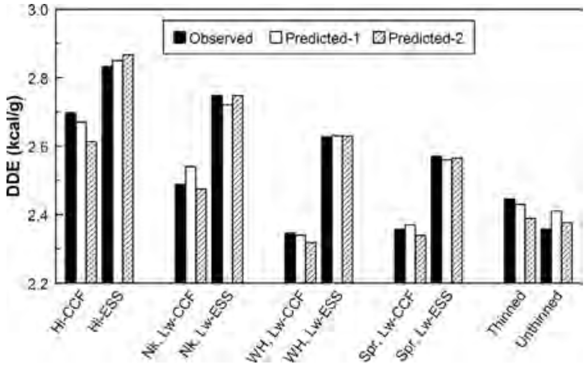


Figure 8. Means of predicted and observed dietary digestible energy (DDE) for elk by categories of potential natural vegetation, successional stage, and thinning for the Nooksack (Nk), Willapa Hills (WH), and Springfield (Spr) study areas in western Oregon and Washington, USA, 2000–2002. Codes are Hi = Pacific silver fir and mountain hemlock zones at high elevations across all study areas; Lw = western hemlock zone (WHZ) at lower elevations; CCF = closed canopy forests; ESS = early-seral stages; Thinned = thinned stands; and Unthinned = unthinned stands. Comparisons of thinned and unthinned were limited to stands in WHZ ranging in age from 20 to 60 years. Predicted-1 means were derived from DDE equations using actual field measures for accepted, neutral, and selected biomass of elk forage; predicted-2 means were derived from the same DDE equations but using predicted values of the 3 forage classes from the biomass prediction equations.

Nutrition Model Evaluation

Our analyses indicated strong correlations among modeled DDE levels, resource use, and performance. Elk with GPS collars exhibited strong selection for areas of relatively high DDE based on our selection ratio analysis. From 1 June to 30 August, selection ratios increased with increasing values of DDE (Fig. 11). Elk avoided areas with DDE <2.55 kcal/g and selected for areas with >2.60 kcal/g of DDE (Fig. 11).

Within the 9 populations used to evaluate relations between animal performance and DDE (Table 3), most of the various DDE levels exhibited high, although insignificant, correlations with pregnancy rate. Pregnancy rates of lactating elk were unrelated to percent area with DDE from >2.58 to 2.75 kcal/g but significantly increased with increasing percent area with DDE >2.58 kcal/g (Fig. 12C). Correlations were not significant between pregnancy rates and percent area with DDE >2.75 kcal/g nor >2.90 kcal/g (Fig. 12). The significant equation (i.e., with percent area with DDE >2.58 kcal/g) seemed to simultaneously account for variation in pregnancy for populations with a significant percentage of area (>10%) with DDE >2.75 kcal/g and for variation in populations generally lacking this higher DDE level. Our data also suggest that pregnancy rates >0.9 occurred only on ranges with at least 10% of area with DDE >2.75 kcal/g.

Autumn body fat of lactating elk exhibited a generally similar pattern (Fig. 13) but was increasingly correlated with percent area offering higher levels of DDE, in contrast to pregnancy rate. We concluded that the best regression for body fat was percent area providing DDE >2.90 (although the regression for percent area with DDE > 2.75 was virtually identical; Fig. 13D and E).

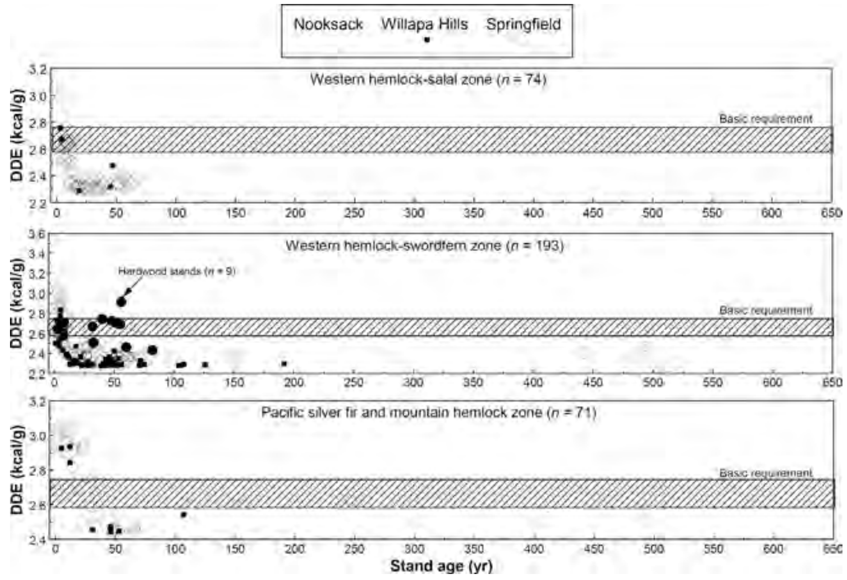


Figure 9. Estimates of dietary digestible energy (DDE) for elk in relation to stand age calculated from equations by study area and potential natural vegetation (PNV) zone at 3 study areas in western Oregon and Washington, USA, 2000–2002 (adapted from Cook et al. [2016]). Values of accepted, neutral, and selected biomass that predict DDE were measured at each field macroplot. The horizontal requirement line indicates the range of DDE levels (>2.58–2.75 kcal/g) needed by lactating female elk to hold constant body fat levels in summer (Cook et al. 2004).

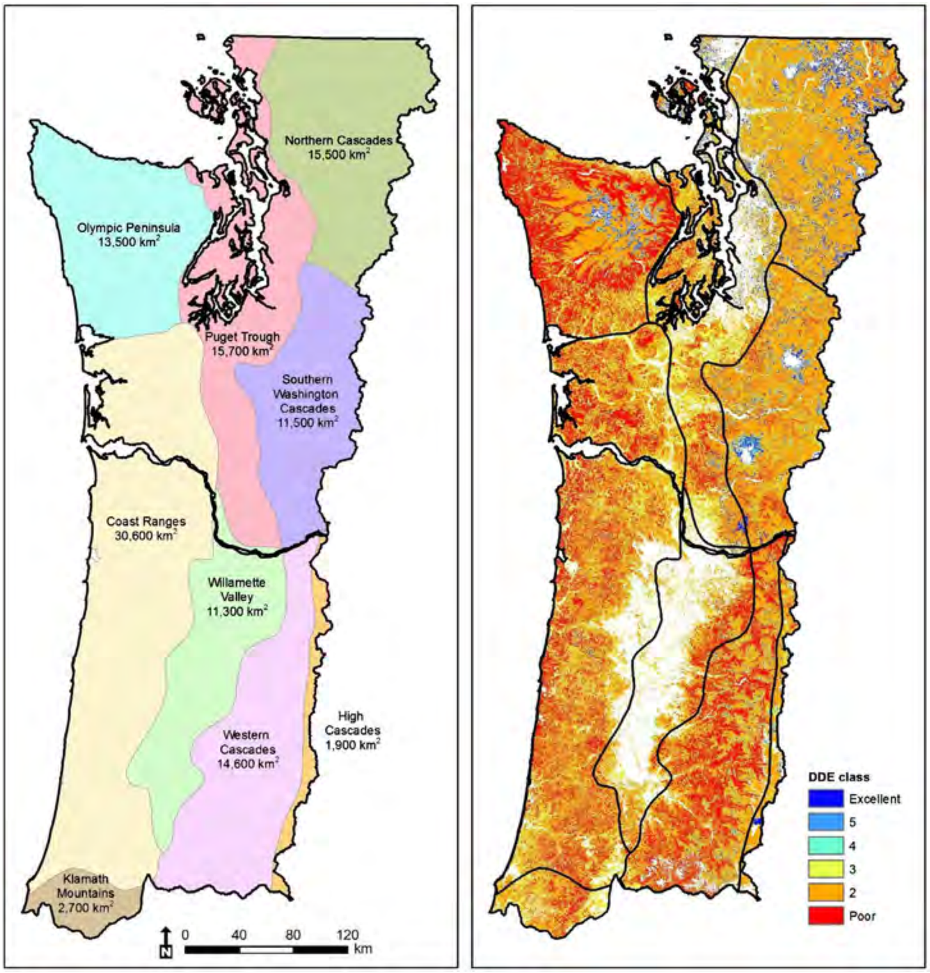


Figure 10. Ecoregions within the Westside region in western Oregon and Washington, USA (left panel). We also present predicted dietary digestible energy (DDE) for elk for 6 classes of DDE (<2.40 [1, poor], ≥2.40–2.58 [2], >2.58–2.75 [3], >2.75–2.83 [4], >2.83–2.90 [5], and >2.90 [6, excellent]). White areas denote agricultural lands and land cover types excluded as non-habitat (e.g., urban, suburban, and ice fields). Existing vegetation data used to predict DDE represent conditions in 2006.

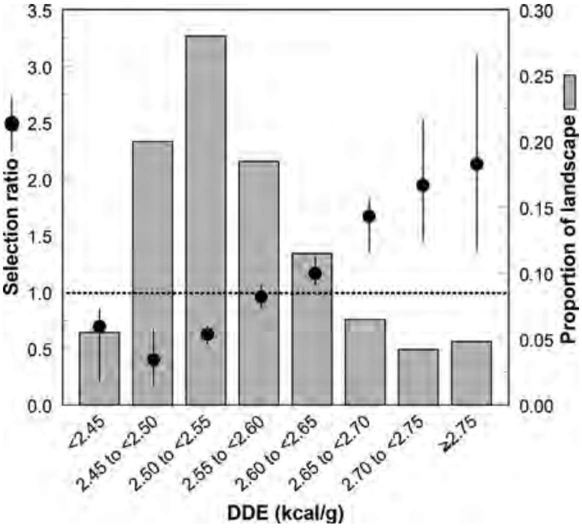


Figure 11. Selection ratios of wild elk equipped with global positioning system (GPS) satellite collars across 5 habitat-use modeling areas in central and western Washington, USA (2004–2009), and proportion of landscape by dietary digestible energy (DDE) classes. Selection ratios >1.0 suggest use greater than available; ratios <1.0 suggest use less than available. Vertical lines indicate 90% confidence intervals.

Regional Nutrition Patterns

Approximately 75%, 20%, and 5% of our entire region offered DDE levels below, around (>2.58–2.75 kcal/g), and in excess of basic requirement for lactating elk, respectively (Fig. 14). Among ecoregions, the greatest percentage of area providing DDE in excess of requirement was in the Cascades, with general declines from north to south from the Northern Cascades (15%), Southern Washington Cascades (11%), and Puget Trough (9%) in Washington to the Western Cascades in Oregon (5%). Areas with predicted DDE above requirement (>2.75 kcal/g) were virtually absent from the Coast Ranges and Willamette Valley ecoregions, and were largely absent except at higher elevations in the Olympic Mountains (Fig. 14).

Summaries of DDE levels among landowners were partitioned by PNV zones because land ownership tended to vary among zones (Fig. 15). Of the 5 major landowners in the WHZ, private, state, NPS, USFS, and BLM had 32.1%, 15.5%, 9.3%, 7.7%, and 6.5%, respectively, of area with DDE at basic requirement levels or better (>2.58 kcal/g). Private, NPS, BLM, USFS, and state had 39.4%, 34.2%, 30.9%, 29.4%, and 25.4%, respectively, of area with DDE at or above requirement in the SFMHZ. Across the entire study region, private lands provided 1.56 million ha of this DDE level, compared to 0.56 million ha on National Forest System lands, the second highest among other landowners (Fig. 16).

Temperature and precipitation patterns during the years DDE and forage data were collected were very similar to 30-year averages for May–July and August–October at Springfield and Willapa Hills, although the August–October period was drier than normal at Nooksack. During May–October, precipitation was 92% of the 30-year average (480 mm) at Springfield and was 96% of the 30-year average (505 mm) at Willapa Hills. At Nooksack, precipitation was 80% of the 30-year average (275 mm) during May–July and 29% of the 30-year average (450 mm) during August–October. Average daily temperature was virtually identical at Springfield compared to 30-year averages and about 1°C cooler over both summer periods at Willapa Hills and Nooksack.

DISCUSSION

Our results indicate that nutritional resources, as indexed by DE levels that elk acquire while foraging, were generally inadequate to satisfy nutritional requirements of lactating elk and their calves over vast areas of our Westside study region. Under these conditions, elk strove to compensate for inadequate nutritional resources by selecting areas that provided nutrition levels that satisfied or exceeded their basic requirements. We also found strong correlations between DDE levels available to elk and autumn body fat and pregnancy rates, supporting our prediction that significant links exist between nutritional resources and performance of elk populations across the vast landscape of our

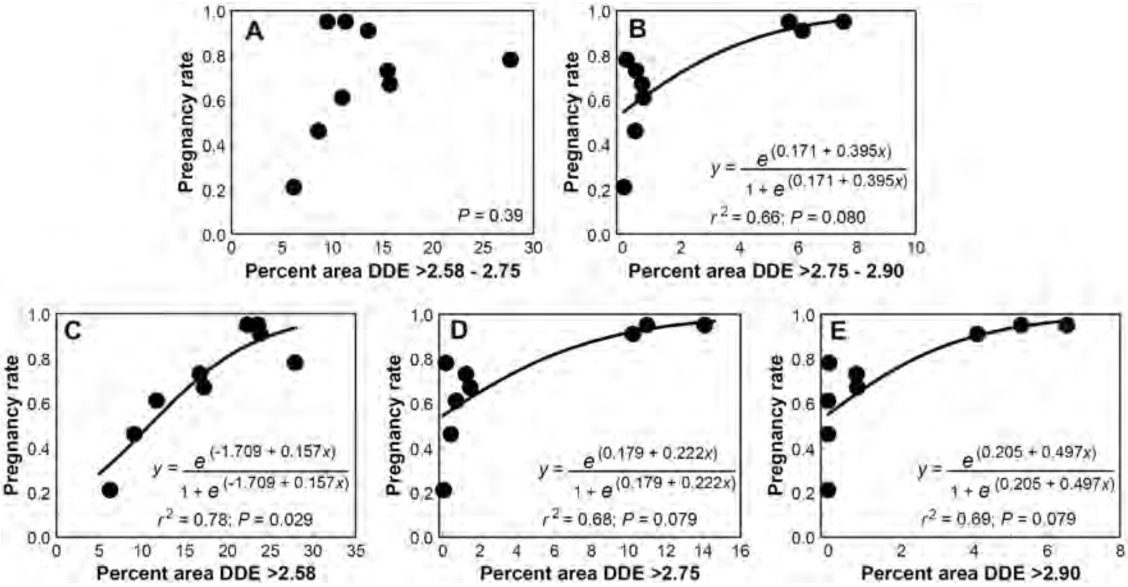


Figure 12. Relations between percent area in selected classes of predicted dietary digestible energy (DDE in kcal/g) and pregnancy rates of lactating wild elk in 9 populations in western Oregon and Washington, USA, 1998–2007. Note that r^2 values presented are pseudo-r^2.

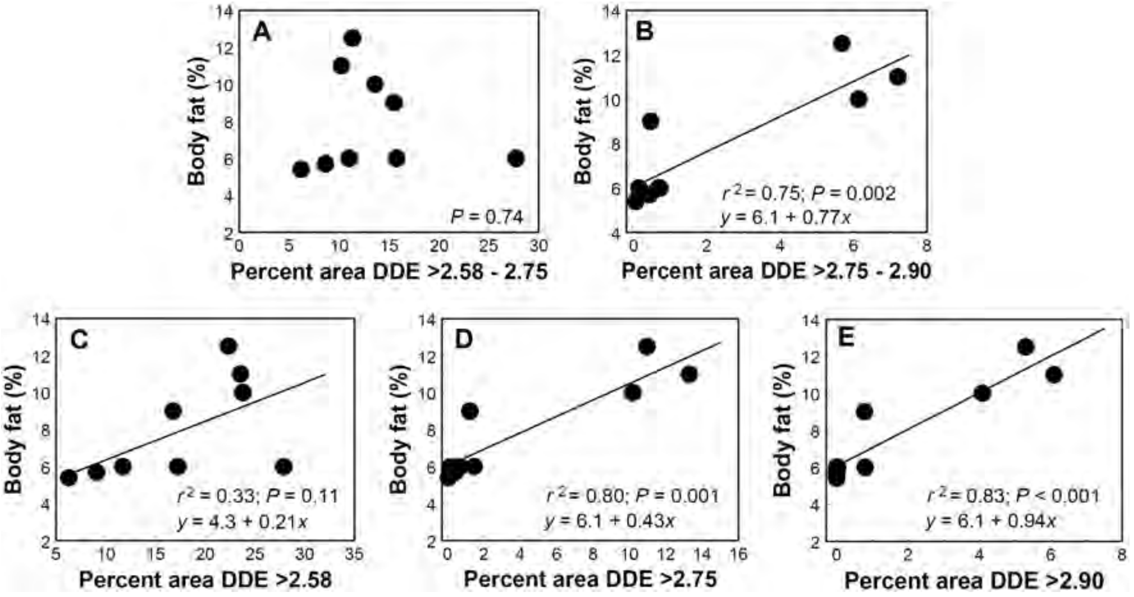


Figure 13. Relations between percent area in selected classes of predicted dietary digestible energy (DDE in kcal/g) and body fat in autumn of lactating wild elk in 9 populations in western Oregon and Washington, USA, 1998–2007.

study region. On ranges where nutritionally superior areas existed, autumn body fat levels and pregnancy rates were high, and where these areas were generally absent, performance suffered significantly. As such, our data strongly support 2 concepts pertaining to summer nutritional ecology and landscape planning. First, including summer nutrition as a key component of landscape models is required in the Westside region if these models are intended to adequately account for environmental influences on habitat use (Rowland et al. 2018), nutritional condition, and reproductive performance of elk. Second, data on elk nutrition dynamics collected at relatively fine scales can be effectively used to account for elk performance metrics at landscape scales in the Westside region. Evidence of the importance of nutrition in summer and early autumn for ungulates in western North America continues to increase (Dale et al. 2008, Cook et al. 2013, Hurley et al. 2014, Monteith et al. 2015, Proffitt et al. 2016), but our results are among the first to confirm that nutrition and foraging dynamics in summer measured at fine scales can be used to predict variation in higher-order population responses across broad, regional landscapes.

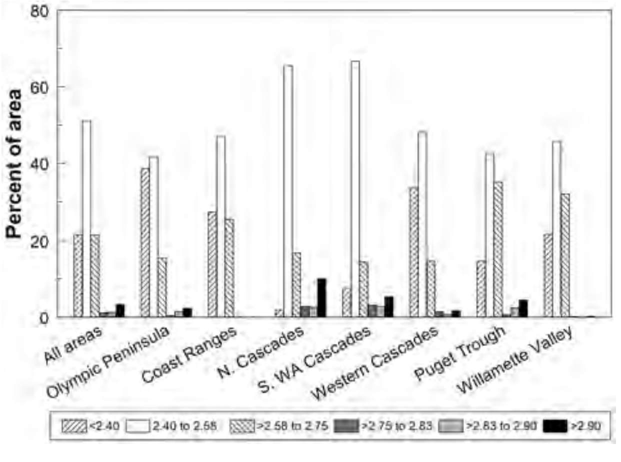


Figure 14. Percent area by ecoregion in each of 6 classes of predicted dietary digestible energy (DDE) for elk, with agricultural lands excluded, in western Oregon and Washington, USA. We excluded 2 peripheral ecoregions (Klamath Mountains and High Cascades) from summaries. Existing vegetation data used to predict DDE represent conditions in 2006.

Largely because of the pioneering work of Trainer (1971), many studies evaluating nutritional condition and pregnancy rates of elk populations conducted in our study region have suggested that low nutritional condition in autumn and depressed pregnancy rates are widespread (Trainer 1971, Smith 1980, Harper 1987, Stussy 1993, Cook et al. 2013). We found that levels of DDE below basic requirement (≤2.58 kcal/g) composed 70–80% of our study region and 75% to >90% of the land base in the WHZ, which dominated across low to mid-elevations. Dietary DE levels that exceed the basic requirement (>2.75 kcal/g) were virtually non-existent in this zone, particularly on public lands. This bleak nutritional environment for elk in summer not only contributes to reduced elk performance but also may contribute to long-term shifts in elk distribution to areas providing better nutrition. Areas that provided substantial area of DDE >2.75 kcal/g (i.e., in excess of basic requirement) existed at relatively high elevations in the SFZ and MHZ, mainly in the mountains of the Olympic Peninsula and the Cascades (Fig. 14) in early seral stages with low overstory canopy cover. Here, opportunities for elk to acquire DDE in excess of basic requirement were substantially greater than in the WHZ at lower elevations.

Elk selected for areas providing at least basic requirement and showed strong selection for areas providing DDE in excess of basic requirement, supporting the prediction that elk recognize and actively seek these areas. Such strong selection undoubtedly is a strategy to avoid the negative fitness consequences of foraging at random (Moen et al. 1997)—the highest levels of pregnancy and body fat occurred on ranges with just 10–15% of area with DDE levels above basic requirement (Figs. 12 and 13), indicating the considerable ability of elk to exploit areas of superior nutritional resources within their seasonal ranges. Nevertheless, on ranges that provided ≤2% of areas with DDE above basic requirement, performance was compromised, indicating elk were

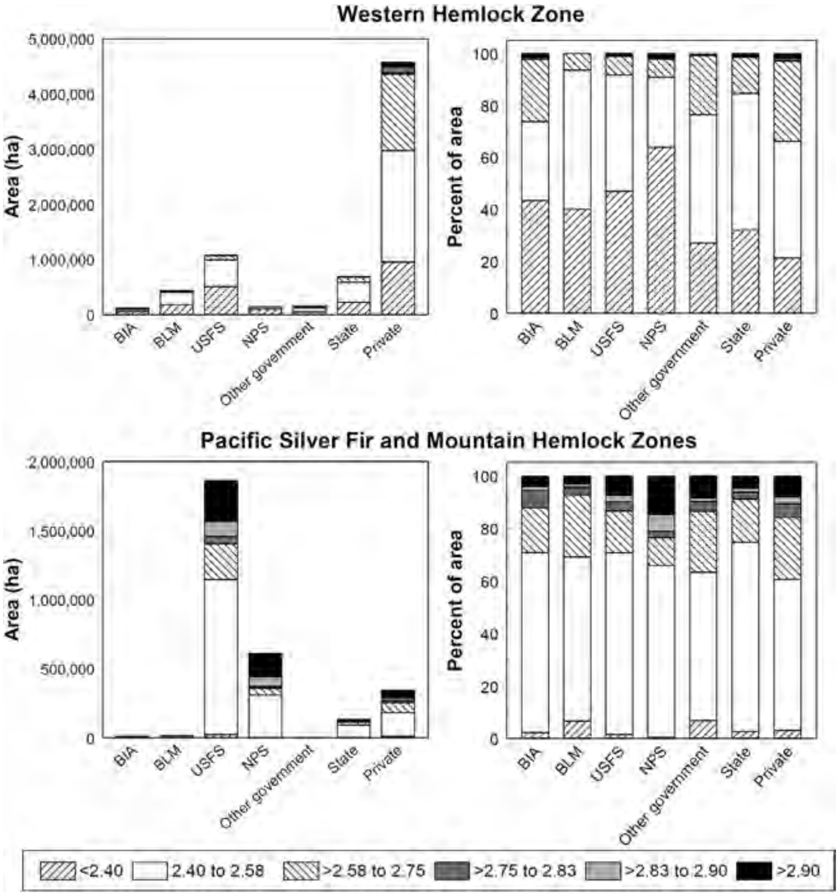


Figure 15. Total area and percent area by landowner in each of 6 classes of predicted dietary digestible energy (DDE) for elk in western Oregon and Washington, USA. We partitioned summaries by potential natural vegetation zones to reduce the influences of ecological conditions on results. Landowner codes are BIA = Bureau of Indian Affairs; BLM = Bureau of Land Management; USFS = United States Forest Service; NPS = National Park Service; Other government = state parks and local municipalities; State = Washington Department of Natural Resources or Oregon Department of Lands; and Private = non-governmental holdings (primarily private forest management companies). Predictions excluded suburban, urban, and agricultural lands. Existing vegetation data used to predict DDE represent conditions in 2006.

unable to fully compensate for poor nutritional resources on these depauperate ranges.

Our results supported our prediction that ranges that provided better nutritional resources during summer also supported greater autumn body fat levels and pregnancy rates of lactating elk. Similar results have been reported before, although across smaller land areas (Albon and Langvatn 1992, Hebblewhite et al. 2008, Proffitt et al. 2016). Perhaps what is most surprising in our study was the strength of the relationships between our 2 measures of performance (Figs. 12 and 13) and DDE levels despite the vast area of our evaluations and the relatively simple approach we used to quantify nutritional resources across elk ranges (i.e., percent of area offering different levels of DDE). In light of the strength of the relationships we found and the causal linkages between summer and early-autumn nutrition and animal performance that are becoming increasingly recognized (Hjeljord and Histol 1999, Dale et al. 2008, McArt et al. 2009, Hurley et al. 2014, Proffitt et al. 2016), we find little support for alternative explanations despite the fact that our analyses did not directly consider their possible influences. One alternative pertains to influences of weather and nutrition during winter. Detailed analyses by Cook et al. (2013) for our 9 populations indicted no significant influences of overwinter changes in nutritional condition, winter weather, or spring body fat on subsequent pregnancy rates and autumn body fat. This finding held for

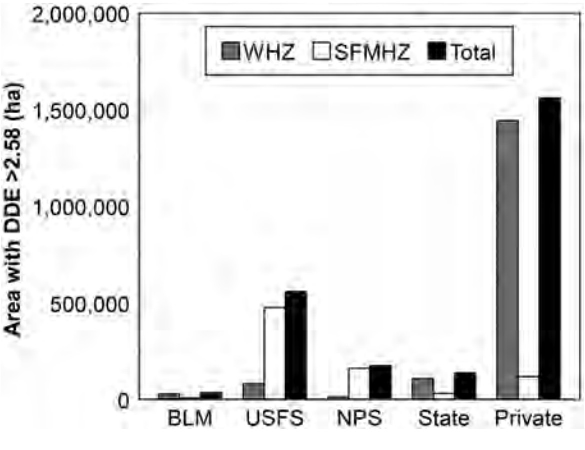


Figure 16. Total area with predicted dietary digestible energy (DDE) for elk >2.58 kcal/g by primary landowners in western Oregon and Washington, USA. Data are partitioned by the western hemlock (WHZ) and the Pacific silver fir and mountain hemlock (SFMHZ) potential natural vegetation zones. Landowner codes are BLM = Bureau of Land Management; USFS = United States Forest Service; NPS = National Park Service; State = Washington Department of Natural Resources or Oregon Department of Lands; and Private = non-governmental holdings (primarily private forest management companies). Predictions excluded suburban, urban, and agricultural lands. Existing vegetation data used to predict DDE represent conditions in 2006.

additional elk populations in areas of substantially harsher winter weather conditions. Based on analyses of all these ranges, they concluded that summer nutrition levels largely dictate both the apex and annual cycle of body fat levels (i.e., the summer-nutrition convergence hypothesis; Cook et al. 2013:29–30). Likewise, in controlled experiments, Cook et al. (2004) demonstrated that both pregnancy rate and autumn body fat in elk were driven by summer, not winter, nutrition, even for elk that exited winter with virtually no body fat. However, in ecological settings where winter weather is colder and snow accumulation is substantially deeper than the Westside region, and especially where inadequate summer nutrition limits body fat accretion and juvenile growth rates in summer, winter conditions certainly may influence performance of elk, especially over-winter survival.

Low levels of body fat and pregnancy might also be attributed to harassment by hunters (e.g., Davidson et al. 2012) and predators (e.g., Creel et al. 2007, but see White et al. 2011*b*, Boonstra 2013, Middleton et al. 2013*b*) that might either increase energy expenditure or force elk to forage in suboptimal vegetation communities. Wolves were absent but black bear and cougar were common in many areas of the region (Wisdom et al. 2018*a*). Studies on 2 populations in our sample (Green River and White River) demonstrated high levels of predation by cougars on elk calves ranging from 20% to 70% annually during the time that our nutritional condition and pregnancy data were collected (Washington Department of Fish and Wildlife 2002*b*). Yet these 2 populations had the second and third highest body fat levels and highest and third highest pregnancy rates of lactating elk in our study (Table 3). Displacement of elk during hunting seasons is increasingly documented, at least in relatively open areas that may offer less security cover than Westside landscapes (Conner et al. 2001; Johnson et al. 2005; Proffitt et al. 2009, 2010; Cleveland et al. 2012), but the strength of the DDE-body fat and pregnancy relationships (Figs. 12 and 13) suggests that such displacement accounts for little variation in performance of elk at broad scales in our region.

The relationships between animal performance and percent area in several DDE classes accorded well with our prediction based on the relationships between DDE and performance reported for elk by Cook et al. (2004). Only our regressions of percent of area providing DDE levels ≥2.75 kcal/g exhibited significant correlations with autumn body fat, agreeing with findings of Cook et al. (2004) that high levels of autumn body fat required over-summer DDE levels of approximately >2.9 kcal/g. The causal mechanism undoubtedly pertains to a declining rate of digestion and passage rates as DE content of forage declines. The overall effect results in a disproportionally large reduction in daily food intake and animal performance despite only modest declines in DE content of forage, a multiplier effect that is increasingly recognized (White 1983, Owen-Smith 2002, Cook et al. 2004, Hebblewhite et al. 2008).

Pregnancy rates were well-correlated to percent of area offering relatively high, but not necessarily the highest, levels of DDE, supporting our prediction and suggesting that nutrition levels required for successful breeding are lower than those needed to accrue relatively high levels of body fat. This relationship supports findings that calf and yearling growth rates, body fat accretion rates and subsequent autumn body fat, age-at-first breeding, and timing of breeding were reduced at DDE levels that nevertheless supported high pregnancy rates (Cook et al. 2004; see Gaillard et al. 2000:384). The pregnancy-DDE relationships, however, may be more nuanced. Populations for which we had pregnancy data largely fell into 2 groups, those lacking areas (≤2% of area) providing DDE levels >2.75 kcal/g and those that provided at least a modest level (10–15%) above this DDE threshold. On those ranges with higher DDE, pregnancy rates exceeded 0.9 (Figs. 12D and E). On those lacking higher DDE, percent area providing DDE >2.58 kcal/g seemed well correlated with pregnancy rates, but rates in these populations were <0.8 (Fig. 12C). Because pregnancy rates peaked at 0.8 for those populations that contained virtually no areas of DDE >2.75 kcal/g (Fig. 12D), our data suggest an asymptotic upper limit to pregnancy rates as a function of the percent of area providing DDE >2.58–2.75 kcal/g. Larger sample sizes would be required to provide conclusive evaluation of this possibility.

We note several cautions for widespread use of these regressions, particularly for the relation between DDE levels and pregnancy rates. First, probability of breeding is a complicated physiological function reflecting body fat accumulated over the several months before breeding and, perhaps more importantly, nutrition at the time of breeding (Bronson and Manning 1991, Gerhart et al. 1997, Cook et al. 2013). Thus, in ecological settings where precipitation and temperature are considerably more variable during late summer and early autumn than in our region (e.g., DeYoung et al. 2018), the relationships between pregnancy and percent area by DDE class may be substantially more variable. Second, a more robust analysis would have been to quantify nutritional resources using metrics that included elk density on ranges for various DDE levels, rather than simply percent of area by DDE levels (Figs. 12, 13). Estimates of elk density were unavailable for most of our population ranges, and the markedly different sizes of elk ranges in our sample precluded evaluations based on absolute area, rather than percent of area. If elk populations were considerably larger, then a substantially greater percent of area with DDE > 2.75 kcal/g may be required to support high levels of pregnancy and body fat.

In the following sections, we highlight a number of concerns, caveats, and justifications for the nutrition model and the approach we used to evaluate its reliability. First, the nutrition model is not a carrying-capacity model. For example, a vegetation community with 1,000 kg/ha of accepted forage may provide nutritional levels (DDE and intake rate of digestible energy) identical to those in a similar community but with 500 kg/ha of accepted forage. Clearly, the former would support more elk. Our model thus predicts the levels of nutrition that elk are likely to acquire under the conditions of the study, not the number of elk that potentially might be supported (see Cook et al. [2016] for additional comments regarding carrying capacity and density-dependent versus density-independent food limitations in our study region).

Second, instead of comparing predicted versus observed DDE using independent data as is normally the case for model evaluation, we compared higher-order responses of free-ranging elk (i.e., habitat use, body fat, and pregnancy rates at broad scales) with predicted DDE. We consider the latter approach to be a more useful evaluation strategy than the former (Babin et al. 2011) because it directly evaluates the ability of the model to address higher-order, broad-scale processes despite the fine-scaled data used to develop the model. After all, it is the higher-order processes that really matter. If the nutrition model was invalid (i.e., unable to predict DDE with reasonable accuracy in areas beyond those where it was developed) or inaccurate (e.g., derived from GIS layers with insufficient accuracy or resolution for the predictor variables used), it is likely that 1) DDE predictions from the nutrition model would have been poorly related to nutritional resource selection (Fig. 11); 2) the DDE covariate in the habitat-use model (see Rowland et al. 2018) would have played a minor role compared to the other covariates in the model (other habitat and topographic features, anthropogenic disturbance); and 3) performance of free-ranging elk would have been poorly correlated to DDE (Figs. 12 and 13). Such was not the case for any of these criteria.

Third, many other measures of animal performance could have been used for evaluating the model, including those that largely reflect the direct influences of nutrition on performance (e.g., growth rates of juveniles and subadults, age at first breeding, timing of ovulation and breeding, neonatal calf size; Cook et al. 2004) and those that may or may not be directly influenced by nutrition (e.g., survival and recruitment rates, population trends). Adequately detailed data for these variables were not available for our analysis (see Cook et al. 2013). Further, the value of survival and recruitment rates as evaluation criteria for a nutrition model is potentially greatly confounded by many factors unrelated to nutrition (e.g., predation and hunting). We used body fat and pregnancy rates only for lactating females because their nutritional requirements are greater and thus their performance is markedly more sensitive to nutrition than are non-lactating adult females (Gerhart et al. 1997; Cook et al. 2004, 2013).

Fourth, captive ungulates have never before been used to develop large-scale nutrition models. Important disadvantages of using captive animals exist (e.g., high expense, concerns about disease, challenging field logistics, increasing regulatory limits on holding and transporting). However, their advantages are considerable, mainly by helping to reduce uncertainty about the relationships between vegetation attributes and nutrient content of diets and intake rate of nutrients over various time scales. This advantage is particularly true in structurally and floristically diverse plant communities, where bite mass, nutrient content, and plant defensive compounds may be highly heterogeneous among species and may have influences on elk foraging and nutrition that are difficult to predict (Cook et al. 2016). The detailed analysis of relationships between nutrition and vegetation characteristics using captive elk by Cook et al. (2016) explicitly identified those nutritional currencies that were most limiting, what vegetation characteristics accounted for these limitations, and those attributes of vegetation communities that nutrition modeling and habitat management programs should emphasize. That analysis greatly reduced the likelihood of a nutrition model constructed using nutritional currencies and vegetation characteristics that were not particularly relevant to elk in our ecological setting. Questions about the reliability of captive animals as proxies of wild animals have been answered with multiple ungulate species in a variety of studies (Yarrow 1979, Austin et al. 1983, Olsen-Rutz and Urness 1987, Spalinger et al. 1997). The considerable value of using captive animals for foraging studies was discussed by Hester et al. (2000) and Cook et al. (2016).

Fifth, there may be several vegetation community types in which our model is relatively inaccurate. The data collected in hardwood stands typically dominated by red alder (*Alnus rubra*) were mostly at Nooksack on very wet soils (Cook et al. 2016), but alder and other hardwood species also may dominate on substantially drier sites, particularly in the southern area of our study region (Franklin and Dyrness 1988). Thus the hardwood covariate may be less reliable in these drier settings. In addition, high elevation forest vegetation types that are substantially drier, less productive, and support markedly different plant composition than those sampled by Cook et al. (2016) exist in the southern Cascades (Franklin and Dyrness 1988). We expect that our nutrition model may overestimate DDE in these communities. Moreover, our assumption that overstory canopy cover was a suitable surrogate for tracking succession applies to early-seral stages soon after stand-replacing disturbance as conifers regenerate, but may not hold for mid-successional areas after partial harvests (e.g., commercial thinning). Our model may overestimate DDE in these stands. Our DDE equations probably are unreliable for treatments that alter chemical composition of plants (e.g., fertilization) or replace native vegetation with exotic species (e.g., seedings of legumes on food plots).

Sixth, accuracy of our forage prediction equations depends on the accuracy of existing spatial data that we used as inputs (e.g., overstory canopy cover, PNV zone). Our analyses suggested errors due to inaccurate input data smooth out at broad scales, but errors may be of greater concern at relatively fine scales. The DDE prediction equations in the Westside nutrition model can be used at fine scales, for example to evaluate stand-level effects on DDE of different forest management prescriptions (Wisdom et al. 2018*b*). There are 2 methods of application that may differ in reliability. The first uses field measurements of overstory canopy cover and proportion of hardwoods from individual stands ($\geq$1 ha in size) with the biomass and DDE equations to predict DDE for a variety of fine-scale applications. In contrast, using field-sampled estimates of forage biomass (e.g., by SB, AB, NB classes) to predict DDE should be more accurate than the former and may be most useful for evaluating effects of a variety of harvesting or silvicultural strategies that are not well-represented in the original data of Cook et al. (2016). For such stand-level evaluations, we recommend that Cook et al. (2016) and Rowland et al. (2013) be consulted.

Seventh, an important step for habitat evaluation and landscape planning models normally extrapolates either inferred or measured nutritional values (DDE in our case) at fine scales across large landscapes. Many approaches may inadequately account for underlying influences of ecological context and vegetation succession and thus may fail to provide a suitable basis to predict future conditions (Haufler 1994, Cushman et al. 2008). For example, land-cover classifications are often based on overstory species composition, but understory vegetation from which herbivores acquire nutrition may be poorly related to overstory species composition. Potential natural vegetation classification systems account for understory vegetation composition, and classification for a site does not change as overstory composition changes (Franklin and Dyrness 1988, Henderson et al. 1992). Further, PNV systems integrate the influences of soils, climate, and landform that can strongly influence vegetation composition, growth, and phenology, and all of these in turn influence forage biomass and quality. For these reasons, we chose to use PNV systems on which to base our nutrition model (Haufler 1994). Large differences in plant composition, phenology, and elk nutrition that existed among PNV zones (Cook et al. 2016) attested to the value of such a classification system for our purposes. Nevertheless, the process of extrapolating fine-scale forage and nutrition data across broad landscapes in ways that are relevant to foraging herbivores needs further evaluation, particularly for areas where high quality, ecological-based vegetation mapping systems are lacking.

Finally, temperature and precipitation patterns during the original data collection (Cook et al. 2016) also could be a source of uncertainty about the veracity of the nutrition model. Weather patterns when the data were collected were very similar to long-term averages, except for precipitation in late summer at Nooksack, thereby suggesting that the nutrition model should represent most years within the region. Nevertheless, the reliability of the model in the face of climate change eventually may become an issue. By 2050, temperatures at least in western Oregon are expected to increase 1.7–3.9°C, annual precipitation is expected to increase slightly, whereas summer precipitation may decline, and the frequency of drier, hotter summers may increase (Dalton et al. 2017). For ungulates, we would predict milder winters, earlier initiation of forage growth in spring, and earlier cessation of growth in summer, thereby reducing forage quality and increasing nutritional limitations in summer (Hebblewhite et al. 2008, Post and Forchhammer 2008). Forage quality levels of the recent past are implicitly included in the nutrition model, providing considerable advantages for nutritional resource evaluations under current climate (i.e., detailed forage quality and quantity surveys are not needed to use the model). However, this advantage renders the model invariant to changing climate, and changes in summer climate may reduce the reliability of the model for the Westside region. Nevertheless, we posit that the model should predict at least relative nutritional differences among PNV zones and successional stages with reasonable accuracy despite at least some changes in climate because many of the differences in nutritional responses among these were due to strong differences in plant composition and differences in precipitation and temperature along elevation gradients. We base this conclusion on the assumption that species composition and elevational influences on temperature and precipitation will largely remain unchanged over the medium term ($\leq$2050).

The science associated with incorporating nutritional ecology of ungulates into habitat evaluation and landscape planning models has been relatively slow to develop. Past use of various untested surrogates of nutrition is increasingly criticized (Searle et al. 2007). Assessing only forage quantity excludes the influences of forage quality and would certainly be inadequate for modeling elk nutrition in the Westside region. Even the assumption that estimates of forage quality and quantity combined provide a reliable means to predict dietary quality and nutrient intake rates of herbivores is generally untested. The strength and consistency of explicit relationships between forage and nutritional outcomes largely remain unevaluated for chemically and structurally complex plant communities (Spalinger and Hobbs 1992, Cook et al. 2016). Finally, measures of nutrition variables most suitable for indexing nutritional value also are uncertain. That DE is more important in ungulate nutritional ecology than protein is supported by others (Skogland 1991, Illius and Gordon 1999, Searle et al. 2007), but debate about protein versus DE nevertheless is ongoing (McArt et al. 2009), and their relative importance may vary among ecological settings. Also, instantaneous and daily intake rates of food or nutrients are classically considered for relating forage conditions to higher-order processes of animal performance and distribution (Fryxell 1991, Spalinger and Hobbs 1992, Searle et al. 2007, Babin et al. 2011).

For our ecological setting, where overall forage quality tended to be relatively low and total forage biomass quite high, forage intake rates were largely invariant across a wide variety of ecological and successional states (Cook et al. 2016). Thus, the most suitable nutritional currency for modeling nutritional resources may strongly depend on characteristics of soils, climate, and vegetation among ecological settings. By using captive elk to identify appropriate covariates and nutritional currencies for modeling, it should be well-tailored to the Westside region. However, the model may not be robust in different ecological settings. If a similar nutrition model is desired for other areas, choices will have to be made between the reliability that using captive animals offers and other approaches that may not as effectively index nutritional resources.

MANAGEMENT IMPLICATIONS

Our results identified a key role of active habitat management for improving nutritional resources across Westside landscapes. Ecological conditions within PNV zones largely set the lower and particularly the upper limits of DDE, but disturbance and succession strongly influenced DDE levels within these limits. Levels of DDE that satisfied or exceeded basic requirement were restricted almost entirely to early-seral stages following stand-replacing disturbance (Fig. 9), confirming the importance of these communities for elk nutrition (Hett et al. 1978; Merrill 1987, 1994; Jenkins and Starkey 1996; Hutchins 2006). Extent of benefits accrued from vegetation management will vary by elevation. Duration of early-seral areas supporting high levels of DDE was much shorter in the WHZ (15 yr) than in the higher elevation PNV zones (~30 yr in the SFMHZ; Fig. 9). Thus, over the long term, a more aggressive habitat improvement program would be required in the WHZ than in the higher elevation zones to maintain nutritionally adequate landscape mosaics for elk and to support productive elk populations for substantial hunting opportunities.

The primary type of disturbance reflected in our data was clearcut regeneration harvest, although thinning also was evaluated in the WHZ by Cook et al. (2016). Dietary DE levels were modestly elevated but remained below basic requirement in thinned stands, and others reported that vegetation responses to thinning are variable (Alaback and Herman 1988, Thomas et al. 1999) and provide little improvement in forage for elk (Jenkins and Starkey 1996). In the SFMHZ and particularly in the MHZ, the slower rate of succession and the greater dominance of palatable plants even under forest canopies suggest that thinning probably will result in greater increases in DDE that persist longer than in the WHZ (Cook et al. 2016). The management examples provided by Wisdom et al. (2018*b*) also demonstrate the superior nutrition produced from clearcut regeneration harvest versus responses to light commercial thinning.

Prescribed burns and wildfire were not evaluated by Cook et al. (2016), but we predict that nutritional responses after stand-replacing wildfires would be similar to those after clearcut logging, based on early-seral vegetation responses after wildfire described by Franklin and Dyrness (1988; see Proffitt et al. 2016). We also speculate that under-burns in thinned stands may significantly improve forage for elk compared to thinned stands that have not been burned, by reducing unpalatable evergreen shrubs and ferns, and increasing growing space for palatable plant species.

As a result of the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994*a*, *b*), constraints to forest management on public lands may represent significant opportunity costs for production of elk. Our summaries indicate private landowners (primarily forest products companies) provided substantially more land area with levels of nutrition that at least satisfy basic requirement (i.e., >2.58 kcal/g): 32% in the WHZ on private lands mainly due to clearcut logging versus 7% of area of federal public lands due to cessation of timber harvest beginning by the mid-1990s (Wisdom et al. 2018*a*). Within PNV zones at higher elevations (SFMHZ), the percent area providing DDE >2.58 kcal/g of nutrition was less divergent among the landowners (39% on private lands and 29–34% on federal lands). These differences were primarily due to overall higher DDE, slower forest succession, and presence of non-forested alpine vegetation in some areas (for which our model predicted very high levels of DDE). Our data suggest that stand-replacing disturbance provides important opportunities to improve nutritional resources significantly even in the driest communities in the WHZ, although the greatest opportunities for providing high nutrition are in the wetter, cooler communities in the WHZ and particularly in the SFMHZ at higher elevations. The USFS is the predominant land manager of these high-elevation lands (Fig. 16) with greatest potential to support productive elk populations. Where opportunities exist for forest management on high-elevation ranges, these should be carefully planned to effectively bolster their nutritional value for elk, if providing good habitat for elk is a management priority.

Linking Nutrition With Landscape Features in a Regional Habitat-Use Model for Elk in Western Oregon and Washington

MARY M. ROWLAND, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RYAN M. NIELSON,[1] *Western EcoSystems Technology (WEST), Inc., 2121 Midpoint Drive, Suite 201, Fort Collins, CO 80525, USA*
MICHAEL J. WISDOM, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
PRISCILLA K. COE,[2] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
JOHN G. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
JENNIFER M. HAFER, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
BRUCE K. JOHNSON,[2] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
BRIDGETT J. NAYLOR, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RACHEL C. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
MARTIN VAVRA,[2] *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
DAVID J. VALES, *Muckleshoot Indian Tribe, 39015 172nd Avenue SE, Auburn, WA 98092, USA*
ROBERT G. ANTHONY,[†] *Oregon State University, 1500 Southwest Jefferson Way, Corvallis, OR 97331, USA*
ERIC K. COLE, *U.S. Fish and Wildlife Service, National Elk Refuge, P.O. Box 510, Jackson, WY 83001, USA*
CHRIS D. DANILSON,[3] *Washington Department of Fish and Wildlife, Region 4, 111 Sherman Street, La Conner, WA 98257, USA*
FRANK GEYER, *Quileute Tribe, 401 Main Street, La Push, WA 98350, USA*
SCOTT HARRIS, *Washington Department of Fish and Wildlife, 48 Devonshire Road, Montesano, WA 98563, USA*
ROBERT MCCOY, *Makah Forestry, P.O. Box 116, Neah Bay, WA 98357, USA*
MICHAEL D. POPE, *Greenbelt Land Trust, P.O. Box 1721, Corvallis, OR 97339, USA*
KIM SAGER-FRADKIN, *Lower Elwha Klallam Tribe Natural Resources, 760 Stratton Road, Port Angeles, WA 98363, USA*

INTRODUCTION

Studies that reveal habitat selection and use by wildlife—especially large mammals—are foundational for understanding their ecology and management, especially if predictors of use can be linked to demography or fitness. Many ungulate species not only serve societal needs as game animals or tribal foods (McCabe 2002, Vales et al. 2017) but also affect native vegetation and agricultural crops because of their large body size, diet choices, and extensive distributions (Hobbs 1996, Schoenecker et al. 2004, Wisdom et al. 2006). Improved understanding of habitat relationships of large mammals, such as elk, can inform current wildlife conservation and management (Fortin et al. 2008) and provide a framework for evaluating future hypothesized environmental conditions (e.g., under climate change; Hebblewhite 2005, Durner et al. 2009). Habitat studies are often fraught with challenges, from inconsistent terminology to choosing research designs and metrics that properly evaluate use or selection (Garshelis 2000, Gaillard et al. 2010, Morrison 2012). We adopt a niche-based definition of habitat (i.e., functional habitat) that includes the resources and environmental conditions that lead to a given level of performance (Hutchinson 1957, Hall et al. 1997, Gaillard et al. 2010). We chose to model intensity of habitat use, rather than habitat selection, in part because it captures not only the probability of selection but also how often a specific resource is encountered (Lele et al. 2013; see section Methods).

A key challenge in managing broadly distributed species like elk is to correctly identify the ecologically relevant variables that most influence habitat use. These variables can be integrated to generate landscape-level predictions of how animal distributions respond to different patterns of land management and habitat attributes over time and space. Habitat characteristics that drive spatial and temporal patterns of elk distributions have been studied since the 1970s, initially in response to widespread timber harvest, livestock grazing, and road construction across landscapes supporting important elk habitat in the western United States (Leege 1984, Lyon et al. 1985). Biologists used these findings to develop a diverse suite of elk habitat models (e.g., Lyon 1979; Thomas et al. 1979, 1988; Wisdom et al. 1986; Roloff 1998; Unsworth et al. 1998).

Contemporary analytical approaches to modeling habitat use and resource selection (Manly et al. 2002, Johnson et al. 2006, Long et al. 2008, Nielson and Sawyer 2013), coupled with the increasing availability of broad-scale spatial data and large telemetry data sets (Frair et al. 2010), have facilitated development of more advanced, spatially explicit models of elk

---

[1] *Current affiliation: Eagle Environmental, Inc., 30 Fonda Rd., Sante Fe, NM 87508, USA.*

[2] *Retired.*

[3] *Current affiliation: Washington Department of Natural Resources, Northwest Region, 919 North Township Street, Sedro-Woolley, WA 98284, USA.*

[†] *Deceased.*

distributions and habitats (e.g., Johnson et al. 2000, Coe et al. 2001, Boyce et al. 2003, Sawyer et al. 2007, Proffitt et al. 2010). Moreover, previously unavailable predictors such as phenology-based metrics of greenness (Hebblewhite et al. 2008, Bischof et al. 2012) or LiDAR-based measures of forest structure (Ewald et al. 2014, Lone et al. 2014) have augmented more traditional model covariates. Research elucidating combined effects of gray wolves and human disturbance (Proffitt et al. 2009) or wolves and climate change (Hebblewhite 2005) on elk further demonstrate the expanding complexity of elk habitat studies. Despite widespread application of elk habitat models in land-use planning (Edge et al. 1990, USDA Forest Service 1990, Christensen et al. 1993), few have been validated with independent data (but see Rowland et al. 2000, Roloff et al. 2001, Benkobi et al. 2004, Sawyer et al. 2007, Coe et al. 2011). Rigorous evaluation of model performance is essential (Johnson 2001, Shifley et al. 2009, Morrison et al. 2012), especially for models guiding public land management decisions that may be challenged in court or applied across thousands of hectares.

A limitation of many prior habitat models for elk and other wildlife species is the appropriate inference space for model application (Morrison 2012). Studies of habitat use or resource selection by animals commonly rely on a single sample of animal locations obtained via GPS or VHF technology. Although some studies span years, most are designed to focus on a specific management question within a limited area, and thus are viewed in isolation. For example, Sawyer et al. (2009) monitored changes in mule deer (*Odocoileus hemionus*) distributions in response to development of a gas field, McDonald et al. (2006) identified how northern spotted owls (*Strix occidentalis caurina*) selected nest locations on a large tract of privately owned land, and Goldstein et al. (2010) tracked brown bears (*Ursus arctos*) on the Kenai Peninsula, Alaska to evaluate the potential for human recreation to disturb denning females. Inferences from these single studies are constrained in both space and time; very few studies focus on estimating habitat use across larger populations at spatial extents that cross multiple jurisdictional boundaries.

Similarities among studies in how animals were sampled, data collection protocols, and data quality, however, may allow for synthesis of information on a larger scale. For example, Durner et al. (2009) combined over 19,000 polar bear (*U. maritimus*) locations recorded over 22 years from 8 of 19 polar bear subpopulations to investigate the potential for global climate change to influence the loss of optimal polar bear habitats. In another unique study, Guldemond and Van Aarde (2008) conducted a meta-analysis on 21 studies published from 1961 to 2005 to evaluate effects of elephants (*Loxodonta africana*) on woody vegetation in savanna landscapes.

We can develop more precise estimates of the size of an effect by examining multiple investigations, rather than a single study (Borenstein et al. 2009). Analysis of data from multiple studies with similar data collection techniques, albeit different primary goals, also may reduce dependence on individual studies and identify general animal-habitat relationships that are robust across the sampled populations (Johnson 2002, Borenstein et al. 2009) or that vary along geographical gradients (Fortin et al. 2008). Similar to Durner et al. (2009), we sought to use data from several disparate telemetry studies in a meta-analysis approach to develop a model that identified commonalities in habitat-use patterns across a large geographic range for a single species. However, unlike Durner et al. (2009), we also sought to recognize the hierarchical nature of the animal location data (thousands of locations from dozens of animals within several model development areas) in the variable selection and model estimation process by adopting a 2-stage approach that modeled patterns of use within modeling areas and then summarizing use at a regional level (Fieberg et al. 2010). Further, we recognized that most regional habitat-use models cannot be simultaneously general, realistic, and precise. We chose to focus on generality and realism in our approach, rather than precision (Levins 1966). Such an approach emphasizes qualitative, versus quantitative, results, and is thus more widely applicable within the intended inference space.

The biological hypothesis and predictions guiding our habitat modeling objectives were as follows. We hypothesized that elk habitat use during summer is driven by a suite of interacting covariates related to energy balance: acquisition (e.g., nutritional resources, juxtaposition of cover, and foraging areas), and expenditure (e.g., proximity to open roads, topography). Among covariates, we predicted that nutrition and human disturbance would function as key drivers of elk distribution because of the preponderance of support from the literature on their role in influencing habitat use by elk. Specifically, we predicted that elk would seek areas offering the best nutritional resources but avoid roads because of associated human disturbance and avoid areas far from cover-forage edges because of their preference for foraging sites with secure patches of cover nearby. We also predicted that sites of similar nutritional value might differ in their realized use by elk because of environmental constraints such as human disturbance or rugged terrain. We describe a structured, multi-step process to develop and validate new habitat-use models for elk in in western Oregon and Washington (hereafter Westside), using multiple telemetry data sets. We then report results of applying this process, interpret modeling results, and describe potential implications for managing elk.

Given our overarching hypothesis about elk habitat use and its relation to energy balance, our primary objective was to construct and validate a summer, landscape-scale model of habitat use for elk across Westside land ownerships that integrated ecologically relevant covariates characterizing nutrition, human disturbance, vegetation, and physical conditions. The covariates considered were directly related to elk habitat use (e.g., elk dietary digestible energy), rather than surrogates that could be more difficult to manage or interpret (Sawyer et al. 2007, Wisdom et al. 2018*a*), such as normalized difference vegetation index (NDVI; Hebblewhite et al. 2008, Pettorelli et al. 2011). Our emphasis on summer habitat use was driven by the inadequacy of many Westside vegetation communities to provide sufficient nutritional resources to meet maintenance requirements of lactating elk during summer (Cook et al. 2013, 2016) and the potential to evaluate and address this limitation by developing nutrition and habitat-use models (Cook et al. 2018, Wisdom et al. 2018*a*).

A second objective was to explicitly incorporate mechanistic covariates reflecting concepts of energy balance (Wisdom et al. 2018*a*). Several studies of elk have demonstrated avoidance of humans and predators, which can affect foraging dynamics and resource acquisition (Frair et al. 2005, 2008; Muhly et al. 2010, 2013; Ciuti et al. 2012*a*, *b*; White et al. 2012), as well as movement rates (Hurley and Sargeant 1991, Wisdom et al. 2005*a*, Naylor et al. 2009). A third objective was to develop a robust regional habitat-use model, an outcome possible only if patterns of elk habitat use were consistent across the range of conditions found in the Westside model development areas. Fourth, we wanted to develop a desktop GIS tool for managers to 1) identify locales where nutritional resources and elk use are relatively high or low and 2) evaluate relative improvements in nutritional resources and elk use as a result of management actions at multiple scales and land ownerships (see Rowland et al. 2013, Wisdom et al. 2018*b*).

METHODS

For the Westside elk project, we modeled intensity of habitat use by evaluating elk locations in relation to habitat features (covariates; Gaillard et al. 2010, Nielson and Sawyer 2013), which is considered an analysis of habitat use. This analysis differs somewhat from an analysis of habitat selection (Manly et al. 2002), which Lele et al. (2013:1185) defined to be strictly a "binary [behavioral] decision, with outcomes of use or non-use of a resource unit." Such behavioral decisions result in patterns of intensity of use of a habitat or resource unit. The intensity of use depends not only on the probability of selection but also on the frequency with which a specific resource unit will be encountered (Lele et al. 2013). Modeling habitat use along a continuum can provide more information about the relationships between habitat characteristics and probability of use by the animal. This modeling approach reveals where animals are on the landscape and the relative amount of time spent by them in each sampling unit, rather than presence or absence of animals as typically reported in use-availability studies (Manly et al. 2002, Nielson and Sawyer 2013). The habitat-use approach met our primary objective of modeling distributions of elk across land ownerships of the Westside region. We considered our modeling to represent a population-scale analysis; at this scale, spatial variation in habitat features should account for differences in elk use (Gaillard et al. 2010).

Defining Areas for Habitat-Use Modeling and Validation

We obtained elk locations from several studies, most spanning multiple years, conducted during 14 years in the Westside region (Fig. 17; Tables 1 and 7). We identified 13 independent capture efforts and associated telemetry data sets from these studies for use in model development and validation (Tables 1 and 7). All wild elk used in our analyses ($n = 173$) were adult females captured and fitted with GPS or VHF collars, and locations were obtained systematically at intervals ranging from 20 min (GPS) to 1 week (VHF). Locations for GPS collars were recorded automatically at shorter intervals, whereas those for VHF collars were obtained via ground or aerial triangulation at least weekly. For GPS collars, location accuracy was high and precision was typical of such collars (<100 m; Hebblewhite and Haydon 2010, Tomkeiwicz et al. 2010); fix success (range: 93–98%; Table 7) and relocation frequency (15–20 min in all but the Pysht data set, which was every 4 hr) were also high. We limited our analyses to elk subjected to autumn hunting pressure, which represents most Westside elk populations, thus excluding telemetry studies for non-hunted elk that resided entirely within national park boundaries or suburban areas. Prior studies have documented that responses of these elk to human disturbance would likely be different and affect predictions of habitat use (Thompson and Henderson 1998, Haggerty and Travis 2006, Stankowich 2008, Starr 2013).

From each data set, we selected elk locations recorded between 1 June and 31 August to define the summer modeling period (Wisdom et al. 2018*a*). We excluded telemetry data that overlapped hunting and rutting periods because elk movements and habitat use may change substantially during those times (Conner et al. 2001; Johnson et al. 2005; Storlie 2006; Proffitt et al. 2010, 2013). Thus, predictions of the habitat-use model do not extend beyond August, when several hunting seasons begin in western Oregon and Washington, including archery hunts for elk and rifle hunts for black-tailed deer. All animal handling was conducted following regulations set forth for implementing the Animal Welfare Act of 1966 and its subsequent amendments and adhered to standards adopted and published by the American Society of Mammalogists (Sikes et al. 2011).

We chose 5 of the GPS data sets for model development because of their superior quality, as noted previously. We used these telemetry data sets to delineate 5 areas for habitat-use modeling (modeling areas; Table 1). Although some GPS collars were programmed to collect locations frequently (e.g., every 15 or 20 min; White River 2004, 2005, 2007), we followed the advice of Kernohan et al. (2001) and assumed independence between locations to avoid constraining estimates of the local (population-level) seasonal ranges.

We defined perimeters of the 5 areas used for habitat model development based on 99% contours for fixed kernel density estimates (KDEs; Wand and Jones 1994) using Hawth's Analysis Tools (v3.27 ArcGIS extension, http://www.spatialecology.com/htools, accessed 5 Apr 2009) with smoothing parameter $h = 1,000$ (default). Model development areas were located in 3 regions of Washington (Pysht, Green River, and White River; Table 1) and ranged in size from 7,135 ha (Pysht 2009) to 35,019 ha (White River 2007; Table 7; Appendix A). Some modeling areas overlapped modestly (Fig. 17), but each was defined by a unique year and capture effort. For example, the Muckleshoot Indian Tribe collared 13 elk in the White River drainage of western Washington in early 2004, and those collars were retrieved via animal capture in late 2004 (White River 2004; Table 7). An additional 6 collars were deployed on a new sample of elk in early 2005 (White River 2005). Then in 2007, another sample of 13 elk was captured and fitted with GPS collars within the same region (White River 2007).

We used the remaining 8 independent elk data sets for model validation and calculated MCPs to delineate model validation areas (Fig. 17; Table 1). These averaged 23,226 ha and ranged from just over 2,700 ha (Quileute 2006–2008) to 53,630 ha (Green-Cedar 2006–2009). We used MCPs rather than KDEs to define validation areas because data collection in these sites was most often with VHF collars, which provided fewer and less-precise locations. The MCPs were more robust to the smaller sample sizes of many of our validation data sets and included more available area compared to KDEs. Further, we anticipated that when biologists or managers used our models, they would

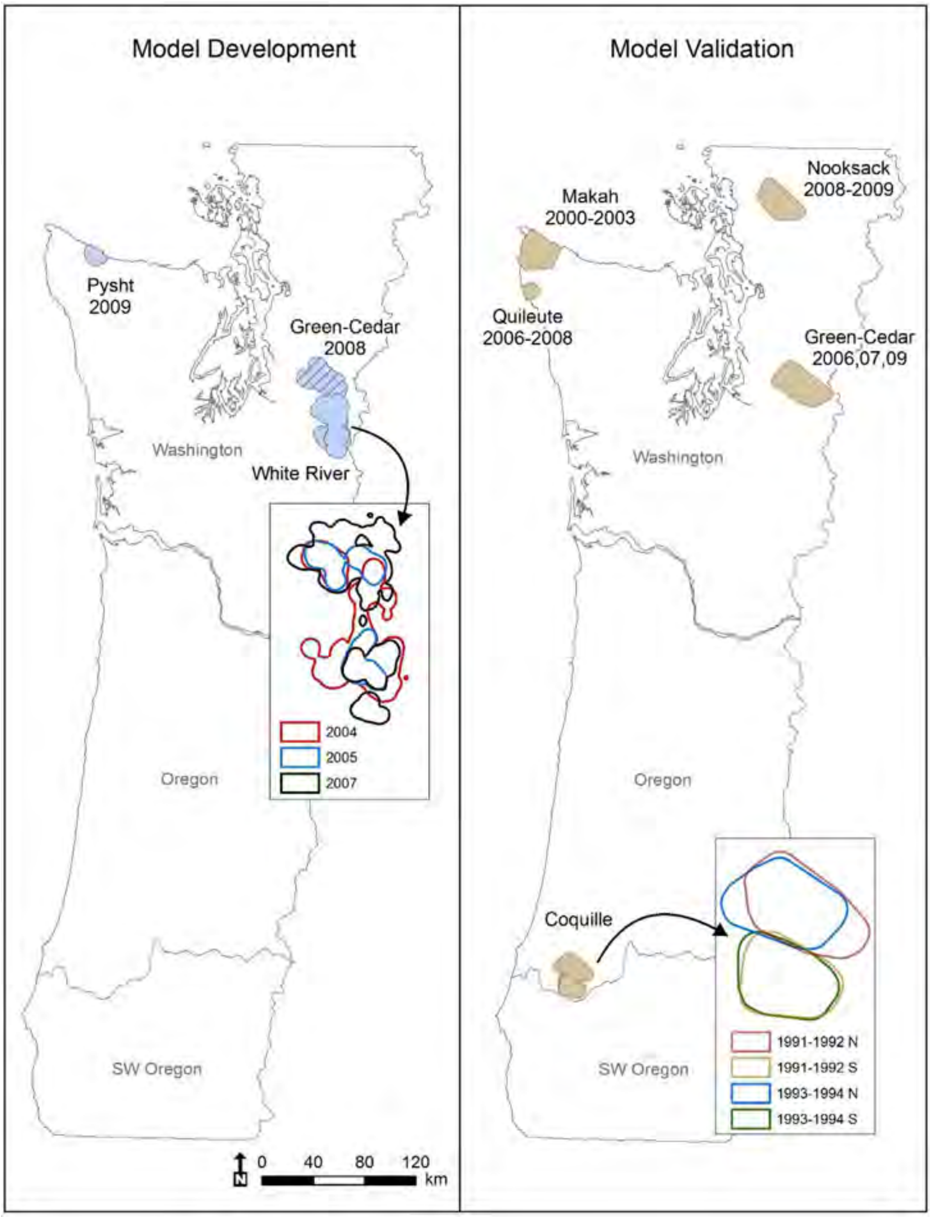


Figure 17. Western Oregon and Washington, USA (Westside region) and areas associated with telemetry data sets used for elk habitat-use model development (left) and validation (right).

seldom create kernels based on a representative sample of elk in the area but instead would identify project areas or larger regions. Collectively, these validation areas represented a diverse cross-section of environmental conditions in the Westside region (Appendix A).

Development of Habitat-Use Models

We adopted a hierarchical modeling approach by considering individual model development areas as replicates in generating a regional habitat-use model. This approach is analogous to that of treating individual animals as the primarily sampling units when creating a population-level model for a single study site (e.g., Sawyer et al. 2006, Fieberg et al. 2010). We used a 4-step process to develop a regional elk habitat-use model by 1) measuring covariates at systematically selected circular sampling units within each habitat-use modeling area, 2) estimating the relative frequency of use in the sampling units for all collared elk within each modeling area during summer, 3) modeling the relative frequency of use as the response variable in a generalized linear model (GLM) using a negative binomial (NegBin) habitat-use model, and 4) averaging coefficients across modeling areas to generalize habitat relationships and develop a regional model.

Following identification of population-level seasonal ranges for each data set, we took a systematic sample, based on a random starting location, of non-overlapping circular sampling units with 350-m radii from each modeling area (Sawyer et al. 2006, Nielson and Sawyer 2013). We then calculated the number of elk locations within each sampling unit (Fig. 18) along with values of covariates of interest (Appendix B). Center points of all sampling units were within a KDE, but portions of some circles may have fallen outside the 99% contours. These sampling units provided the response (number of elk locations) and covariates for

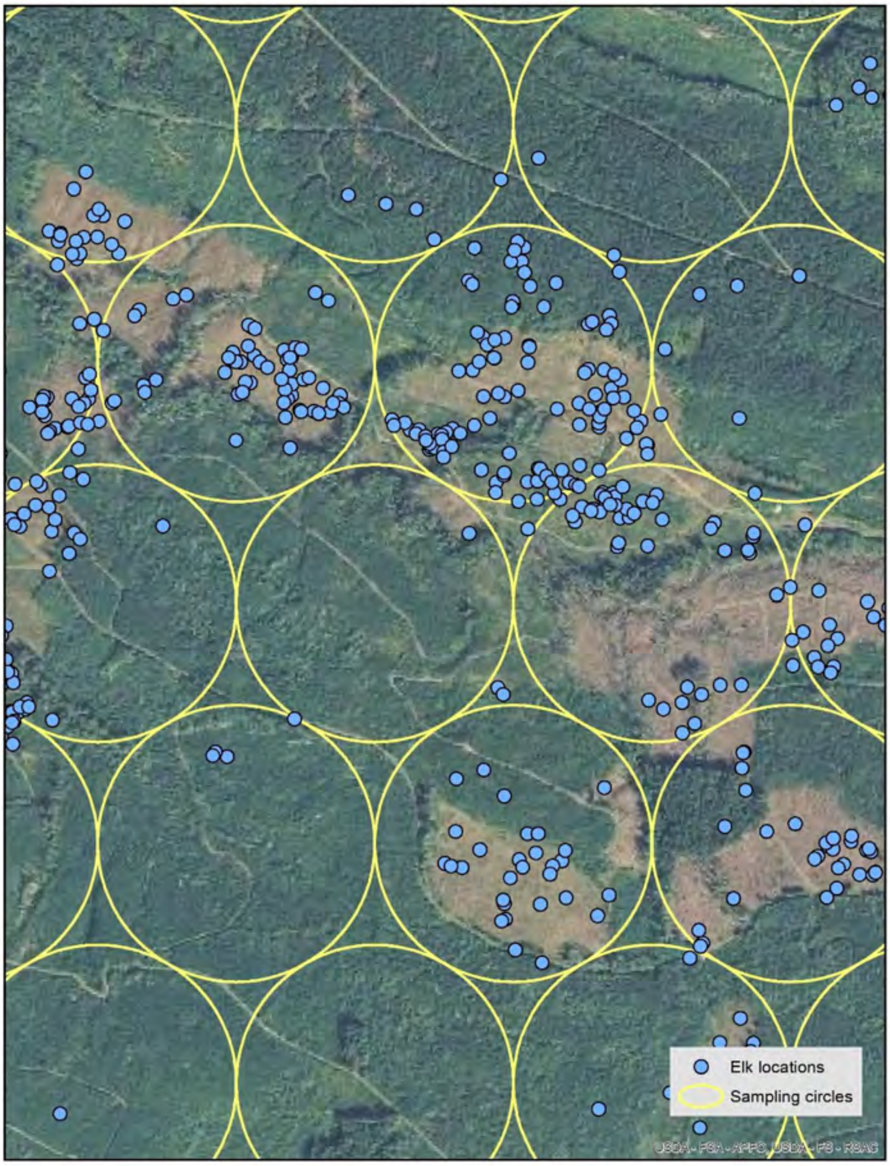


Figure 18. Example of a systematic sample of circular sampling units and elk telemetry locations.

estimating the habitat-use model. The number of sampling units for each modeling area ranged from 166 (Pysht 2009) to 805 (White River 2007). Nielson and Sawyer (2013) recommended choosing a sampling unit that is small enough to detect changes in animal movements while providing counts of locations that approximate a negative binomial distribution. During pre-analysis investigations, we considered sampling units of various sizes and determined that a 350-m radius circle was appropriate, largely based on the distribution of the number of GPS locations within the units, landscape heterogeneity, and mobility of sampled animals during summer. In addition, we ensured that the size of the sampling units exceeded the inherent error in GPS locations and in covariate layers considered during modeling (Nielson and Sawyer 2013).

We used a GLM to estimate the intensity of use for each modeling area as a function of covariates using the NegBin habitat-use model. This method is described by Nielson and Sawyer (2013) and is also found in Millspaugh et al. (2006) and Sawyer et al. (2006, 2007, 2009). We considered a Bayesian hierarchical model estimated via Markov chain Monte Carlo methods, but the combined size of our data sets and the complexity of our model development process precluded use of this modeling approach because of its computational demand. We also attempted to fit a generalized linear mixed model with random effects for model development areas, but we experienced convergence issues even with the simplest models; thus we adopted a 2-stage approach to estimating a regional elk habitat-use model (Fieberg et al. 2010).

Potential for habitat-induced data loss (Frair et al. 2004, 2010; Nielson et al. 2009) was not a concern in modeling because of the high GPS fix success during the summer period (Table 7). All GPS fix schedules covered the 24-hour period during summer. We were not interested in creating a foraging-period model because our goal was to develop a more general habitat-use model that integrated multiple covariates, not just nutrition, to predict elk distributions. Moreover, we could not restrict our analysis to periods presumed to capture foraging (e.g., crepuscular hours) because we would have been forced to discard all VHF data, which was largely diurnal (Table 7). Large numbers of locations recorded at regular intervals (e.g., 15–20 min), as was true for all but one of our GPS telemetry data sets, can result in counts of use within the circular sampling units that are quite large (hundreds or thousands). Although the NegBin is not influenced by temporal autocorrelation in animal locations, too many locations within some of the circular sampling units can result in counts of use that are not NegBin distributed (Nielson and Sawyer 2013). Thus, we elected to use at most the first location obtained every hour.

The NegBin involves regressing the number of animal locations within each circular sampling unit onto the covariates measured on those units. We applied the model in each individual modeling area; it was based on the commonly used NB2 formulation of this function (see below; Cameron and Trivedi 1998), which can be represented by

$$\ln[E(t_i)] \approx \ln(T) + \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} \ldots + \beta_p x_{pi} \qquad (1)$$

where t_i is the number of GPS locations within sampling unit i, E represents the expected value, T represents the total number of GPS locations within the modeling area, β_0 is an intercept term, $\beta_1, \beta_2, \ldots, \beta_p$ are coefficients to be estimated, and $x_{1i}, \ldots, x_{pi}$ are the values of p covariates measured on sampling unit i. Inclusion of the offset term, ln(T), in Equation (1) simply scales the response to ensure modeling of relative frequency, or intensity of use (e.g., 0, 0.003, 0.0034, ...) instead of integer counts (e.g., 0, 1, 2, ...; Nielson and Sawyer 2013). We used the natural log of the number of locations obtained from a particular modeling area in summer as the offset term in Equation (1). The errors follow a negative binomial distribution.

Various NegBin model parameterizations exist, and distinctions are made based on the link function used and the assumed distribution of var(Y). The NB2 (log link) is the most common parameterization (Cameron and Trivedi 1998), which specifies that $\mathrm{var}[Y] = u + u^2/\theta$ (Hilbe 2008). The term var[Y] is the variance of the observed count of use (Y), u is the expected count of use, and theta (θ) is the dispersion parameter. The likelihood for the NB2 formulation can be found in Cameron and Trivedi (1998:71).

Covariate derivation and selection.—We developed an *a priori* list of potential landscape variables (covariates) by reviewing previously published elk habitat models (e.g., Wisdom et al. 1986, Edge et al. 1987, Roloff 1998, Sawyer et al. 2007). We initially considered >30 covariates (Appendix B, Table B1), but consultation with biologists and land managers helped us refine our list (Tables B2 and B4) by identifying factors believed to affect local elk populations and those most likely to be manageable (e.g., plant community attributes such as acceptable biomass or canopy cover) or easier to derive accurately and efficiently (e.g., roads open to the public vs. estimates of vehicle traffic).

We grouped covariates into 4 categories to predict elk habitat use: 1) nutrition, 2) human disturbance, 3) vegetation, and 4) physical (Fig. 19). Our initial process of covariate selection and reduction resulted in 6 nutrition covariates, 10 human disturbance covariates, 11 vegetation covariates, and 13 physical covariates for evaluation (Appendix B, Table B1). Nutrition covariates reflected potential energy accrual, whereas human disturbance covariates generally reflected energy costs, such as flight responses to motorized traffic. Vegetation covariates may correspond to either energy gain or loss (for example, higher quality and abundance of forage in open-canopy forests versus energy costs incurred in traveling to distant cover patches). Likewise, physical covariates may relate to energy balance, such as increased energetic costs when traveling on steep slopes (Kie et al. 2005) versus thermal benefits of north aspects in summer (Ager et al. 2003). Although physical covariates like aspect cannot be managed directly, we retained this group because these features have been consistent predictors of habitat use by elk in prior studies (Johnson et al. 2000, Ager et al. 2003, Sawyer et al. 2007,

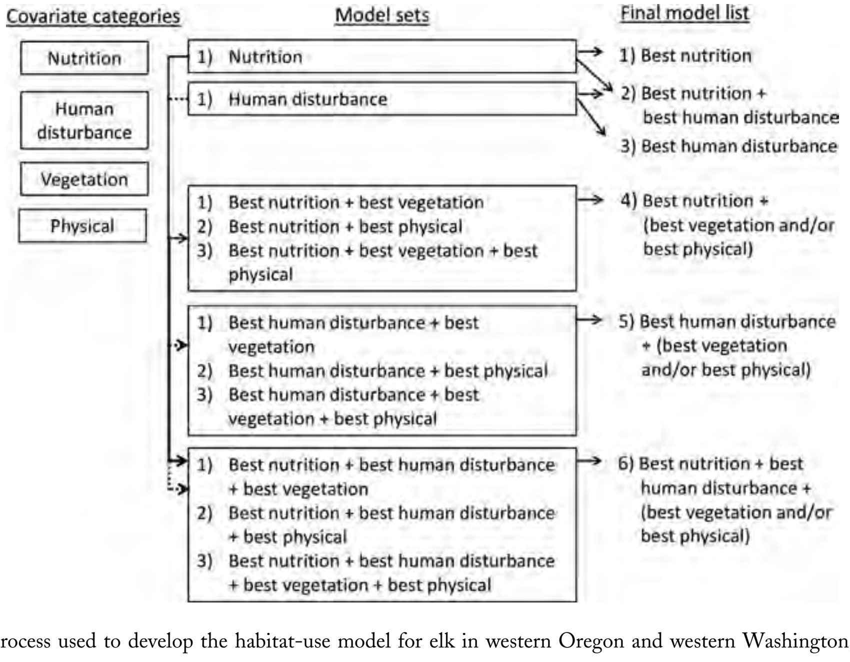


Figure 19. Description of the process used to develop the habitat-use model for elk in western Oregon and western Washington, USA.

Barbknecht et al. 2011, Coe et al. 2011, Harju et al. 2011) and provide context for model predictions. We also modified some covariates, such as canopy cover, when required to match the vintage of associated elk telemetry data. When telemetry locations spanned multiple years for a single data set, we selected covariate values from the year in which most elk locations were obtained (Appendix B).

We calculated covariate values within each cell on a 30-m × 30-m grid encompassing our modeling areas, using either the average (e.g., mean slope), percent coverage (e.g., percent canopy cover), or distance from the center point of each 350-m radius sampling unit (e.g., distance to nearest forage patch). Distance to nearest road open to public motorized use (distance to open road) was based on grids extending 4 km beyond the modeling area boundaries. Our intent was to account for elk reacting to roads close to, but outside, the defined modeling area. The 4-km buffer for distance to open road was based on earlier studies (e.g., Rowland et al. 2000, Sawyer et al. 2007) and preliminary analyses suggesting elk did not respond to roads beyond 4 km. Thus, if distance to nearest open road was >4 km, distance was truncated at 4 km for analysis. Similarly, the distance to nearest cover-forage edge covariate (distance to edge; Appendix B) accounted for edges outside the modeling area but within 4 km of the boundary. Before analysis, we removed circular sampling units centered on or encompassing >38.5 ha (50% of the circle) of a land cover type considered non-habitat, such as rock, water, ice, or development-urban (Appendix B, Table B3).

We derived some covariate layers in a GIS with >1 data source, which allowed us to compare sources (e.g., X*a* and X*b*) and qualitatively evaluate their accuracy. If we thought a data source had potential for large errors, or errors appeared small but inconsistent on a regional scale, we dropped the covariate derived from that source. To further screen covariates, we used histograms to identify substantial differences in distributions of covariates between data sets or across the larger regional landscape. These differences could indicate potential problems in either identifying a common relationship between elk habitat use and that covariate, or applying our final elk habitat-use model(s) to the region. With large differences in distributions, we would err by predicting elk habitat use outside the range of the data used for model estimation (Neter et al. 1996). Thus, if we identified a marked difference in distributions across data sets, we dropped the covariate.

We used a pairwise correlation analysis to further reduce the number of covariates in each category prior to modeling, which diminished the potential for deleterious effects of collinearity on model estimates. If ≥2 covariates had a Pearson's correlation coefficient of $|R| > 0.6$, we took 1 of the following approaches to reduce chances of collinearity destabilizing the NegBin model: 1) we dropped 1 of the 2 correlated covariates; 2) we did not allow both covariates to enter the same model together; or 3) we carefully monitored model estimates to ensure that model stability was not compromised. If 2 or more covariates were highly correlated, and 1 was clearly easier to derive and interpret and had more relevance to management, we retained only that covariate and dropped the other(s) prior to modeling. However, if this choice was unclear and the correlated covariates were in the same category (e.g., nutrition, physical), we allowed only 1 of the covariates to enter the model based on support in the data according to Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Although a pairwise correlation analysis prior to modeling is useful for identifying potential multicollinearity issues, smaller pairwise correlations can affect model estimates, and the method cannot identify scenarios where the linear combination of 2 or more model covariates is correlated to another covariate. Major changes in estimates of coefficients (e.g., negative to positive) and likelihood-based estimates of standard errors (small to large) provide direct evidence of multicollinearity issues. Thus, we carefully monitored estimates of coefficients and standard errors during the model building procedure to ensure that multicollinearity was not influencing model estimates.

Model selection.—With our refined set of covariates, we fit a univariate model for each covariate within a covariate category, such as physical, to data from each habitat modeling area. We discarded covariates if AIC results revealed inconsistent coefficients across study areas or confidence intervals spanned 0. We then ranked the remaining models by AIC values. A rank of 1 indicated the model had the lowest AIC score in the category. Finally, we summed ranks of models within each category across modeling areas to identify the consistently best model for that category (lowest AIC rank). For example, consider a covariate category with 3 univariate models, for which AIC ranks indicate that model 1 has a rank of 1 in 3 of the 5 habitat-use modeling areas and ranks of 2 and 3 in the 2 remaining areas. Thus, model 1 has a sum of ranks = 8 ($3 \times 1 + 2 + 3$). If models 2 and 3 have summed ranks of 10 and 12, respectively, then model 1 has the most support from the data. Using this approach, rather than the sum of likelihoods or AIC values, gives equal weight to each data set in identifying the best models. The ranks also highlight differences and similarities across modeling areas.

We used a 2-stage information-theoretic approach (Burnham and Anderson 2002, DeVore et al. 2016) in model development. This approach allowed us to avoid evaluating all possible combinations of covariates as competing models without regard to their ecological meaning or intended uses, and ensured that we primarily considered mechanistic covariates relevant to management. First, we identified sets of candidate models that combined covariates from different categories (Fig. 19). Then, we fit each model within a model set to telemetry data from each habitat modeling area (Table 7) and ranked the models by AIC values, as described previously for covariate selection. The lowest of the summed ranks of individual models within each model set across modeling areas identified the consistently best model.

Following identification of the top model within each set, we created a final model set by combining the competitive models from each set representing the best nutrition, human disturbance, vegetation, and physical models. This process resembled that of Beck et al. (2006) in developing habitat models for elk based on alternative explanations of factors influencing selection such as forage and distance to roads versus forage and topography. We required that each model in the final list contain either the best nutrition or best human disturbance model. This decision was based on our confidence that nutrition and human disturbance had stronger mechanistic support than other covariate groups (vegetation and physical). These covariates have clearly demonstrated relationships to ecological processes of energy

Table 7. Telemetry data used to develop and validate elk habitat-use models in western Oregon and Washington, USA.

Model use	Data set (study area and year)	Technology[a]	Number of animals	Number of locations	Fix success[b]	Data source
Development	Green-Cedar 2008	GPS	17	26,480	94	Muckleshoot Indian Tribe
	Pysht 2009	GPS	6	3,228	97	Lower Elwha Klallam Tribe
	White River 2004	GPS	13	28,355	93	Muckleshoot Indian Tribe
	White River 2005	GPS	6	11,923	97	Muckleshoot Indian Tribe
	White River 2007	GPS	13	28,692	98	Muckleshoot Indian Tribe
Validation	Coquille North 1991–1992	VHF	16	316		Oregon State University
	Coquille North 1993–1994	VHF	20	180		Oregon State University
	Coquille South 1991–1992	VHF	13	225		Oregon State University
	Coquille South 1993–1994	VHF	15	113		Oregon State University
	Green-Cedar 2006, 2007, 2009	GPS	23	69,150	96	Muckleshoot Indian Tribe
	Makah 2000–2003	VHF	21	820		Makah Indian Tribe
	Nooksack 2008–2009	GPS	7	3,618	88	Nooksack Indian Tribe
	Quileute 2006–2008	GPS	3	14,686	94	Quileute Tribe

[a] Global positioning system (GPS) or very high frequency radio telemetry (VHF).

[b] Mean fix success of GPS collars, reported as percentage of attempted locations for which a successful location was obtained. Not applicable for VHF collars.

acquisition (nutrition) or energy loss (human disturbance) and can be manipulated by managers to change habitat use by elk. There is less empirical evidence of underlying mechanisms for patterns of elk use in relation to vegetation covariates. Moreover, some vegetation covariates were predictors in the nutrition model (e.g., overstory canopy cover), and thus would have been redundant in habitat-use modeling. Our model development process used the AIC ranking procedure described above. In summary, we first identified the best model in each of the 4 covariate categories, and then identified the best models using combinations of these 4 models, culminating in a final list of models from steps 1–4 (Fig. 19).

From the final list of 6 models (Fig. 19), we identified the top-ranked model for each model development area using AIC. We then summed AIC ranks across areas to identify a final habitat-use model for the region. We estimated this regional model (hereafter referred to as the Westside habitat-use model) by averaging coefficients from the final model across the 5 modeling areas. This 2-stage approach (Millspaugh et al. 2006, Fieberg et al. 2010) allowed us to investigate differences in elk habitat use among studies during model development yet synthesize results through meta-analysis of disparate data sets into 1 final regional model for distribution to managers. Although each study-area model represents a measure of probability of use, the regional model based on the average of coefficients from individual modeling areas represents the relative probability of use because predictions from the regional-level model reflect geometric means of study-area probabilities rather than true probabilities (Nielson and Sawyer 2013).

To estimate 90% CIs for coefficients in the Westside habitat-use model, we bootstrapped (Manly 2006) the primary sampling units—individual elk habitat modeling areas—1,000 times and re-estimated regional model coefficients for each sample. We used the central 90% of the 1,000 estimates for each coefficient as the CI (percentile method). We used a similar approach to calculate 90% CIs for coefficients of the 5 individual modeling areas, except the primary sampling units at that level were the collared elk. We followed the premise of Adams et al. (1997), who concluded that bootstrapping methods are more conservative than standard confidence limits for meta-analysis of ecological data.

We evaluated the final model for goodness of fit using the sum of the deviance residuals in a chi-square test (Hilbe 2008). A P-value <0.1 from the chi-square test would indicate lack of fit and the potential that the data were not distributed as a NegBin. We also investigated whether spatial correlation existed in model residuals among the circular sampling units within each model development area using Moran's I (Moran 1950). A high Moran's I value would indicate a violation of independence in the residuals and model assumptions.

Model Interpretation

To aid in model interpretation, we calculated use ratios and marginal plots for coefficients in the Westside habitat-use model. We computed use ratios, similar to selection ratios (McDonald et al. 2006), from the estimated coefficient for each covariate using $\left[\exp\left(\hat{\beta}_j\right) - 1\right] \times 100\%$, which identifies the change in percentage increase or decrease in the predicted probability of use with a 1-unit increase in the covariate X_j, holding all other variables constant. Although it is unrealistic to expect the value of 1 covariate to change while others remain constant, use ratios are useful for evaluating the marginal contribution of individual covariates. Similarly, we used marginal plots to visualize how predictions of elk use changed across the range of observed values for a single covariate while values of other covariates remained constant.

In addition to producing marginal plots, we calculated standardized partial regression coefficients (Zar 2010) for all variables in the Westside habitat-use model. The absolute values of standardized coefficients can indicate the relative importance of covariates in predicting use by elk (Millspaugh et al. 2006, Zar 2010). However, strict interpretation requires the covariates to be independent, which is usually not true. Thus, we used a combination of use ratios, marginal plots, standardized coefficients, and CIs for the final model to help identify and understand the relative importance of each covariate in the habitat-use model.

We mapped predictions of the Westside habitat-use model on a 30-m × 30-m grid that covered each modeling area, excluding cells identified as non-habitat (Appendix B). We then assigned the model prediction for each grid cell a value of 1 to 4 based on the quartiles of the distribution of predictions for each modeling area and classified areas as low use (first quartile), medium-low use (second quartile), medium-high use (third quartile), or high use (fourth quartile); each quartile represented 25% of the specific modeling area. We also mapped covariates of the Westside habitat-use model within each modeling area to display the range of values in each area and aid in interpretation of observed spatial patterns of predicted elk use.

Model Validation

We evaluated performance of the regional model with 8 independent data sets using locations of female elk not used during covariate selection and model estimation (Table 1). Many of these locations were recorded with VHF radiotelemetry (Table 7) and thus were limited in number and to daylight or crepuscular hours only. For validation data collected via GPS (Table 7), fix success averaged >84% for data collected at Nooksack, >93% for Quileute, and >90% for Green-Cedar. For each validation data set, we mapped predictions of the regional model on a 30-m × 30-m grid that covered an MCP developed using all elk locations collected in that area between 1 June and 31 August. We categorized elk locations from Coquille as separate north and south data sets for 1991–1992 and for 1993–1994 because of the original sampling scheme of this study (Cole et al. 1997), and used all recorded locations from the 4 data sets to create MCPs (Table 1; Appendix A).

We assigned each cell of the grid to 1 of 20 equal area-sized prediction bins using percentiles of the distribution of predictions for that grid. Thus, prediction bin 1 had the lowest 5% of predicted values on the grid, and bin 20 had the highest 5%. We calculated a Spearman rank correlation (r_s) between bin rank and the number of elk locations that occurred in each of the 20 bins (Boyce et al. 2002, Sawyer et al. 2009). We performed all statistical analysis in the R language and environment for statistical computing (R version 2.11.1, www.r-project.org, accessed 6 May 2010). We estimated the NegBin using the glm.nb function and the NB2 formulation available in the MASS contributed package (Venables and Ripley 2002).

RESULTS

Covariate Selection and Model Development

Following model selection in AIC and removal of candidate models with inconsistent or nonsignificant coefficients across study areas, we ultimately retained 4 covariates from the nutrition category for model development: mean DDE, mean accepted biomass (AB), mean of pixels with DDE ≥2.4 (marginal, good, or excellent [MGE]; Cook et al. 2004, 2018), and percentage of the circular sampling unit with DDE values ≥2.4 (% MGE; Appendix B, Tables B1 and B2). For human disturbance, we brought forward only 1 covariate, distance to open road. For the vegetation and physical covariate categories, only 1 covariate remained in each after pre-analysis screening and model selection: distance to edge (vegetation category) and mean slope (slope; physical category; Appendix B, Table B2).

We developed 3 models from the 4 covariates in the nutrition model set; 2 were univariate (DDE, AB), and the third combined 2 covariates (MGE and % MGE) with an interaction term (Table 8). Three of the nutrition covariates (DDE, AB, and MGE) were highly correlated and thus could not be included in the same model. We created the third model in this set to combine aspects of diet quality (MGE) and forage quantity (% MGE), predicting that elk seek patches that offer high levels of DDE. The best nutrition model, DDE, had a summed rank of 8 and was the top performer in 3 of 5 modeling areas (Table 8). The AIC weights (i.e., model strength of evidence) for the DDE model ranged from 0.005 to 0.534 among modeling areas (Appendix D, available online in Supporting Information).

We created 2 human disturbance models with the distance to open road covariate: a univariate model and one with both linear and quadratic terms. Exploratory analysis of elk locations in relation to roads revealed that elk use did not consistently increase linearly

Table 8. Ranks of models to predict habitat use by elk in summer in western Oregon and Washington, USA, within each of 5 model development areas. Models are organized by model set and listed in order within each set from best to worst as indicated by the sum of ranks (lower sum is better) for each model across areas.

		Model development area[a]					
Model set	**Model**	**GC08**	**PY09**	**WR04**	**WR05**	**WR07**	**Summed rank**
Nutrition	DDE[b]	1	1	2	1	3	8
	AB[c]	2	2	3	2	1	10
	MGE[d], %MGE, MGE × %MGE	3	3	1	3	2	12
Human disturbance	Distance to open road	1	1	2	2	1	7
	(Distance to open road)^2	2	2	1	1	2	8
Nutrition + (vegetation and/or physical)	DDE, distance to cover-forage edge, slope	1	2	1	2	1	7
	DDE, slope	2	1	2	1	2	8
	DDE, distance to cover-forage edge	3	3	3	3	3	15
Human disturbance + (vegetation and/or physical)	Distance to open road, distance to cover-forage edge, slope	1	2	1	1	1	6
	Distance to open road, slope	2	1	3	2	2	10
	Distance to open road, distance to cover-forage edge	3	3	2	3	3	14
Nutrition + human disturbance + (vegetation and/or physical)	DDE, distance to open road, distance to cover-forage edge, slope	1	2	1	2	1	7
	DDE, distance to open road, slope	2	1	2	1	2	8
	DDE, distance to open road, distance to cover-forage edge	3	3	3	3	3	15

[a] Codes indicate model development area and year: GC08 = Green-Cedar 2008; PY09 = Pysht 2009; WR04 = White River 2004; WR05 = White River 2005; WR07 = White River 2007.

[b] Dietary digestible energy (kcal/g) within a circular sampling unit.

[c] Accepted biomass (kg/ha; biomass of plants that elk neither significantly avoided nor selected and those that elk significantly selected).

[d] Marginal, good, or excellent categories of DDE; values ≥2.4 kcal/g.

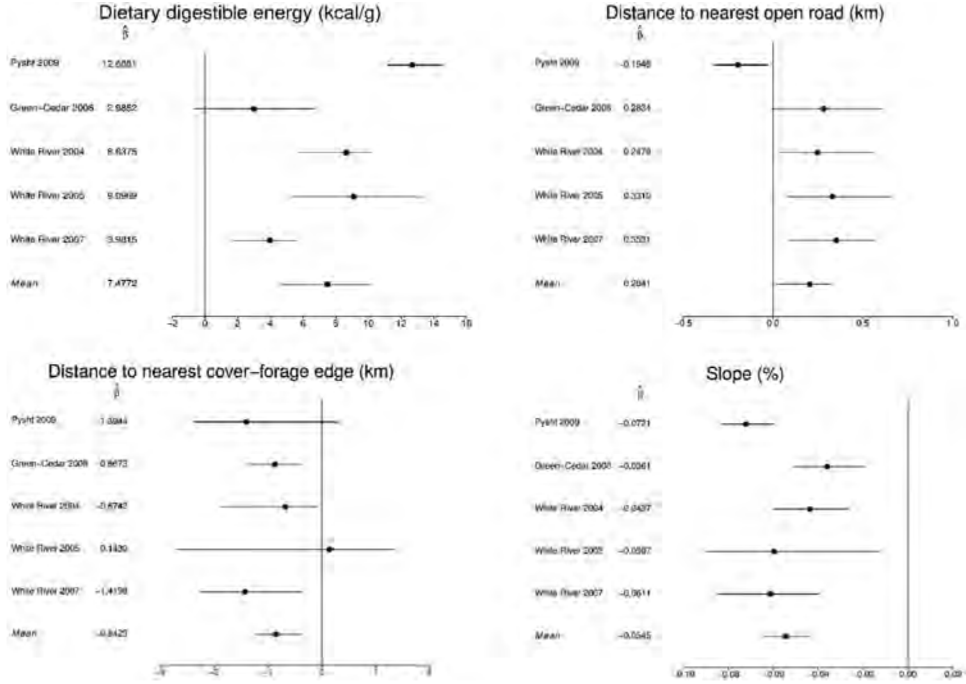


Figure 20. Coefficients ($\hat{\beta}$) and 90% confidence intervals for the 4 covariates in the best elk habitat-use model estimated for each of 5 model development areas and averaged across areas, western Oregon and Washington, USA.

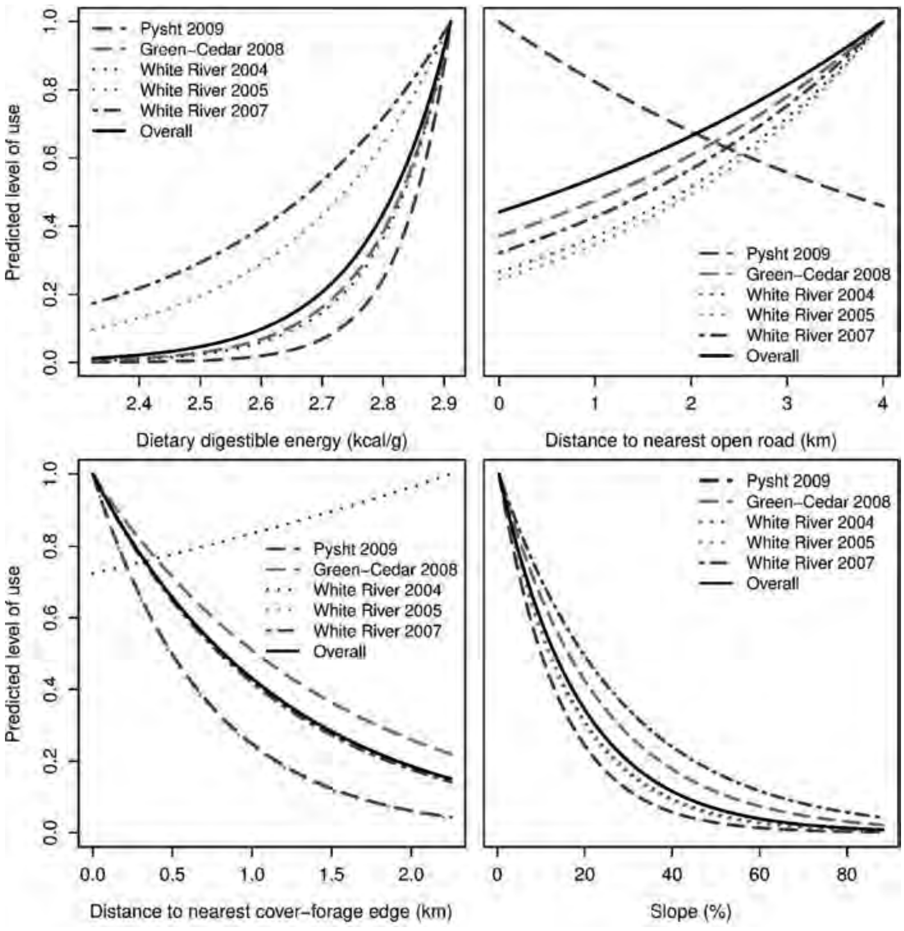


Figure 21. Marginal plots of the 4 covariates in the best elk habitat-use model estimated for each of 5 model development areas and averaged across areas, western Oregon and Washington, USA.

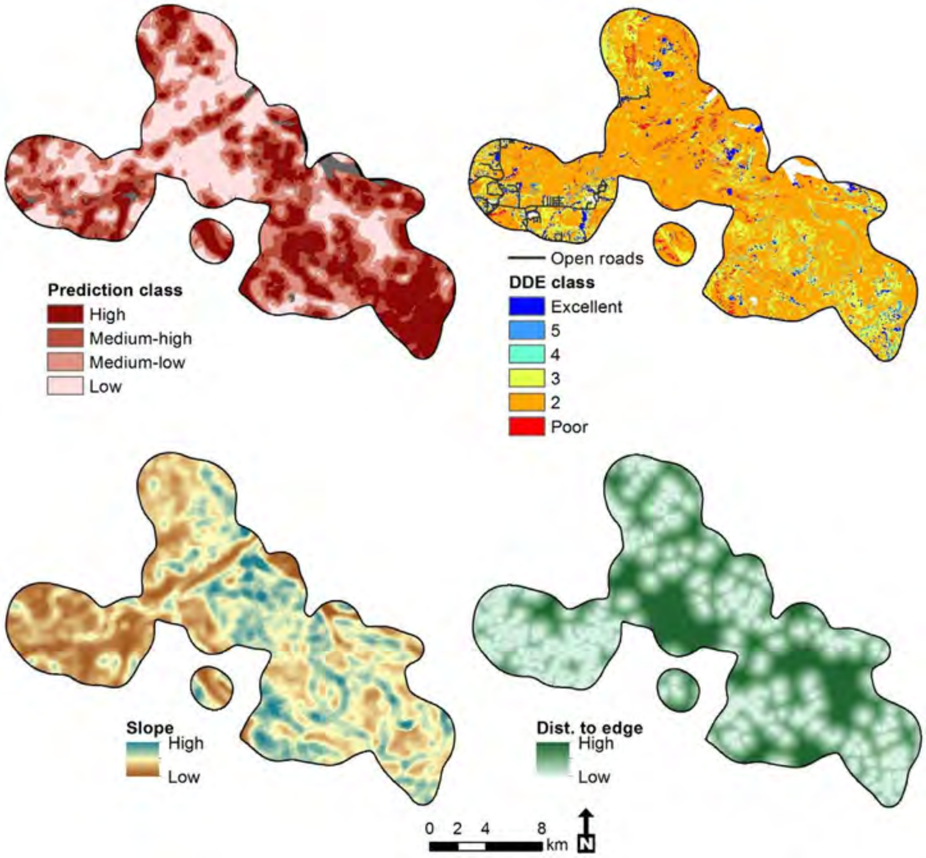


Figure 22. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the Green-Cedar 2008 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

among modeling areas as distance to open road increased. However, the best model, distance to open road, ranked first in 3 of the 5 modeling areas (summed rank = 7; Table 8). In these 3 sites AIC weights were relatively high (>0.63), indicating strong support for this model in contrast to the quadratic form (Appendix D).

We next combined distance to edge and slope with the best nutrition and human disturbance models to create new model sets (Fig. 19). For the nutrition + (vegetation and/or physical) model set, we evaluated 3 models that contained DDE and either slope or distance to edge or both; the best model contained all 3 covariates (Table 8). This model ranked first in 3 of 5 modeling areas (summed rank = 7), and AIC weights ranging from 0.271 to 0.972 indicated uniformly strong support, especially in the Green-Cedar 2008 and White River 2004 data sets (Appendix D). We then compared 3 models in the human disturbance + (vegetation and/or physical) model set. Similar to results for the previous model set, the best model in this group contained all 3 covariates: distance to open road, distance to edge, and slope (Table 8). The summed rank of 6 for this model indicated that it was the best performer for all but 1 data set (Pysht 2009), where it ranked second behind distance to open road and slope.

We then combined the best nutrition, human disturbance, vegetation, and physical models in another model set, with the constraint that each model contained nutrition and human disturbance covariates. The best model included all possible covariates (i.e., DDE, distance to open road, distance to edge, and slope; Table 8). This model ranked first in 3 areas and second in the remaining 2; AIC weights ranged from 0.277 to 0.990 (Appendix D).

We evaluated one additional candidate model, combining the best nutrition and human disturbance models (i.e., DDE and distance to open road) with the best performers from the 5 model sets described above (Fig. 19). The best model in the final set ranked first in every habitat-use modeling area (summed rank = 5) and included 4 covariates: DDE, distance to open road, distance to edge, and slope (Table 9). The AIC weights for this model ranged from 0.553 (PY09) and 0.750 (GC08) to >0.890 in the 3 remaining modeling areas, indicating consistent, and strong regional support (Appendix D). The second-best model had a summed rank of 12 and was similar to the best model but lacked the distance to open road covariate (Table 9). Two covariates, distance to edge and slope, occurred in each of the 3 best models (Table 9). Distance to open road was the model least supported by the data in our final list; the summed rank was 35 and all AIC weights approached zero (Appendix D).

We created the Westside habitat-use model by averaging estimated coefficients for each covariate in the final model across the 5 model development areas (Table 1). Predicted use ($\hat{w}$) from the Westside habitat-use model was:

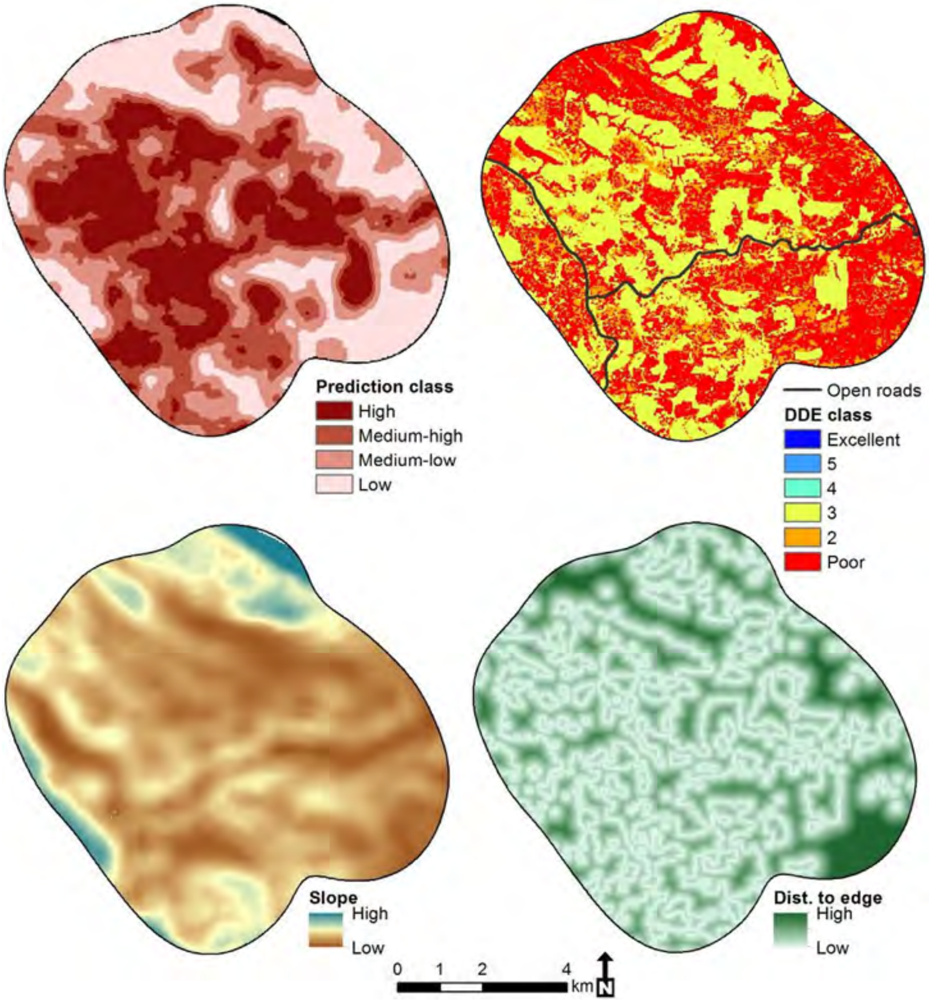


Figure 23. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the Pysht 2009 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map.

$$\widehat{w} = \exp(-24.2389 + [7.4772 \times \text{DDE}] + [0.2041 \times \text{distance to open road}] - [0.8423 \times \text{distance to edge}] - [0.0545 \times \text{slope}])$$

Goodness-of-fit tests for each study area resulted in P values between 0.20 (White River 2005) and 0.84 (Pysht). There was no evidence of lack of fit (i.e., that the data did not fit a negative binomial distribution), and spatial correlation in the residuals for the circular sampling units was extremely low in each study area. All Moran's I values for distances equal to 700 m (nearest neighbors) ranged from 0.07 to 0.21. Spatial correlation declined to near 0 within 2,100 m.

Model Interpretation

Coefficients for the final habitat-use model indicated that elk were most likely to occupy sites with greater DDE, far from roads open to the public, close to cover-forage edges, and with relatively gentle slopes (Table 10). Coefficients were generally consistent among modeling areas, with some exceptions (Fig. 20). For example the estimated coefficient for distance to edge in White River 2005 was positive, but the 90% CI included 0; thus the relationship was not statistically significant at an alpha level of $\alpha = 0.10$. The estimate for DDE in Green-Cedar 2008 was also not statistically significant (Fig. 20). Moreover, there was a negative and statistically significant ($\alpha = 0.10$) relationship between elk habitat use and distance to open road in Pysht (2009). None of the CIs for the averaged coefficients for the 4 predictor covariates included 0, however, indicating that we identified elk habitat-use relationships that were consistent and robust among data sources (Fig. 20). Based on standardized coefficients, changes in slope (−0.949) were relatively most important in predicting habitat use, followed by DDE (0.656), distance to edge (−0.305), and distance to open road (0.300). Use ratios for the Westside habitat-use model indicated an increase in relative probability of use by elk with increases in DDE and distance from open roads, but decreases in relative probability of use with increasing distance to edge and slope (Table 10).

Predicted probability of use by elk, as demonstrated by marginal plots, increased steadily with increasing DDE across all 5

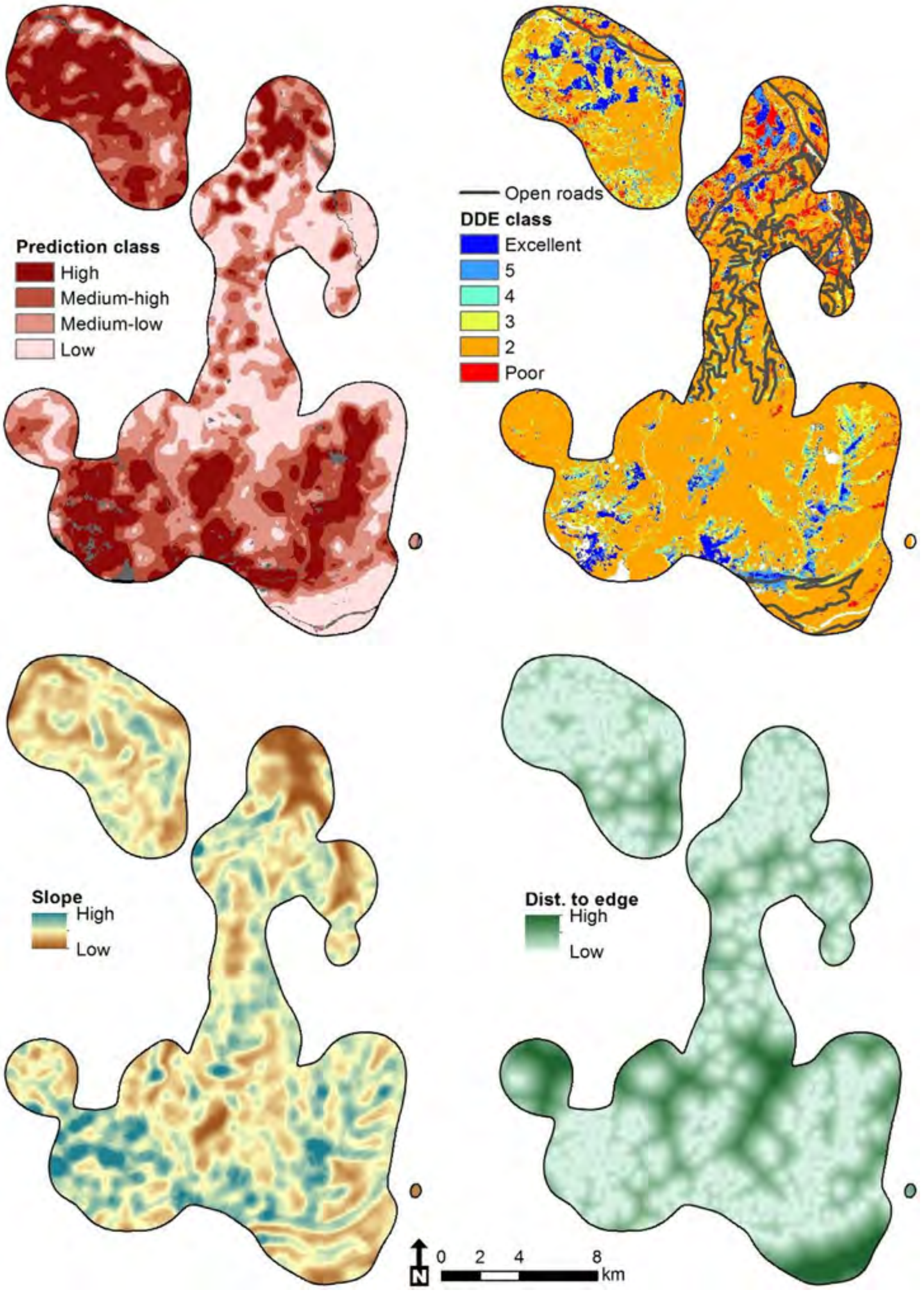


Figure 24. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the White River 2004 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

modeling areas, with the curvilinear response rising markedly at DDE levels exceeding 2.7 (Fig. 21). Predicted use also increased with increasing distance from roads in all areas, with the exception of Pysht 2009. Elk use was predicted to decline with increasing distance to edge, with the exception of White River (2007). Last, predicted use decreased sharply in all areas as slope increased between 0 and 40%.

Patterns of predicted use mapped in each model development area revealed high variability and patchiness of use as a result of the distribution and interaction of model covariates in each site (Figs. 22–26). For example, in Pysht (2009), where only 2 highways transected the site and nutrition was the most depauperate among modeling areas, predicted use was strongly aligned with nutrition but not roads (Fig. 23). Areas of steep slopes that were far from edges also showed low predicted use (Fig. 23). By contrast, in White River 2007, bands of low levels of predicted use closely aligned with open roads, especially in the southeastern edges of the area (Fig. 26). In Green-Cedar 2008 (Fig. 22), nutrition was uniformly low (predominantly low-marginal; Table 2) and not closely aligned with patterns of habitat use other than in the southeastern lobe of the kernel, where pockets of higher DDE values co-occurred with the

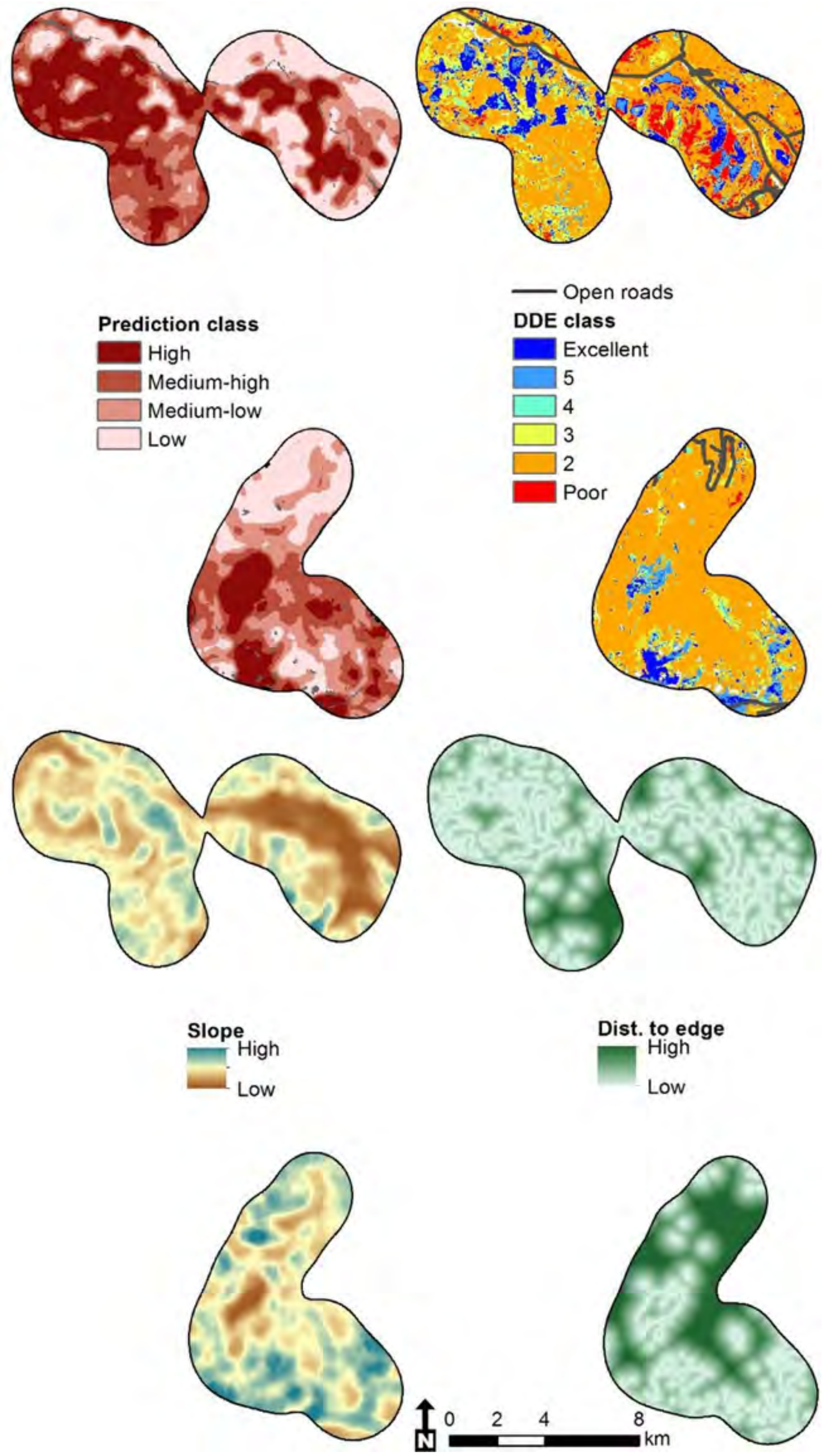


Figure 25. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the White River 2005 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

absence of open roads. By contrast, the western lobe had similarly good patches of DDE and several open roads that likely had low traffic rates, but these roads led to several small subdivisions that were masked from our analysis but may have influenced use by elk.

Model Validation

Spearman rank correlation coefficients between predicted and observed use for the final Westside habitat-use model ranged from 0.32 in Coquille North 1993–1994 to 0.99 in Green-Cedar (2006, 2007, 2009; Table 11). The mean correlation coefficient across

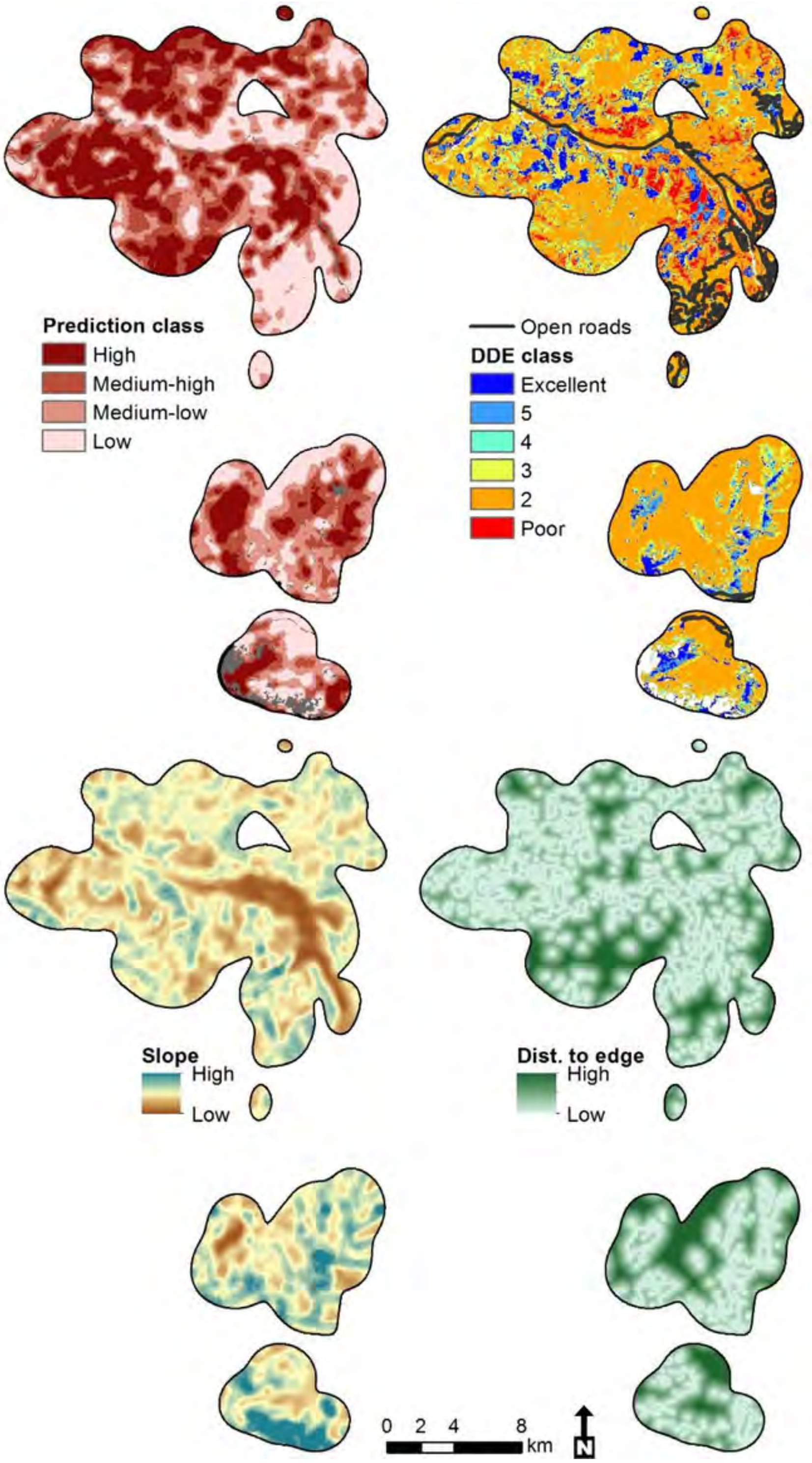


Figure 26. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the White River 2007 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

validation areas was 0.77 (90% CI = 0.63–0.90). Correlations were higher in the 4 validation sites in Washington ($r_s \geq 0.96$) than in the 4 in Oregon ($r_s = 0.32$–0.87). Elk telemetry locations were generally clustered within higher prediction classes, with few observations of elk in the lowest-ranked classes (Appendix E, available online in Supporting Information).

DISCUSSION

Our hypothesis that habitat use by elk in western Oregon and Washington would be driven by a suite of covariates related to energy balance was well supported; our final model included 1) a direct measure of energy acquisition (DDE); 2) a metric of

Table 9. Ranks of the final set of candidate models used to predict habitat use by elk in summer within 5 model development areas in western Oregon and Washington, USA. Models are listed in order from best to worst as indicated by summed ranks; a summed rank of 5 would indicate that a model was the best performer in all 5 areas.

		Model development area[a]					
Model number	**Model**	**GC08**	**PY09**	**WR04**	**WR05**	**WR07**	**Summed rank**
6	DDE[b], distance to open road, distance to cover-forage edge, slope	1	1	1	1	1	5
4	DDE, distance to cover-forage edge, slope	3	2	2	2	3	12
5	Distance to open road, slope, distance to cover-forage edge	2	6	3	3	2	16
1	DDE	5	5	5	4	5	24
3	DDE, distance to open road	6	3	4	5	6	24
2	Distance to open road	7	7	7	7	7	35

[a] Codes indicate model development area and year: GC08 = Green-Cedar 2008; PY09 = Pysht 2009; WR04 = White River 2004; WR05 = White River 2005; WR07 = White River 2007.

[b] Dietary digestible energy (kcal/g) within a circular sampling unit.

human disturbance and thus potential energy loss (distance to open roads); 3) topography, which can affect both locomotion energy and foraging conditions (slope); and 4) an index of either foraging efficiency or security (distance to cover-forage edge). Three of the 4 covariates—DDE, distance to open road, and distance to edge—have analogs in the Wisdom et al. (1986) model, whose improvement was the impetus for our modeling effort (Wisdom et al. 2018*a*)*:* forage quality, density of open roads, and size and spacing of cover and forage areas. Signs of coefficients and marginal plots of the 3 covariates in our Westside model agreed with relationships hypothesized in the 1986 model, suggesting that these covariates are robust predictors of elk use across time and space in the Westside region (Wisdom et al. 2018*a*). Elk consistently chose habitat features that maximized energy acquisition and minimized the potential for energy loss and mortality via hunters or poachers, supporting the hypothesis that animals choose habitats that benefit performance (Gaillard et al. 2010). Study designs that link habitat choices to demographic consequences are requisite for improving habitat models for wildlife (Morrison et al. 2012).

Our prediction that nutrition and human disturbance would function as key drivers of elk distributions was corroborated by their strong relation to predicted use (Fig. 21). The model containing only these 2 covariates, though, had a relatively high summed rank (i.e., little support from the data), and Akaike weights for the model approached 0 in all but one modeling area (Appendix D, final set of candidate models). Results from an example application of the regional model in western Washington (example 1 in Wisdom et al. 2018*b*) supported our prediction that elk use of areas of similar nutrition may be compromised by other, interacting covariates such as human disturbance and topography. In this example, the greatly improved levels of DDE in a local landscape did not translate into increased predicted use because roads remained open following timber harvest (option 3).

Our regional model was successful in predicting habitat use by elk. Multiple lines of evidence suggested that the model was robust, including its top rank in all 5 model development areas (Table 9), high correlation of predicted and observed use in validation with independent telemetry data (Table 11; Appendix E), and consistent trends in covariate values relative to predicted use. This generality, and the successful melding of study-area models into a regional model using a hierarchical, meta-analysis approach, resulted in a large inference space (>11 million ha) compared with that of most ungulate habitat models. In a formal statistical sense, the inference space of the models applies only to the model development and validation areas (Fig. 17; Table 7), which were not selected randomly but opportunistically. These 13 areas, however, were large and encompassed a wide range of environmental conditions, management regimes, and land ownerships across the Westside region.

The meta-analysis approach we adopted allowed for study area (unit-level) summaries that can help clarify the amount of information in the data (Murtaugh 2007); the approach was clearly sufficient in meeting our objectives. Our analysis was generally a more accessible and transparent approach compared to a Bayesian or frequentist hierarchical model. We also attempted to fit a generalized linear mixed model, which would provide estimates of the regional and study area coefficients simultaneously, but that process is not only complicated but also requires additional assumptions about the distribution of the random effects. Moreover, correlation patterns need to be correctly specified within individual modeling areas (Fieberg et al. 2010).

Although modeling results were generally consistent among areas, we found some exceptions, such as elk response to open roads in Pysht (2009) (Figs. 20 and 21). Two Washington State highways were the only roads open to public access in this landscape (Fig. 23), and mean distance to open roads was lowest among all modeling areas (Appendix B, Table B4). Traffic patterns and motorist behavior likely differ between highways

Table 10. Coefficients, confidence intervals (CI), and use ratios for the final Westside habitat-use model for elk in western Oregon and Washington, USA.

Covariate	$\hat{\beta}$	90% CI lower limit	90% CI upper limit	Use ratio
Intercept	−24.2389			
DDE[a] (kcal/g)	7.4772	4.8053	10.1349	111.2% increase for each 0.1-unit increase in DDE
Distance to open road (km)	0.2041	0.0242	0.3252	22.7% increase for each 1-km increase from road
Distance to cover-forage edge (km)	−0.8423	−1.2554	−0.3855	8.1% decrease for each 100-m increase in distance to edge
Mean slope (%)	−0.0545	−0.0630	−0.0441	5.3% decrease for each 1 %-increase in slope

[a] DDE = dietary digestible energy.

Table 11. Spearman rank correlation coefficients (r_s) for tests of predicted versus observed use by elk in summer for the regional version of the best habitat-use model (Westside habitat-use model) using 8 model validation data sets from western Oregon and Washington, USA.

Data set (study area and years)	Westside habitat-use model
Coquille North 1991–1992	0.50
Coquille North 1993–1994	0.32
Coquille South 1991–1992	0.87
Coquille South 1993–1994	0.55
Green-Cedar 2006, 2007, 2009	0.99
Makah 2000–2003	0.97
Nooksack 2008–2009	0.96
Quileute 2006–2008	0.97

such as these and less-traveled roads, where drivers may slow down or even stop and leave a vehicle to hike or photograph wildlife. We suspect that elk did not avoid traffic on these highways but responded instead to the high-quality forage on small farms adjacent to them (K. Sager-Fradkin, Lower Elwha Klallam Tribe Natural Resources, personal communication).

For distance to edge, White River 2005 was the only data set with a positive coefficient, indicating higher predicted use farther from edges (Fig. 20). The small sample size in this data set ($n = 6$ elk) may have contributed to the relatively large variability and lack of significance for this covariate. Although the coefficient for distance to edge was negative in Pysht (2009), it was not significant; this site contained extensive private timberland (Appendix A) with many harvest units, and had the shortest average distance to edge among modeling areas (Appendix B, Table B4). Last, the coefficient for DDE was lowest in Green-Cedar 2008, and the lower CI included 0 (Fig. 20). This finding may stem from the overlap of relatively good nutrition with the only open roads in this site (western portion of the area; Fig. 22).

Each covariate in the Westside habitat-use model is strongly supported in published literature. Slope had the largest standardized coefficient among the 4, and its coefficient was the only one for which no CIs spanned 0 in any study area (Fig. 20). Thus, slope remains an important consideration in planning and siting habitat improvements for elk, such as road closures or silvicultural prescriptions, which are best positioned on gentle slopes. Predicted use by elk declined sharply as slope increased from 0 to 40%, with very low probability of use (<0.10) predicted for slopes $>60\%$ (Fig. 21). Preference by elk for gentle to moderate slopes has been documented previously in western Oregon (Witmer 1981, Witmer et al. 1985, Wisdom et al. 1986) and elsewhere (Hershey and Leege 1982, Edge et al. 1987, Johnson et al. 2000, Sawyer et al. 2007). Energetic costs for elk moving on a horizontal plane are nearly 3 times lower than those of moving upslope (Parker et al. 1984), and elk in eastern Oregon preferred to move along ridgelines rather than on steeper slopes perpendicular to drainages (Kie et al. 2005).

Many elk habitat models have included some form of forage variable (e.g., Wisdom et al. 1986, Thomas et al. 1988, Roloff 1998, Johnson et al. 2000, Benkobi et al. 2004), although it has not always been used in model predictions because of the lack of site-specific information needed for its derivation (Cook et al. 1996, Roloff 1998). Earlier studies hypothesized about effects of summer nutrition on population performance of elk in the Pacific Northwest (Trainer 1971, Harper 1987, Merrill et al. 1995), but only recently have these effects been more widely recognized (Cook et al. 2013, 2018). Moreover, few studies have related distributions of wild elk and performance metrics, such as nutritional condition, to nutritional resources in summer. However, Hebblewhite (2006) demonstrated a positive relation between body mass and pregnancy rates with exposure of elk to high-quality forage, and Middleton et al. (2013*a*) documented declines in pregnancy rates in migratory elk that they hypothesized were in part a function of declining spring-summer forage conditions. In Montana, Proffitt et al. (2016) found elk exposed to lower summer nutritional conditions entered the winter with lower body fat and pregnancy rates. Summer nutrition for elk, defined in our study by DDE rather than by more commonly obtained forage quality or quantity variables, was a strong and consistent predictor of elk distributions in our Westside habitat-use model. The utility of the nutrition model in strategic land-use planning, not only to predict use but also animal performance, is embodied in the examples described by Wisdom et al. (2018*b*), which can serve as a template for holistic elk management in the Westside.

Several elk habitat models reflect elk selection for sites close to cover-forage edges, presumably for security (e.g., Wisdom et al. 1986, Thomas et al. 1988, Brunt et al. 1989, Benkobi et al. 2004), although mechanisms for this selection have not been well-described in the literature (Hanley 1983). In western Oregon, 95% of Roosevelt elk locations were within 130 m of cover (Witmer 1981). In Vancouver, British Columbia, more than 50% of Roosevelt elk locations in forage areas were within 40 m of the edge; by contrast, only 20% of locations in cover were within this distance (Brunt et al. 1989). Elk likely select foraging sites close to cover during summer to reduce predation risk or ameliorate effects of micro-climates or insects, and select sites within cover but close to edges to minimize travel to nutritious forage in more open areas and along cover-forage edges (Skovlin et al. 2002). Elk in southwest Oregon shifted to more open vegetation types during a period of controlled road access (Cole et al. 2004), and elk in Yellowstone National Park were closer to forest edges during daytime but did not alter habitat selection in relation to close (within 1 km) encounters with wolves (Middleton et al. 2013*b*).

Research in Europe on red deer (*Cervus elaphus*; Meisingset et al. 2013) and throughout the range of elk in western North America has demonstrated elk avoidance of roads (Lyon 1979; Cole et al. 1997, 2004; Rowland et al. 2000, 2005; Frair et al. 2008; Ciuti et al. 2012*b*; Montgomery et al. 2012). Roosevelt elk in the coastal range of Oregon generally avoided all roads in summer, with elk use less than expected within 500 m of paved roads (Witmer 1981, Witmer and deCalesta 1985). Cole et al. (1997) found that elk survival in southwestern Oregon increased, and daily movements and core area size decreased, following road closures, presumably from a decline in poaching and disturbance from traffic. Worldwide, roads represent a dominant anthropogenic feature that can lead to foregone foraging opportunities, increased poaching, and higher energetic costs resulting from flight responses to traffic (Coffin 2007). The strong relation between elk distribution and roads exemplified in our regional model demonstrates its utility in managing elk populations and habitats in relation to road networks throughout the Westside.

Model Validation

The Westside habitat-use model performed extremely well ($r \geq 0.96$) in all but the Coquille study area in southwestern Oregon, where performance was much more variable ($r = 0.32$–0.87). Telemetry data from this area were the oldest in our project (early 1990s), and analysis required extensive manipulation of vegetation layers to match the vintage of elk telemetry data (Appendix B). Moreover, elk locations from this study were only diurnal and obtained from VHF collars (mean error ellipse of 1.2 ha), and the sample size was orders of magnitude less than that in other validation data sets (Table 7; Appendix E). Although environmental conditions in Coquille typify those of the southern Oregon Coast Range (Cole et al. 1997), the study area lies at the southern boundary of our modeling region. Landscapes to the south differ substantially, with complex topography, serpentine soils, and flora atypical of much of the Westside (Franklin and Dyrness 1988). Last, road closures established in 1992 for this research only partially limited access (Cole et al. 1997, 2004); thus, we likely under-estimated the extent of open roads in the Coquille data set for 1993–1994. Nonetheless, correlation between predicted and observed elk use in this area was much greater than expected by random chance, indicating the model still performed reasonably well given the limitations of the data. Including this study area was useful because it represented the only data from Oregon, and its location at the boundary of the Westside region offered insights about how robust our validation results might be to higher location error, lower relocation frequency, and unknown fix rate.

A possible contribution to the strong performance of some of our validation data sets may be the spatial overlap of certain areas used for model development versus validation (e.g., Green-Cedar and White River; Fig. 17). Although some of these areas overlapped and thus were not completely spatially independent, model development versus validation data sets always differed by the year in which telemetry data were collected and across years by collared animals from which telemetry data were obtained. Thus, we did not use any individuals for both model development and validation. Moreover, using independent data for model validation is preferred over other methods such as cross-validation or other methods of sub-setting the original data, which may lead to inflated measures of model performance (Johnson 2001).

Sources of Uncertainty in Model Application

We developed competing models based on a combination of ecological rationale, biological hypotheses, and predictions, a structured process for model development, and mechanistic covariates related to energy balance to evaluate habitat use. Such an approach provides a useful modeling framework for advancing knowledge about a species' habitat use and requirements (Morrison 2001, 2012). We included a covariate, DDE, in our habitat-use model that was the response variable of the best nutrition model. Thus we modeled a model, which can compound estimation and prediction errors (Mowrer and Congalton 2000). We used coarse-scale GIS layers as source data (Appendix B), often criticized as having insufficient or unknown accuracy for modeling (Shao and Wu 2008). The spatial resolution, extent, and classification of coarse-scale data to estimate, map, and validate habitat-use and resource-selection models can affect modeling results or their interpretation (Morris et al. 2016). These approaches could lead to an inability to detect causal relationships and represent them in habitat-use modeling. However, our modeling produced ecologically meaningful results (i.e., not detecting anticipated results that could be Type II errors) and no unexpected results (i.e., spurious results that could be Type I errors).

Our regional model predictions reflect relations between elk and current environmental conditions. How climate change or other processes might affect these predictions, specifically those derived from vegetation-based covariates (distance to edge and DDE), has not been tested. Predicted regional increases in annual temperatures (projected to be highest in summer) of 1.8°C to 5.4°C by 2070–2099 in the Pacific Northwest, coupled with projected 30% decreases in summer precipitation (Mote et al. 2014), will undoubtedly affect forage phenology and associated biomass and quality of forage for elk. However, relative, if not absolute, values of nutrition for elk as predicted by the nutrition model should remain robust, as noted by Cook et al. (2018). Most research to date evaluating impacts of climate change on ungulates does not specifically address habitat use or distributions but rather population dynamics, especially in relation to winter severity (e.g., Patterson and Power 2002, Hebblewhite 2005). Thus these studies are not directly relevant to our summer habitat-use model. Wang et al. (2002), however, evaluated potential impacts of climate change on elk populations in Rocky Mountain National Park in Colorado, USA, and projected that higher summer temperatures would slow population growth in elk. Given the uncertainty of future climate, land management regimes, and other processes such as abundance of invasive plant species, insects, and wildfire, an adaptive management approach will be required to understand best and appropriate applications of our habitat-use model and to guide future research as needed (Wisdom et al. 2018*b*).

We did not incorporate the presence or density of predators as predictors in our habitat-use model, primarily because such data were unavailable across our study areas. Despite this omission, the model performed well in predicting current elk distributions. However, we recognize such data can play an important role in modeling the full suite of functional habitat components that may affect elk distributions (Gaillard et al. 2010). Two common Westside carnivores are known predators of elk. Black bears prey primarily on neonate elk (Zager and Beecham 2006, Griffin et al. 2011), whereas cougars prey primarily on elk calves during summer but also will kill adult elk (White et al. 2011*a*, Clark et al. 2014). If Westside elk do respond to the presence of cougars and black bears, that response is likely reflected in their current distributions because they have shared ranges with these 2 common predators for decades. Moreover, predation by black bears occurs during such a brief temporal window and on calves, which we did not monitor, that adult elk are unlikely to respond to bears at the scale of our models. Similarly, cougars are cryptic predators whose presence may not affect summer elk habitat use at the temporal and spatial scales of our models. For example, birth-site selection of Rocky Mountain elk at larger spatial scales did not appear to be influenced by predation risk but rather by access to nutritional resources (Rearden et al. 2011), which we accounted for in our models. We know of no published literature documenting changes in habitat use by elk in response to either of these 2 predators.

Gray wolves were functionally absent in the Westside region during the years in which our data were collected. Wolves are actively colonizing Washington and Oregon through dispersal from populations in British Columbia, Idaho, and Montana (Oregon Department of Fish and Wildlife 2010, Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service 2017). Currently, there is one pack located just east of our modeling region in Washington (Teanaway; Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service 2017). No packs have been established within the Westside region in Oregon; however, a pair of wolves was documented in early 2018 in southern Wasco County, Oregon, in the Cascade Mountains (Oregon Department of Fish and Wildlife 2018). In contrast to evidence for cougars and bears, wolves can effect changes in elk distributions and habitat use, often with negative consequences for fitness (Frair et al. 2005, Hebblewhite et al. 2005, Mao et al. 2005, Muhly et al. 2010, White et al. 2012). These results, however, are inconsistent (Middleton et al. 2013*b*). If wolves become sufficiently abundant in the Westside, recalibration of the habitat-use model could be required through additional research, although habitat shifts in response to wolves have been most often reported for winter, not summer, and included use of steeper slopes, higher elevations, and denser cover (Mao et al. 2005). Moreover, in some situations, human disturbance (e.g., hunting, other recreation, high-volume traffic on roads) may exert stronger effects on elk habitat use than do wolves (Proffitt et al. 2009, Ciuti et al. 2012*b*). Thus, the inclusion of a roads covariate in our habitat-use model may provide some resilience of the model even with the projected re-establishment of wolves in western Oregon and Washington.

MANAGEMENT IMPLICATIONS

The habitat-use model predicts relative probability of use by elk, and can guide management treatments to improve elk habitat quality and distributions, such as increasing use on national forest lands relative to adjacent land ownerships. It is not a carrying-capacity model, nor is it a model to predict population numerical response. Such models require intensive data about amount and quality of forage and many assumptions about animal density and other factors that may limit the ability of a landscape to support a defined number of animals (Hobbs and Swift 1985, Beck et al. 2006, Cook et al. 2016). However, Vales et al. (2017) successfully applied equations in our Westside nutrition model to create an elk forage index on lands managed by the Muckleshoot Indian Tribe in central Washington. The scale-independent index is intended to guide timber harvest management and reflects the density of female elk that a given landscape can support. Similarly, Roloff (1998:158) developed a habitat potential model for elk that reflects the "inherent ability of the landscape to produce and sustain elk in the absence of human disturbance." Our model integrates nutrition with human disturbance and other factors to predict relative—but not absolute—use by elk within the analysis area.

For successful application of the model, users should understand its multivariable framework. For example, silvicultural treatments to improve nutritional conditions for elk may yield negligible benefits in term of increased elk use in sites with high open road densities or steep slopes (see Wisdom et al. [2018*b*] for specific examples). Similarly, closing roads in locales with relatively low DDE and limited opportunity to improve nutrition through thinning may be futile if managers seek to improve elk habitat, distribution, or elk performance. Wisdom et al. (2018*b*) describe specific applications of the nutrition and regional habitat-use model, and offer caveats and suggestions for management application in the Westside region.

Nutrition and Habitat-Use Models for Elk Management in Western Oregon and Washington

MICHAEL J. WISDOM, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
MARY M. ROWLAND, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RYAN M. NIELSON,[1] *Western EcoSystems Technology (WEST), Inc., 2121 Midpoint Drive, Suite 201, Fort Collins, CO 80525, USA*
JOHN G. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
BRUCE K. JOHNSON,[2] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
JENNIFER M. HAFER, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
RACHEL C. COOK, *National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA*
PRISCILLA K. COE,[2] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*
DAVID J. VALES, *Muckleshoot Indian Tribe, 39015 172nd Avenue SE, Auburn, WA 98092, USA*
BRIDGETT J. NAYLOR, *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
MARTIN VAVRA,[2] *U.S. Forest Service Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*

INTRODUCTION

Landscape modeling of habitat use by wide-ranging animal species such as elk is a topic of increasing focus in the wildlife profession (Ciuti et al. 2012*a, b*; Nielson and Sawyer 2013). Models of habitat use, or related models of resource selection, predict the probability of animal use of a given area and time based on a wide range of environmental covariates (Rowland et al. 2018). These models can provide valuable knowledge about a species' habitat choices in time and space that presumably index the species' habitat needs (Gaillard et al. 2010, Hebblewhite and Haydon 2010). Models are particularly useful when they are based on covariates that are ecologically meaningful to the species' habitat requirements and that can be directly manipulated by managers to achieve desired changes in a species' habitat use, distribution, and performance (mechanistic covariates; Wisdom et al. 2018*a*).

We describe and demonstrate the management utility of elk nutrition and habitat-use models developed and validated for applications in western Oregon and Washington (Westside; Cook et al. 2018, Rowland et al. 2018). We first summarize intended management applications and considerations, with focus on interpretation of predictions and spatial and temporal scales of use. We then provide management examples that highlight types of applications and benefits. Finally, we discuss challenges and implications of elk modeling in the Westside region, given current management direction on different land ownerships, stakeholder involvement, and future sources of management and environmental uncertainty.

Management Applications and Predictions

The nutrition and habitat-use models evaluate summer range during June–August, a period of nutritional stress for lactating female elk in the Westside region (Cook et al. 2018). Explicit rationale and empirical support for evaluating summer range was detailed by Cook et al. (2004, 2013, 2016, 2018). Evaluation of the nutrition model, which showed the strong positive relationship between landscape composition of summer predictions of DDE (kcal/g) and pregnancy rates and body fat of associated elk populations, supported the focus on summer as a period of nutritional limitation in the Westside region (Cook et al. 2018). These relationships further justified the focus on modeling habitat use during summer on Westside landscapes (Rowland et al. 2018).

The nutrition model predicted DDE during summer in the Westside region using a combination of covariates, including PNV zone, overstory canopy cover, and hardwood composition (Cook et al. 2018). Model predictions were evaluated with independent data on selection ratios, elk performance, and habitat use. Results supported the predictions that fine-scale nutrition data (i.e., DDE) collected with captive elk represent the actual nutrition levels of wild elk, and that these levels can be re-scaled to produce reasonably accurate, broad-scale predictions of nutrition across the Westside region (Cook et al. 2018).

The habitat-use model predicted the relative probability of elk use on Westside landscapes during summer (Rowland et al. 2018). Predictions were based on 4 covariates: DDE outputs from the nutrition model and 3 non-nutrition covariates (distance to open roads, slope, and distance to cover-forage edge; Rowland et al. 2018). The 4 covariates best predicted use by elk across the Westside region at landscape scales based on data from multiple study areas used for model development. Model predictions were validated with independent data on habitat use from additional study areas not included in model development (Rowland et al. 2018). Results supported the hypotheses that elk use of landscapes is consistent across the Westside region, as captured in 1 regional model; and that the regional model would include "a suite of interacting covariates related to elk energy balance" often found to account for elk use in prior research (Rowland et al. 2018:32).

The nutrition and habitat-use models, when used together, predict elk nutrition, habitat use, elk distribution, and

---

[1] *Current affiliation: Eagle Environmental, Inc., 30 Fonda Rd., Sante Fe, NM 87508, USA*
[2] *Retired.*

performance at landscape scales of direct relevance to elk management (Fig. 2; Wisdom et al. 2018*a*). The nutrition model predicts the spatial distribution of nutritional resources (Cook et al. 2018); the habitat-use model can predict the extent to which those resources will be used (Rowland et al. 2018). Landscapes managed for nutrition therefore require simultaneous management of non-nutrition covariates to facilitate desired nutritional use. Effective management thus relies on both models (see Management Examples).

The nutrition and habitat-use models further predict landscape distribution (Rowland et al. 2018) and performance (Cook et al. 2018) of elk populations. Landscape distribution is estimated by summing the predictions of relative probabilities of habitat use across different management boundaries of interest, such as land ownerships (see Management Examples). Animal performance is predicted by regression equations showing that pregnancy rates and body fat of lactating female elk increase in response to increasing landscape area of higher levels of DDE in Westside elk populations (Cook et al. 2018). Increasing animal performance based on increasing area of higher nutrition, however, implicitly assumes that such areas will be used by elk, as predicted by the habitat-use model (Rowland et al. 2018). Our management examples demonstrate these model uses.

METHODS

Scales of Application

Nutrition model.— The nutrition model can applied in 2 ways: spatially explicit or tabular. Equations in the model to predict forage biomass and DDE are the same for both applications (Cook et al. 2018). Spatially explicit model application can occur at any spatial scale of interest, ranging from an individual stand to the entire Westside region. Applying the model at a stand level requires accurate field data that reflect site-specific conditions (Cook et al. 2018). By contrast, coarse-scale GIS data are often sufficient (Appendix B) for applying the nutrition model over large landscapes like those in which the nutrition and habitat-use models were developed and validated (Appendix A).

The tabular application is not scale-dependent but instead can be used in gaming scenarios to understand potential effects on DDE values of changes in overstory canopy cover and hardwood composition in a given PNV zone (Vales et al. 2017, Cook et al. 2018). For example, a manager may want to evaluate how nutrition differs under 4 timber harvest prescriptions in conifer stands that reduce canopy cover to 0%, 20%, 40%, and 60% with either constant or varying levels of hardwood composition (Table 12). For the tabular application, estimates of canopy cover and hardwood composition can be used to drive the model, first to predict forage biomass and then DDE, although estimates of forage biomass (i.e., selected, neutral, accepted) derived directly from field sampling in the stands would provide more accurate predictions of DDE.

Table 12. Dietary digestible energy (kcal/g) of forage for elk in relation to example levels of overstory canopy cover and hardwood composition of coniferous forests in the Pacific silver fir-mountain hemlock potential natural vegetation zone of the Westside region, western Oregon and Washington, USA, based on the elk nutrition model (Cook et al. 2018).

	Overstory canopy cover			
Hardwood composition	**0%**	**20%**	**40%**	**60%**
0%	2.93	2.84	2.74	2.63
5%	2.94	2.86	2.76	2.66
10%	2.95	2.88	2.78	2.68
20%	2.96	2.92	2.82	2.72
50%	3.00	3.03	2.95	2.86

For landscape assessments, the spatially explicit form of the nutrition model can be used to predict DDE as a stand-alone evaluation or in tandem with predictions from the habitat-use model. Applying the habitat-use model by definition requires first applying the nutrition model because DDE predictions are a required covariate in the habitat-use model (Rowland et al. 2013, 2018). When using the nutrition model as a stand-alone tool for landscape assessment, the size of area should be large enough to affect conditions for a local population. Minimum size should be approximately 800–1,000 ha (Rowland et al. 2013), which equates roughly to the area of summer home ranges of elk in the Westside region (Cole et al. 1997, McCorquodale 2003, Witmer et al. 1985, Wisdom et al. 1986).

Predictions of the nutrition model are made to each pixel (grid cell) within an analysis area. Results are directly comparable across all pixels in the analysis area, and across different analysis areas for a given time period (Cook et al. 2018). Results from the spatially explicit nutrition model can then be used to predict pregnancy rates and body fat of lactating female elk in a given summer range, based on the percentage of the analysis area occurring in the higher nutritional classes of DDE (Figs. 12 and 13; Cook et al. 2018), as demonstrated in our management examples.

Habitat-use model.— Assessing habitat use involves 2 general steps. The first is applying the habitat-use model in an area of $\geq$10,000 ha, referred to as a regional landscape. This scale is compatible with the range of study area sizes used to develop and validate our models (Appendix A; Cook et al. 2018, Rowland et al. 2018). Areas $\geq$10,000 ha also encompass multiple populations of summering elk, thus providing an appropriate area in which to evaluate summer range conditions at a regional scale.

The specific size and boundaries of a regional landscape depend on objectives (Rowland et al. 2013). Smaller regional landscapes might be appropriate for focusing on habitat conditions in a given land ownership or drainage (see Example 1). Larger regional landscapes might be appropriate for evaluating conditions across multiple land ownerships that encompass cumulative management activities at large spatial extents (see Example 2).

After the boundary of the regional landscape is established, a 4-km buffer must be placed around the boundary before applying the habitat-use model (see Management Examples). All roads open to public motorized use are to be mapped within this buffer, as are all cover-forage edges (Rowland et al. 2013, 2018). Open roads and cover-forage edges outside the analysis areas but within the 4-km buffer may affect elk use within the analysis areas and thus should be considered (Rowland et al. 2013, 2018).

A second, optional step beyond assessment of a regional landscape is a summary of results for smaller areas, referred to as local landscapes, which are embedded within the regional landscape. In this case, results from applying the habitat-use model for the regional landscape are subsetted to evaluate local conditions or projects, as defined by boundaries of the local landscape. The minimum area for designating a local landscape is

800–1,000 ha; this size is compatible with summer home ranges for elk in the Westside region as described earlier, and reflects a scale of management that would be ecologically meaningful to a local population of elk. This is the same minimum area for applying the nutrition model as a stand-alone landscape assessment. Changes in pregnancy rates and body fat of lactating elk associated with management actions to improve nutrition are thus assessed over an area large enough to affect a population and ensure that associated changes in use in response to changes in nutrition are evaluated at a meaningful scale. Similarly, changes in elk distribution in response to habitat management are summarized at this same scale in which the distribution of a population may be affected (see Management Examples).

Habitat-use modeling does not require the designation or analysis of local landscapes, and their inclusion depends on objectives. Once local management projects are identified (e.g., specific timber harvest units or new road network) as the basis for establishing boundaries of a local landscape, a buffer distance of approximately 1.6 km should be placed around those project areas for summarizing habitat use (see Example Management Uses). The buffer accounts for the effects of the distance to cover-forage edge covariate on elk use, based on the new edges created from timber harvest units or other changes to forest structure (Rowland et al. 2013).

Habitat-use model predictions (Rowland et al. 2013, 2018) are made for each pixel within a regional landscape. Predictions are not standardized on a 0 to 1 scale but are relative to all other values in the area in which the habitat-use model was applied. It is possible to standardize these predictions but they remain relative to other values within the area, and are not directly comparable to predictions made during separate model runs for other areas (although patterns of predicted use may be compared qualitatively between different regional landscapes). Thus, the key to making predictions of elk use comparable across a landscape of interest is to apply the model over the entire area. This point illustrates the benefits of applying the model over a larger regional landscape versus a smaller one: results are comparable across the entire area in which the model is applied, and can be subsetted to any local landscapes of interest. Similarly, model results are comparable across time periods but only when the regional landscape boundary is constant across time periods (Rowland et al. 2013).

Management Examples

We provide 2 examples to demonstrate nutrition and habitat-use modeling applications for landscape management. Example 1 considers 3 management options within 1 land ownership to evaluate effects of proposed silvicultural prescriptions and management of open roads. This example highlights the complementary use of results at scales of regional and local landscapes. Example 2 is an evaluation of multiple land ownerships to quantify and understand elk distribution across ownerships. Results can be used to establish and implement broad-scale objectives for elk distribution and performance (pregnancy rates and body fat of females).

For both examples, we highlight key results and management interpretations but do not address details of how to apply the models in a GIS framework. Rowland et al. (2013) describe and illustrate these details, give additional examples for data summary and display, and provide information about using spatial data sets needed to derive model covariates. The Westside elk modeling website provides downloadable GIS programs to apply the models and example data layers (https://www.fs.fed.us/pnw/research/elk/toolbox/index.shtml). Doerr (2016) and Vales et al. (2017) provide

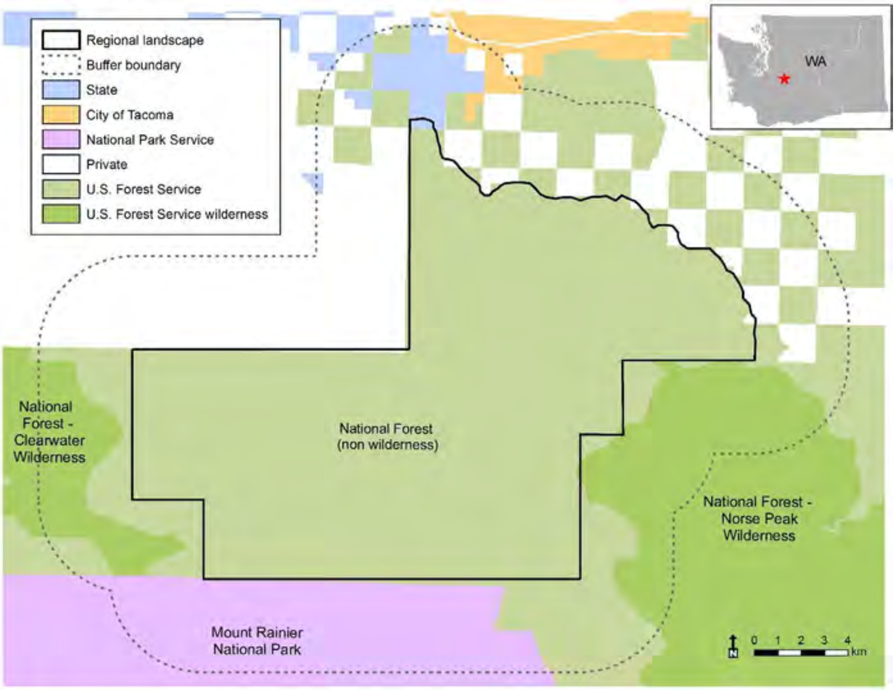


Figure 27. Example 1 study area (27,980 ha) in the White River drainage of western Washington, USA (see upper right inset) showing land ownership and allocations present in 2010 that were used to estimate current conditions for example 1.

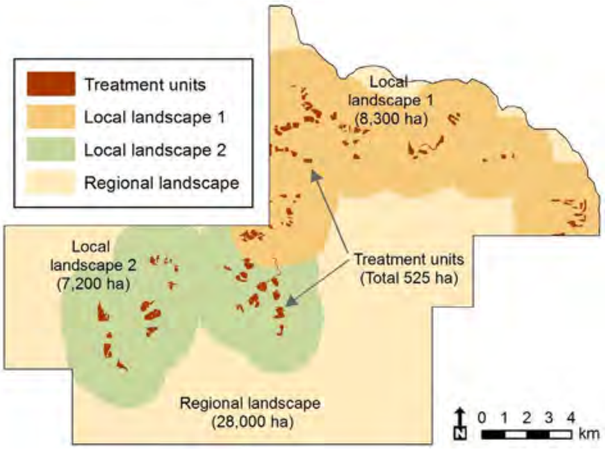


Figure 28. Example 1 had 3 management options. Option 1 included 256 ha of clearcut regeneration harvest in 61 units within local landscape 1 plus 269 ha of commercial thinning in 46 units within local landscape 2. Option 2 included commercial timber harvest on the same units as option 1, except that all units will be clearcut (no commercial thinning). Option 3 was the same as option 2 except 71 km of roads closed as part of timber harvest remained open.

additional examples of applying the Westside models, which complement those provided here. Our examples use land ownerships and environmental conditions for 2010 as the reference or base condition (Appendix B).

Example 1.—The first example encompasses 27,980 ha in the White River drainage of western Washington within the Mt. Baker-Snoqualmie National Forest and adjacent areas of the Wenatchee National Forest (Fig. 27). The area overlaps portions of the White River study areas where telemetry data on elk were obtained for habitat-use modeling (Appendix A). The example is based on discussions and management decisions made between Forest Service managers and the Muckleshoot Indian Tribe on ways to improve elk nutrition and habitat use in the area (USDA Forest Service 2001*a*, *b*). These management options were formally evaluated by Forest Service managers as a result of these discussions (USDA Forest Service 2001*a*, *b*), and implementation of option 1 began in 2012 (USDA Forest Service 2012*a*, *b*).

Different combinations of forest silvicultural prescriptions and management of open roads were considered under 3 management options (Fig. 28). This illustrates the effects of proposed management within 1 land ownership, and how results for regional and local landscapes can be used in complementary ways.

We identified 61 forested units encompassing 256 ha (mean unit size = 4.2 ha, range = 0.3–12.3 ha) for timber harvest under option 1, based on clearcutting as the harvest regeneration method (local landscape 1; Fig. 28). We identified 46 additional units encompassing 269 ha (mean unit size = 5.8 ha, range = 0.3–23.1 ha) for commercial thinning under this option (local landscape 2; Fig. 28). Overstory canopy cover would be reduced from >70% before timber harvest to 0% after clearcutting and to 60% after commercial thinning.

Option 2 included commercial timber harvest on the same units as option 1, except that all units in local landscape 2 would use clearcut regeneration harvest (i.e., no commercial thinning). Option 3 included the same units and silvicultural treatments as option 2 but differed in road management. Under option 3, 71 km of roads used for log hauling would remain open to public motorized use after timber harvest but would be closed under options 1 and 2 (Fig. 29).

For example 1, we selected the boundaries of the regional landscape to evaluate the 3 management options at a regional extent encompassing all national forest management activities and lands that could be managed with active silviculture (non-wilderness areas of national forest). Boundaries of the regional landscape thus followed national forest boundaries with private and state lands to the north, wilderness or roadless areas to the east and west, and NPS lands to the south (Fig. 27). We included a 4-km buffer beyond the boundaries to accurately evaluate distance to open roads and cover-forage edges within the regional landscape, as described earlier.

We selected the boundaries of the 2 local landscapes to evaluate smaller areas adjacent to proposed harvest units (Fig. 27). We established boundaries using a 1.6-km buffer around the harvest units to evaluate spatial effects on elk use in relation to distance to cover-forage edges created during timber harvest. This buffering distance for summarizing habitat use in a local landscape was supported by results from the distance to cover-forage edge covariate in the habitat-use model; most elk use occurred within 1.6 km from an edge.

Example 2.—The second example encompasses 94,403 ha in the White River drainage of western Washington (Fig. 30). This area includes portions of the White River study areas

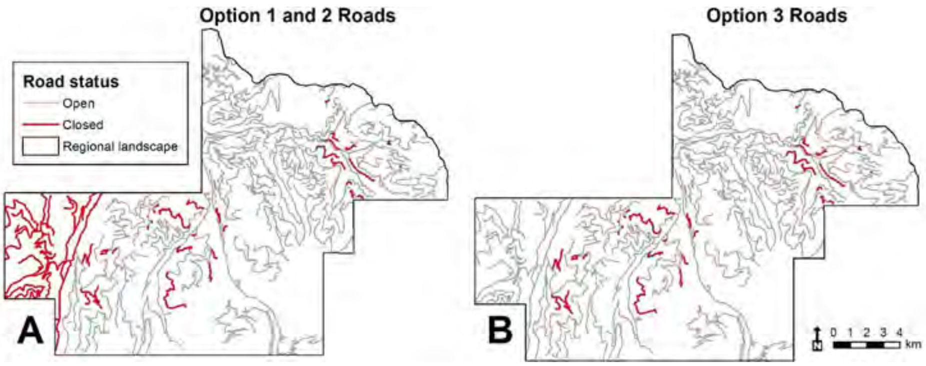


Figure 29. Roads open versus closed to public motorized use under options 1 and 2 (A) versus under option 3 (B) for example 1. Approximately 71 km of roads in the western part of the regional landscape would remain open after timber harvest under option 3. However, the majority of roads (524 km) remain open to public motorized use under all 3 options.

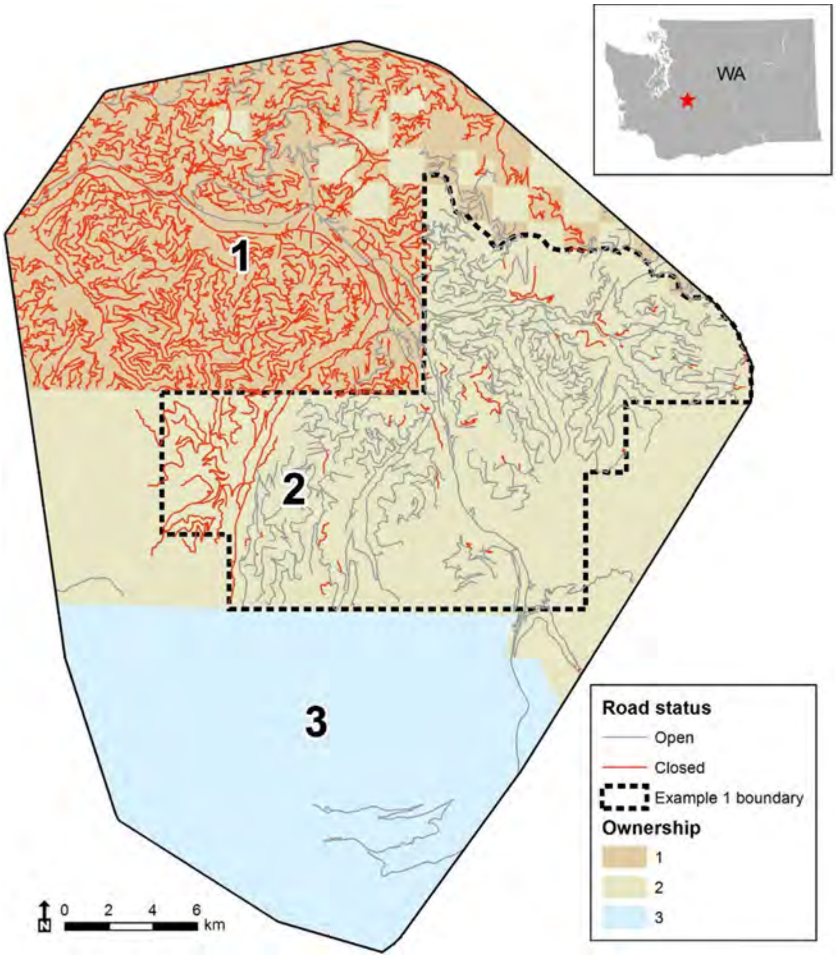


Figure 30. Year 2010 land ownership in the 94,403-ha area of example 2, composed of 3 major ownerships: private industrial forest (ownership 1), Mt. Baker-Snoqualmie and Wenatchee National Forests (ownership 2), and Mount Rainier National Park (ownership 3), Washington, USA. Ownership 1 included a small percentage of state lands because small tracts of state lands were interspersed among large areas of private industrial forest. Example 1 lies entirely within example 2, as outlined in dotted lines. Roads open versus closed to public motorized varied widely by land ownership.

where elk telemetry data were analyzed as part of habitat-use modeling (Appendix A). It encompasses the entire portion of national forest included in example 1, as well as private industrial forest and state lands to the north and Mount Rainier National Park to the south (Fig. 30). The Mt. Baker-Snoqualmie and Wenatchee National Forests compose 45% of the area, followed by Mount Rainier National Park (26%) and private industrial forest (24%). State lands compose the remaining 5%, which is sparsely distributed among private industrial forest and thus is combined with surrounding private industrial forest for our analysis. Estimation of model covariates in our examples used the same environmental data that we used to derive covariates for model development in the White River study areas (Appendices A and B).

RESULTS

Nutrition Predictions, Example 1

Over 85% of the regional and local landscapes under the existing condition in Example 1 are composed of the 2 lowest nutrition classes, poor and low-marginal (DDE <2.58 kcal/g; Tables 2 and 13; Fig. 31). These classes represent conditions below basic requirement of lactating female elk during summer and are associated with lowest levels of female body fat and pregnancy rates (Cook et al. 2018).

The 4 highest nutrition classes (classes 3–6) composed 14.2% of the regional landscape and 12.4% and 13.6% of the 2 local landscapes under the base (existing) condition (Table 13; Fig. 31). These classes represent levels of nutrition that meet or exceed the basic requirement of lactating female elk during summer (Cook et al. 2018). The 3 highest nutrition classes (classes 4–6; Table 2) exceed basic requirement and composed 5.9% of the regional landscape and approximately 6% of each of the 2 local landscapes under the base (existing) condition (Fig. 31; Table 13).

For the regional landscape, the proposed silvicultural treatments would increase the area of DDE in classes 3–6 from 14.2% currently to 15.7% and 16.5% under options 1 and 2, respectively (Table 13). The proposed treatments also would increase the regional landscape area of DDE in classes 4–6 from 5.9% currently to 6.9% and 8.3% under options 1 and 2 (Table 13).

Nutrition classes 3–6 (high-marginal to excellent; Table 2) capture levels of DDE in which pregnancy rates are responsive to nutritional change (Table 13). Similarly, nutrition classes 4–6 (low-good to excellent; Table 2) capture levels of DDE that affect percent body fat of lactating female elk (Table 13). For the

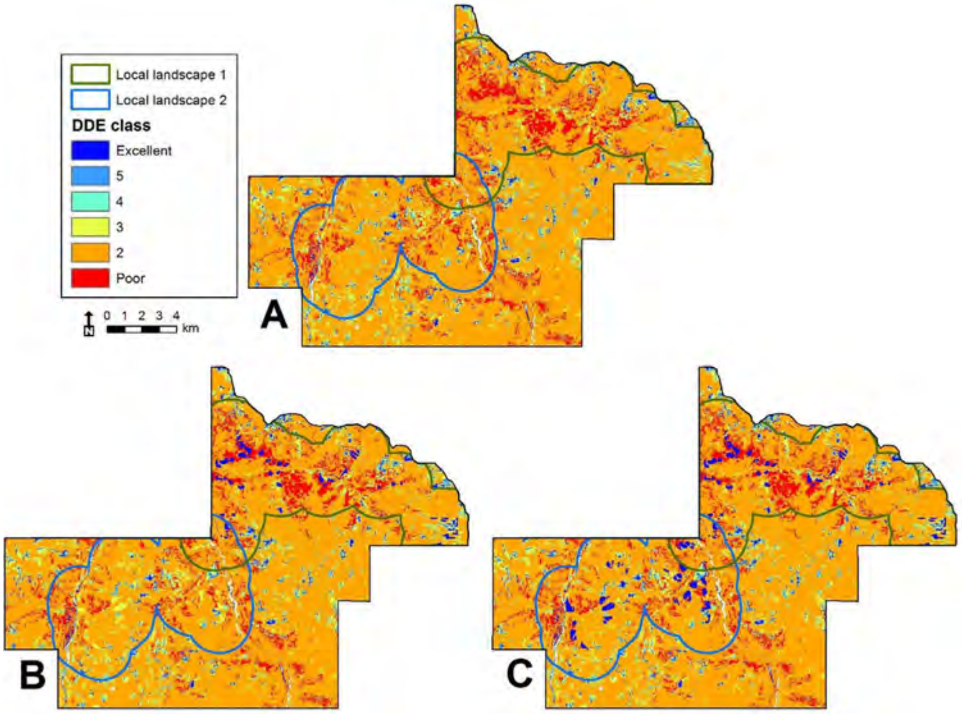


Figure 31. Six classes of elk nutrition in the White River drainage of western Washington, USA for the base condition (A), option 1 (B), and options 2 and 3 (C) for example 1. Land ownerships and environmental conditions for 2010 were used as the base condition (Appendix B).

regional landscape, the increased area of nutrition classes 3–6 is predicted to increase pregnancy rates for lactating female elk from 0.63 currently to 0.68 under option 1 and 0.71 under option 2, using the equation for percent area in DDE >2.58 kcal/g (Fig. 12C; Table 13). Similarly, the increased area of nutrition classes 4–6 is predicted to increase percent body fat in lactating female elk on the regional landscape from 9% currently to 10% under both options, using the equation for percent area in DDE >2.75 kcal/g (Fig. 13; Table 13). Silvicultural treatments and nutritional results for option 3 are the same as option 2 for the regional landscape.

Although the predicted improvements in pregnancy rates and body fat under options 1 and 2 may appear biologically insignificant, these improvements are substantial in relation to the small land area treated: only 1.9% of the regional landscape is being treated silviculturally under these options to achieve the improvements. These results suggest that even a slightly higher percentage of land area treated silviculturally to improve nutrition (e.g., 3–4% of the regional landscape) for option 2 would result in a substantial increase in pregnancy rates and body fat. For example, a 4% increase in area of nutrition classes 3–6 above that for option 2 in the regional landscape

Table 13. Percent area by dietary digestible energy (DDE) class for the regional landscape and 2 local landscapes for the current time period (base) and under 3 management options presented for example 1, and the predicted pregnancy rate and body fat for lactating female elk based on the percent area of DDE in nutrition classes 3–6[a] and 4–6[b], respectively (Cook et al. 2018). We used year 2010 conditions for base.

	DDE class[c]							
	1	**2**	**3**	**4**	**5**	**6**	**Pregnancy rate (%)**	**Body fat (%)**
Regional landscape								
Base	9.1	76.6	8.3	2.4	1.9	1.6	0.63	9
Option 1	8.6	75.7	8.8	2.4	1.9	2.6	0.68	9
Option 2 and 3	8.6	74.9	8.2	2.4	1.9	4.0	0.71	10
Local landscape 1								
Base	15.8	71.9	6.8	2.6	1.5	1.5	0.56	9
Option 1	14.6	69.9	6.7	2.5	1.5	4.8	0.67	10
Option 2 and 3	14.6	69.9	6.7	2.5	1.5	4.8	0.67	10
Local landscape 2								
Base	10.2	76.2	7.6	2.8	1.6	1.6	0.60	9
Option 1	9.5	74.6	9.7	2.8	1.6	1.8	0.69	9
Option 2 and 3	9.5	71.4	7.5	2.8	1.6	7.2	0.78	11

[a] Equation for predicting pregnancy rates of lactating female elk (Y), where x = % area with DDE >2.58 kcal/g and $y = e^{(-1.709\ +\ 0.157x)}/1 + e^{(-1.709\ +\ 0.157x)}$.

[b] Equation for predicting percent body fat of lactating female elk (Y), where x = % area with DDE >2.75 kcal/g and $y = 6.1 + 0.43x$. For landscapes with 0% area of DDE >2.75 kcal/g, percent body fat = 6.1%, which is the Y intercept of above equation. Predictions of body fat are capped at 15% when using this equation because of limitations in inference in making body fat predictions at higher levels.

[c] The DDE values (kcal/g) for classes were 1 = <2.40; 2 = 2.40–2.58; 3 = >2.58–2.75; 4 = >2.75–2.83; 5 = >2.83–2.90; 6 = >2.90.

would increase pregnancy rates from the baseline of 0.63 currently to 0.81; this level of increase is biologically significant (Proffitt et al. 2016).

The shifts to higher nutrition classes are primarily from class 2 to class 3 under option 1, and from class 2 to class 6 under option 2 (Table 13). Thus, the nutritional change under option 2 shifts more area to the highest nutritional class than option 1. Superior nutrition under option 2 is due to clearcutting used as the silvicultural approach for timber harvest, which provides the lowest canopy cover and highest nutritional response (Table 12; Cook et al. 2018). Nutritional results for option 3 are the same as option 2.

Nutritional improvements and effects on pregnancy rates and body fat within the 2 local landscapes illustrate the additional, positive effects of silviculture (Table 13). On local landscape 1, the percent area of DDE in classes 3–6 would increase from 12.4% currently to 15.5% under options 1 and 2 (Table 13); the percent area of DDE in classes 4–6 would increase from 5.6% currently to 8.8% under options 1 and 2 (Table 13). The increased area of better nutrition classes in local landscape 1 is predicted to increase pregnancy rates for lactating female elk from 0.56 currently to 0.67, and increase percent body fat from 9% to 10% under both options (Figs. 12 and 13; Table 13). Changes in pregnancy rates and percent body fat of female elk on local landscape 2 resulting from option 2 are superior to those of local landscape 1 (Table 13). The higher pregnancy rates and body fat predicted on local landscape 2 under option 2 reflect the larger area of clearcutting resulting in a greater spatial shift to the highest nutrition class (class 6; Table 13). Nutritional results for option 3 are the same as option 2.

As with results for the regional landscape, nutritional increases for local landscape 2 are superior for option 2 versus 1 because clearcutting was used as the regeneration method compared to commercial thinning under option 1. Clearcutting produces an overhead canopy cover of 0%, which yields the highest increase in DDE (Cook et al. 2018). Clearcutting under option 2 thus results in substantially higher levels of DDE, with the most increase in the highest nutrition class (class 6; Fig. 31; Table 13).

Commercial thinning under option 1 does not reduce overhead canopy cover sufficiently to detect a measureable increase in higher nutrition classes and associated animal performance compared to the base condition (Table 13). Canopy cover levels of 40% or 60%, often associated with commercial thinning under the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994*a*, *b*), yield substantially lower levels of DDE compared to an overhead canopy cover of 0% that is associated with clearcutting (Table 12).

Interpreting the nutritional improvements and their predicted benefits to pregnancy rates and body fat of females in local landscapes 1 and 2 are similar to those for the regional landscape. Specifically, only small percentages of the landscapes are being treated silviculturally to improve nutrition. Resulting improvements in pregnancy rates and body fat are apparent, but their biological significance could be increased substantially with even a slight increase in areas treated silviculturally beyond the levels treated in local landscapes 1 and 2.

Habitat-Use Predictions, Example 1

Elk use (relative probability of use) is predicted to increase under options 1 and 2, with increased use concentrated in the 2 local landscapes that encompass the proposed silvicultural treatments (Figs. 32 and 33). For options 1 and 2, the proposed silvicultural activities required motorized road access, and 109 km of these roads

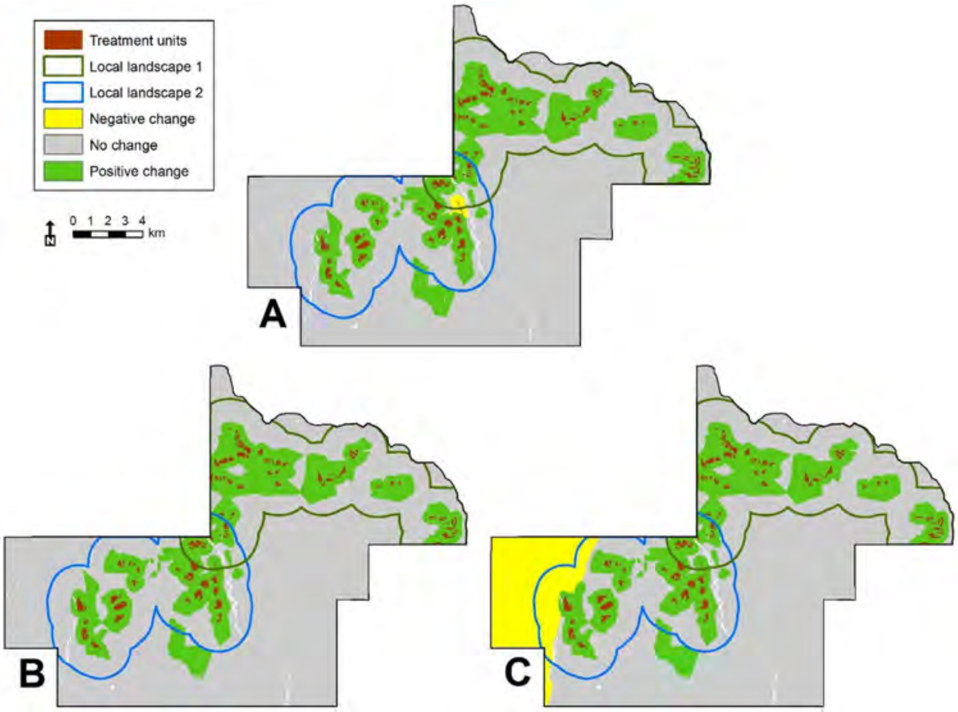


Figure 32. Areas shown as increasing, decreasing, or remaining the same for predicted elk use in the White River drainage of western Washington, USA under option 1 (A), option 2 (B), and option 3 (C) in example 1.

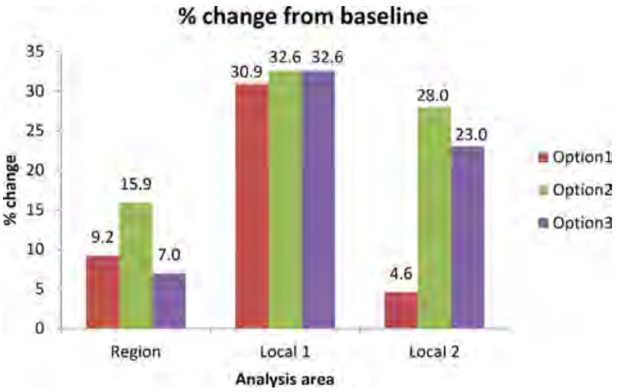


Figure 33. Percent change in relative probability of elk use in the White River drainage of western Washington, USA under each management option relative to the base condition under example 1, as summarized for the regional landscape (region) and local landscapes 1 and 2 (local 1, local 2).

would be closed to public motorized use after timber harvest. For option 3, 71 km of the roads closed under options 1 and 2, providing access to areas of timber harvest, would remain open to public motorized use after harvest. As a result, the predicted increase in elk use is diminished under option 3 compared to options 1 and 2 for the regional landscape, despite the increased nutrition provided by timber harvest (Figs. 32 and 33).

Many of the predicted increases in elk use are substantial: >30% increase in elk use in local landscape 1 under all options, a 28% and 23% increase in local landscape 2 under options 2 and 3, and a 16% increase in use in the regional landscape under option 2 (Fig. 33). The increase in predicted elk use relative to the existing condition was higher for option 2 than for 1 for both the regional landscape and local landscape 2 because clearcutting was the form of timber harvest under option 2 versus commercial thinning under option 1 (Fig. 33). Predicted elk use under option 2 also is higher than option 3 for the regional landscape and local landscape 2, owing to the road closures implemented under option 2 compared to 3 (Fig. 33).

Nutrition Predictions, Example 2

The 3 major land ownerships in the White River under example 2 provide a strong contrast in nutritional conditions (Fig. 34). Private industrial forest supported highest levels of nutrition, followed by Mount Rainier National Park. These 2 land ownerships had 39.4% and 28.4% of their respective areas in nutrition classes 3–6, which are associated with predicted

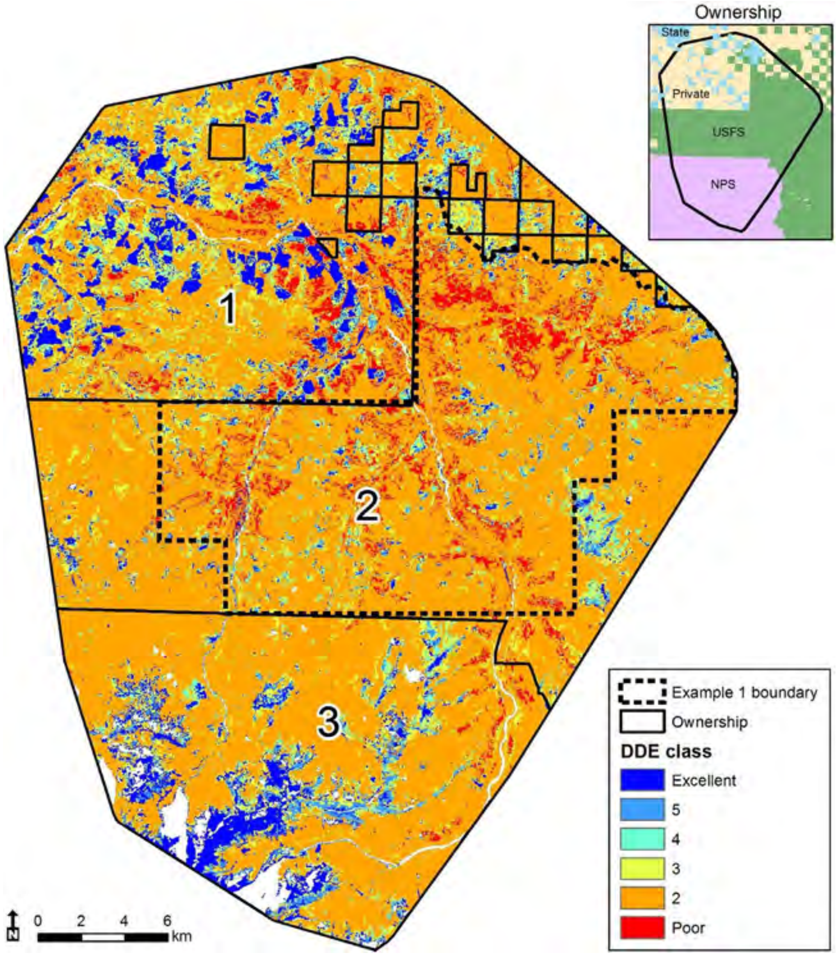


Figure 34. Six elk nutrition classes of dietary digestible energy (DDE) for example 2 mapped by 2010 land ownership, composed of private industrial forest (private, ownership 1), Mt. Baker-Snoqualmie and Wenatchee National Forests (USFS, ownership 2), and Mount Rainier National Park (NPS, ownership 3), Washington, USA. A small percentage of state lands was included in the private category because small tracts of state-owned lands were interspersed among large areas of private industrial forest. Boundaries of the example 1 area lie entirely within the national forest portion of the example 2 area, as outlined in dotted lines. Nutrition classes are estimated for conditions in 2010. Masked areas represent non-habitat (e.g., rock, water) and are displayed in white.

Table 14. Percent area by dietary digestible energy (DDE) class for the regional landscape for the current time period by the 3 major land ownerships discussed in example 2, and the predicted pregnancy rates and percent body fat of lactating female elk based on percent area in nutrition classes 3–6[a] and 4–6[b], respectively. A small percentage of state lands was included in the private category because small tracts of state lands were interspersed among large areas of private industrial forest. We used year 2010 conditions to estimate DDE.

	DDE class[c]							
	1	**2**	**3**	**4**	**5**	**6**	**Pregnancy rate (%)**	**Body fat (%)**
Private	6.0	54.7	17.7	5.9	2.9	12.9	0.99	15
National forest	6.6	79.2	8.4	2.4	1.7	1.7	0.63	9
National park	0.9	70.7	10.1	2.5	5.6	10.2	0.94	14

[a] Equation for predicting pregnancy rates of lactating female elk (Y), where $x = \%$ area with DDE >2.58 kcal/g and $y = e^{(-1.709\ +\ 0.157x)}/1 + e^{(-1.709\ +\ 0.157x)}$.

[b] Equation for predicting percent body fat of lactating female elk (Y), where $x = \%$ area with DDE >2.75 kcal/g and $y = 6.1 + 0.43x$. For landscapes with 0% area of DDE >2.75 kcal/g, percent body fat = 6.1%, which is the Y intercept of above equation. Predictions of body fat are capped at 15% when using this equation because of limitations in inference in making body fat predictions at higher levels.

[c] The DDE values (kcal/g) for classes were 1 = <2.40; 2 = 2.40–2.58; 3 = >2.58–2.75; 4 = >2.75–2.83; 5 = >2.83–2.90; 6 = >2.90.

pregnancy rates approaching 1.0 (Table 14). National forest lands, by contrast, had 14.2% of area in nutrition classes 3–6 and a predicted pregnancy rate of 0.63 (Table 14). Private industrial forest and Mount Rainier National Park also had large areas in nutrition classes 4–6; associated predictions of body fat of lactating females on these ownerships were 15% and 14%, respectively (Table 14). National forests had 5.8% of area in classes 4–6 and predicted body fat of 9% for lactating female elk (Table 14).

Areas of higher nutrition were associated with recent clearcut harvest on private industrial forest or high-elevation meadows within Mount Rainier National Park (Fig. 34). By contrast, national forest lands were dominated by canopy cover levels >70% and associated low nutrition. This high canopy cover reflects the lack of active silviculture during the past 25 years on USFS lands, and lack of wildfire in wilderness and roadless areas over the same period (USDA Forest Service 2012*a*, *b*). However, if option 2 from example 1 is implemented on the national forest portion of example 2 (Fig. 30), the percent area in higher nutrition classes will increase substantially on USFS lands, as shown earlier (Fig. 31; Table 13). Moreover, a slightly larger increase in clearcutting area under option 2 would result in substantially higher elk performance, as discussed earlier.

Habitat-Use Predictions, Example 2

Elk use was predicted to be highest on private industrial forest, followed by Mount Rainier National Park (Fig. 35), as would be expected by the higher levels of nutrition on these land ownerships and limited open roads (Figs. 30 and 34). Only 14% of elk use was predicted to occur on national forest, in contrast to 49% and 37% of use predicted on private lands and Mount Rainier National Park (Fig. 35).

Although these patterns of elk use across ownerships were associated with like patterns in nutrition, the differences in habitat use across ownerships were magnified and diverged further by additional differences in road management (Fig. 30). Mount Rainer National Park had limited open roads. Private lands included a large network of 1,660 km of roads, but only 254 km of these roads were open to unrestricted motorized use by the public. By contrast, national forest lands had 843 km of roads with 666 km of roads open to public motorized use. The combination of higher nutrition and lack of open roads on private land, in contrast to the lower nutrition and a large network of open roads on national forests (Figs. 30 and 34), explains predicted elk use being 3 times higher on private lands than on the adjacent national forests (Fig. 35). Similar differences in nutrition and open roads between Mount Rainier National Park and national forest lands explain the substantially higher predicted elk use in the Park.

Implementation of option 2 of example 1 on national forest lands would reduce differences in elk use across ownerships in example 2. Elk use increases from 13% beforehand (Fig. 35) to 15% afterward on national forest lands. This increase in elk use may seem biologically insignificant, but only a small percentage (1–2%) of the national forest land under example 1 is being treated to achieve this increase. Although predicted elk use would remain higher on private industrial forest and NPS lands, the implementation of option 2 under example 1 illustrates how changes in elk use, and associated distributions of elk, are possible to achieve through coordinated management across ownerships. Obviously, implementing nutritional improvements and road closures over a substantially larger percentage of the national forest lands would increase elk use far more than occurred in example 1, and could be implemented to a degree that shifts in elk distribution to public lands may start to occur.

DISCUSSION

Modeling Applications

The 2 examples illustrate key management uses and benefits of the models, which can be applied to regional and local landscapes to evaluate regional and local conditions. The models also can be applied within and across land ownerships to evaluate current conditions and management options that consider the dominant land uses in Westside landscapes. Results can be used as the basis for setting elk management objectives on public or private lands and for designing management prescriptions to meet the objectives.

Use of the nutrition model in example 1 demonstrated how different types and areas of silvicultural treatments can be evaluated for nutritional improvements, and in turn, how pregnancy rates and body fat of lactating female elk are affected. Regeneration harvest such as clearcutting, for example, resulted in a much stronger nutritional response compared to commercial thinning. That is, a reduction in canopy cover to 0%, *via* clearcutting, or to <10% via shelterwood or seed-tree regeneration harvest, results in a substantially higher increase in DDE per unit area treated than does commercial thinning. Regeneration harvest shifts DDE to the highest nutrition class (class 6; Table 13), which has the greatest

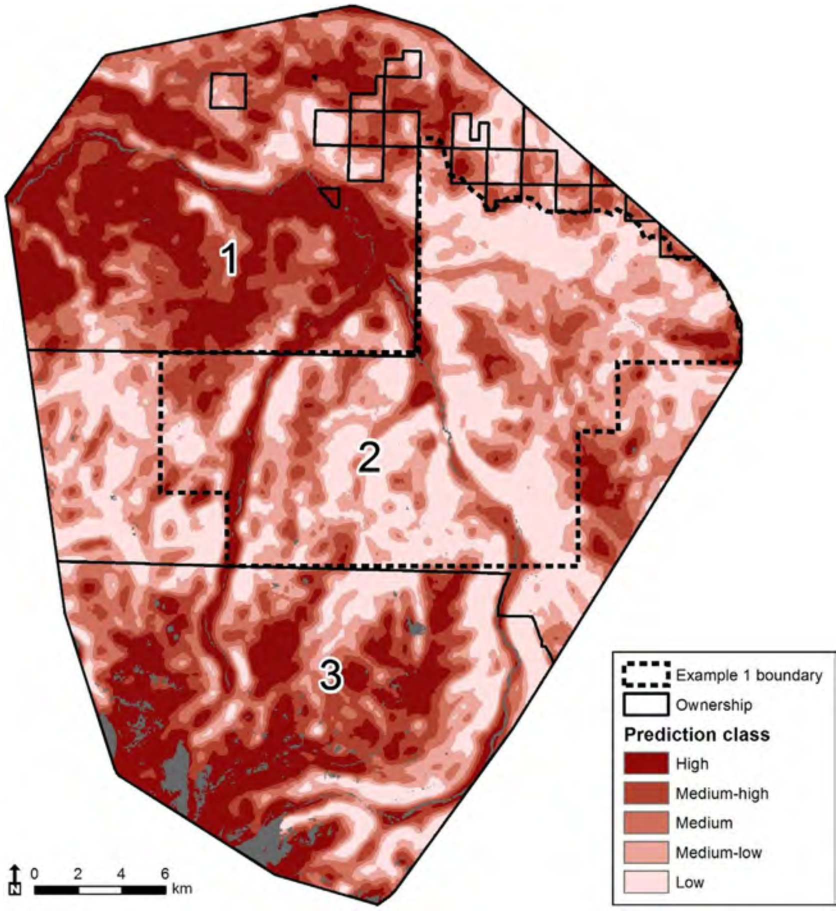


Figure 35. Relative probability of elk use for example 2 mapped by 2010 land ownership, composed of private industrial forest (ownership 1), Mt. Baker-Snoqualmie and Wenatchee National Forests (ownership 2), and Mount Rainier National Park (ownership 3), Washington, USA. A small percentage of state lands was included in the private category because small tracts of state-owned lands were interspersed among large areas of private industrial forest. Example 1 area lies within the national forest portion of the example 2 area, as outlined by dotted lines. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray.

benefit to pregnancy rates and body fat. Commercial thinning or other limited-entry silvicultural practices associated with a moderate reduction in canopy cover (e.g., to 40%) do not shift DDE to the highest nutrition class, and thus have more limited benefits to nutrition and animal performance (e.g., Table 12). However, the nutritional and animal performance benefits of any silvicultural practices that reduce canopy cover are clear, thus demonstrating the benefits of limited-entry silviculture such as commercial or pre-commercial thinning.

Habitat-use modeling in example 1 further demonstrated the need to consider all covariates that affect elk use. An increase in open roads under option 3 offset some of the benefits of increased nutrition, with a reduction in elk use under this option compared to options 1 and 2, despite a substantial increase in nutrition. The patch size of forage enhancements was small, which decreased the distance to cover-forage edges and increased elk use, as reflected by the distance to cover-forage edge covariate. In addition, forage enhancements occurred on gentle slopes, further increasing habitat use based on the slope covariate. Thus, all non-nutrition covariates in the habitat-use model contributed to increased use of the areas of improved nutrition. These results demonstrated how each covariate in the habitat-use model can be managed strategically, in combination, to achieve objectives for elk nutrition, habitat use, performance, and distribution. Results further demonstrate the need to integrate management of all covariates in the habitat-use model if the benefits of increased nutrition are to be realized.

Example 2 demonstrated how a range of management options could be proposed to evaluate the degree to which elk distributions could be shifted to public lands through improved management of nutrition, roads, and arrangement of cover and forage areas, and in context of elk use of slope. If, for example, the objective was to triple elk use on national forest lands in the example 2 landscape, different combinations of silvicultural prescriptions and access management could be identified, mapped, and the models applied to identify which management approaches would meet objectives. Patch size of silvicultural treatments could be designed to further increase use based on distance to cover-forage edges. Silvicultural treatments placed on gentle slopes would further increase elk use of the areas of improved nutrition based on the slope covariate.

Differences in predicted elk use across land ownerships thus provide a foundation to design management strategies and activities to achieve objectives for elk nutrition, habitat use, distribution, and performance. Results can be used for coordinated landscape planning for elk across ownerships, and for consideration of conditions in adjacent ownerships as context for a given land owner's strategy for elk management.

These results have implications for managing elk distributions not only within these landscapes, but in relation to adjacent land ownerships (see Example 2). The substantial increase in habitat use is likely to maintain distribution of elk in the local landscapes, and has potential to shift some of the elk distribution to these areas of national forest from adjacent land ownerships (see Example 2).

The examples also illustrate how the models might be used to address the growing problem of elk shifting their summer distributions from higher-elevation forests to lower-elevation agricultural and urban areas (Thompson and Henderson 1998, Starr 2013). These shifts have been associated with elk finding refuge areas in agricultural and urban areas where they are not hunted, often resulting in long-term, year-round residence (Walter et al. 2011, Starr 2013). Simultaneous with these distributional changes has been the long-term decline in abundance of early-seral forest habitat on public lands in the Westside region (see summary by Wisdom et al. 2018*a*), which may motivate or accelerate landscape shifts by elk to lower-elevation agricultural and urban areas (Starr 2013).

Habitat Modeling for Elk

The Westside nutrition and habitat-use models performed well in predicting elk nutrition, habitat use, distribution, and performance under current conditions. Future sources of uncertainty, however, have the potential to reduce accuracy and utility of the models for management. Rowland et al. (2018) mention future sources of uncertainty that might affect model predictions, which include climate change; associated changes in forest insect dynamics; increased frequency, area, and intensity of wildfires; and changing density and composition of predators and their management. Additional sources of uncertainty include the future role of private forest owners in sustaining areas of high nutrition; the continued trend to further limit or eliminate hunting on private lands, leading to more refuge areas; and increased human activities on public lands, including poaching, that are facilitated by a large network of roads open to motorized access. Future research can address these uncertainties as environmental change continues in the Westside region, and models are modified and adapted to maintain their utility for management.

Despite these future sources of uncertainty, use of the models under current conditions is strongly supported by results from the modeling analyses. Our approach to modeling nutrition and habitat use for elk may provide a useful framework for research and management of wildlife species with coarse-scale habitat requirements. Voluminous but highly disparate data sets on animal use at landscape scales are now commonly available with the advent of GPS and satellite-based telemetry and remotely sensed vegetation parameters. These data can now be assimilated and analyzed for habitat modeling across large areas of a species' range with the use of ubiquitous, coarse-scale GIS data to estimate covariates, and the use of GPS-based telemetry data to estimate animal use. Unfortunately, extensive data sets on animal performance are typically limited for most areas and are more difficult and expensive to acquire.

Taking advantage of these large and disparate data sources for habitat modeling demands more investment in the design of modeling approaches, especially for management uses. New methods of meta-analysis and meta-replication can now be used to develop and validate habitat models across a vast inference space, such as an ecoregion or biome. Our work was based on integration of a wide range of large and disparate data sets to gain knowledge of a species' habitat needs and the evaluation of those needs, at scales meaningful to the species and to management. Use of such methods, and their further improvement with future modeling work, will continue to advance the ecology and management of wildlife species like elk.

MANAGEMENT IMPLICATIONS

Diverse Land Ownerships and Objectives

Elk are typically not the primary focus of management on public or private lands in the Westside region. Public forests throughout the region are under the direction of the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994*a*, *b*), which focuses on sustaining and increasing the abundance of late-seral forest stages for recovery of late-seral wildlife species such as the northern spotted owl and marbled murrelet (*Brachyramphus marmoratus*). During the past 25 years since the Northwest Forest Plan was enacted, the abundance of early-seral vegetation has declined substantially, and now composes a small and declining percentage of public forests in the Westside region (Weisburg and Swanson 2003, Cook et al. 2018). This change contrasts with the historical abundance of early-seral vegetation that occupied up to 35% of forest area in the region (Weisburg and Swanson 2003). The current paucity of early-seral vegetation on public forests has prompted litigation by Native American tribes to prompt restoration of these vegetation types for hunted species such as elk, which are a key subsistence food on public lands ceded for tribal harvest in the region (USDA Forest Service 2001*a*, *b*).

Industrial forest owners, by contrast, typically manage Westside lands for intensive timber harvest, even-aged management, and short rotation lengths. This combination produces large areas of early-seral vegetation with high elk nutrition (Cook et al. 2016, 2018; Geary et al. 2017). However, the degree to which intensive timber management can sustain high elk nutrition also depends on the reforestation methods used to establish commercial conifers after timber harvest (Witmer et al. 1985). Efforts to truncate early-seral forest development and duration to meet goals for industrial forest production may further diminish future maintenance of early-seral conditions (Swanson et al. 2011, 2014). Despite this trend, the large amount of area subjected to clearcutting under short timber harvest rotations (e.g., 30–40 years) on private industrial forest (Geary et al. 2017), and similar rotations on many tribal lands (Vales et al. 2017), are likely to continue to produce substantial areas of high nutrition. Elk use of areas of higher nutrition is further affected by the shape of openings (distance to cover-forage edge), management of roads (distance to roads open to public motorized use), and slope (percent slope), per our habitat-use model.

The challenge of how to address poor and marginal nutritional conditions that dominate public lands throughout the region represents a major dilemma for elk management. Public and private forests occupy an equally large percentage of the Westside region (~44% each; Wisdom et al. 2018*a*); both ownerships thus have a major effect on elk nutrition and habitat use. Under current conditions and those likely to be maintained on public forests under the Northwest Forest Plan, only small areas of public land will meet the summer nutritional requirements of lactating female elk (Cook et al. 2018). This habitat void is likely to result in a population distribution of elk that is largely concentrated on private forests, agricultural lands, and areas closed to hunting near or within smaller towns or areas of rural-urban interface. An elk distribution largely concentrated on private lands will severely limit opportunities for hunting and viewing of elk on public lands, as well as eliminate or substantially curtail traditional tribal hunting on ceded public lands.

To achieve desired objectives for elk nutrition, habitat use, distribution, and performance, within and across land ownerships, explicit management prescriptions for elk must be integrated with other prescriptions for multiple-use management. Research is needed that evaluates the trade-offs and spatial and temporal optimization of different landscape management objectives for different sets of species and habitats, including elk and other early-seral versus late-seral species. The Northwest Forest Plan is currently under review for renewal, following the time requirements for revision established when it was implemented (USDA Forest Service and USDI Bureau of Land Management 1994*a*, *b*). The historically low abundance of early-seral vegetation on public forests in the Westside region will likely be part of the public's discussion of possible refinements to the Northwest Forest Plan; this discussion is further justified by the large number of early-seral wildlife species in the Westside region (Hagar 2007) and strong tribal interest in the topic (USDA Forest Service 2001*a*, *b*).

Poor nutrition and extensive areas of open roads are obviously 2 key factors that pose challenges to achieving desired elk habitat use, population distributions, and associated animal performance across ownerships at landscape scales in the Westside region (Cook et al. 2018, Rowland et al. 2018). These challenges often warrant evaluation and management of elk conditions across multiple land ownerships to identify and maximize opportunities for maintaining elk distributions in desired areas for recreation objectives. New agreements between public and private forest managers could be considered to more fully coordinate the management of nutrition and roads in a manner that provides support for increased elk distribution within and near public lands; or to provide additional public recreational opportunities for elk viewing and hunting on private lands as a mitigation for lack of early-seral vegetation being sustained on public lands. Such coordination is now possible in using the spatially explicit nutrition and habitat-use models. Roads open to public motorized use are common on public lands and have the potential to substantially reduce elk use of areas of higher nutrition and shift or maintain distributions away from public lands (per example 2).

Stakeholder Engagement in the Modeling Process and Applications

Effective development and management applications of the nutrition and habitat-use models were facilitated by long-term engagement of key stakeholders in the Westside region. Ideas for the modeling came from hunting conservation organizations, who organized meetings with public land managers and scientists in the region to discuss elk management issues and associated modeling needs. These discussions led to a federal advisory group's formal recommendations to the Secretaries of Interior and Agriculture to begin a new round of elk habitat modeling in the Westside region (Wisdom et al. 2018*a*). These recommendations prompted federal agency leaders to recruit scientists to lead the modeling process.

Stakeholder engagement continued and grew as part of the formal modeling process. The group of scientists recruited to conduct the modeling was affiliated with a diverse set of tribal, state, federal, university, and private partners who had a direct stake in elk research and management. No interested partners were excluded. Data used for modeling were provided by 5 Native American tribes, a state wildlife agency (Washington Department of Fish and Wildlife), the timber industry (National Council for Air and Stream Improvement and associated timber companies), and a university (Oregon State University; Table 7). Funding and staffing support for the work also was diverse and substantial, including over 20 different tribal, state, federal, private, and university sources.

The diversity of science and management engagement in the modeling process was further enhanced by a series of meetings and 2 formal workshops conducted by the scientists during model development (https://www.fs.fed.us/pnw/research/elk/westside/index.shtml). Meetings and workshops were used to share modeling ideas and preliminary results, and obtain feedback from stakeholders about how the models could be improved for management applications. The process was transparent and continuous throughout, allowing the models to be improved iteratively through stakeholder input. In addition, the draft models were beta-tested by a large group of tribal, state, and federal biologists to further evaluate and improve management utility. Results from these tests helped refine and finalize the models for application in practical ways at spatial and temporal scales of interest to managers. Finally, the draft models underwent early and rigorous peer review before manuscript submission for publication to address the scientific merits and rigor of the work and facilitate timely management uses before formal publication.

In response to these activities, the USFS and USDI Bureau of Land Management formally endorsed the models as official corporate tools to evaluate and manage elk nutrition and habitat use on federal lands in the Westside region. The endorsement was outlined in a joint letter from both agencies dated 21 February 2013 directed to their land managers and biologists. This process and support led to early adoption and effective use of the models on federal (e.g., Doerr 2016) and tribal lands (Vales et al. 2017). The effectiveness of continuous and transparent stakeholder engagement in elk modeling illustrates the benefits of such a process in facilitating management uses of wildlife habitat models as a partnership between scientists and stakeholders.

Adaptive Management Partnerships

Given the significant ecological and economic benefits of elk, their cultural connection with Native American Tribes, and the socio-political status of the species, we anticipate increased focus on restoration of early-seral vegetation to benefit elk and other early-seral species in the Westside region (Swanson et al. 2014). Adaptive management, as originally defined by Walters (1986), is a key part of the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994*a*, *b*); its renewal may provide additional opportunities to design, implement, and test concepts of early-seral management for associated wildlife (Hagar 2007).

Use of adaptive management to enhance elk habitat would be particularly effective if integrated with state wildlife agency goals for elk within and across state wildlife management units. The Washington Department of Fish and Wildlife and the Oregon Department of Fish and Wildlife have established elk population goals for their wildlife management units (Washington Department of Fish and Wildlife 2002*a, b, c*, 2004, 2008, 2013; Oregon Department of Fish and Wildlife 2003, 2005), but detailed objectives have not been established for managing elk distributions and performance within and across land ownerships within the units. These additional objectives would provide essential context for effective management of nutrition and habitat use with model applications. Adaptive management approaches for elk are further complicated by management of roads open to public motorized use, which often is a polarizing issue among many public groups (Stern et al. 2009). Resolving the road management issue to meet elk objectives will require close coordination and planning between elk managers and diverse public interests.

Despite these challenges, our validated models provide a strong scientific basis for management of elk habitats and populations. All landowners now have opportunities to use the models to coordinate management within and across ownerships to achieve goals for elk distribution and performance. Development and use of habitat models like those described here could provide similar opportunities for management in other areas of elk range in North America, where elk constitute a major economic and social resource, and where debate and conflict regarding management of population distributions and performance are currently unresolved (Wisdom and Cook 2000).

SUMMARY

Distributions of elk in western North America are shifting from public to private lands, leading to foregone recreational opportunities for the public and conflicts with private landowners. Tools that predict nutritional resources and distributions of elk across large landscapes can benefit management of elk across land ownerships. We developed and validated regional models of elk nutrition and habitat use for application in western Oregon and Washington, USA (Westside).

We used data collected during foraging experiments with captive female elk and field measurements of site characteristics from 349 macroplots in 3 Westside study areas to develop the nutrition model. The habitat-use model incorporated 13 unique telemetry data sets of female elk from multiple sources and 7 study areas.

- Predictions of dietary digestible energy (DDE) varied widely among predominant potential natural vegetation (PNV) zones, with the preponderance of Westside landscapes failing to meet basic requirements of DDE for lactating female elk. Generally, highest DDE levels occurred in zones occupying higher elevations and in early-seral communities. Lowest DDE levels occurred at lower elevations and in closed-canopy forests.
- We found strong regional gradients in DDE north to south (higher to lower) in the Cascades and east to west from the Cascades to the Coast Range. Autumn body fat and pregnancy rates of wild lactating elk varied similarly across the region.
- We evaluated the nutrition model by comparing predicted DDE levels to higher order responses of elk, including resource selection, autumn body fat, and pregnancy rates. Elk strongly selected for areas providing relatively high DDE. Mean autumn body fat and pregnancy rates of lactating elk in 9 Westside elk populations were positively correlated to percent area providing DDE levels that met or exceeded basic requirement (>2.58 kcal/g DDE).
- Disturbance regime and forest succession also were closely linked to DDE, suggesting that habitat management, such as thinning, on Westside summer ranges can significantly influence elk distributions and productivity (e.g., pregnancy rates).
- The nutrition model demonstrated that data on foraging dynamics and ungulate nutrition collected at fine scales can reliably index performance of elk populations at broad scales in the Westside region.
- We used a hierarchical approach to develop the habitat-use model by considering individual study areas as replicates to predict relative probability of use by elk across the Westside.
- The regional habitat-use model best supported by the empirical data had 4 covariates: DDE, distance to nearest road open to motorized use by the public, distance to cover-forage edge, and slope. Predicted elk use was greater in areas with higher DDE, farther from open roads, closer to cover-forage edges, and gentler slopes.
- Our regional habitat-use model performed well using independent telemetry data, with high correlation between predicted and observed use by elk in most validation sites.
- We demonstrated the management utility of the nutrition and habitat-use models through 2 examples in western Washington, comparing nutritional conditions and predicted use by elk across land ownerships and scales in response to several management scenarios. Results indicated that relatively small-scale improvements in habitat (e.g., road closures, clearcuts, or thinning) can lead to biologically meaningful increases in animal performance and greater relative probability of use by elk.
- We conducted a meta-analysis of disparate data sets on elk habitat use synthesized from multiple areas and years for model selection and validation. We found consistent patterns of habitat use across the populations sampled. This replicable approach can be used for other wildlife species to better understand regional patterns of use and thus improve management efficiency and consistency. We further demonstrated that mechanistic processes of nutrition and human disturbance in our study areas can be successfully modeled with coarse spatial data to accurately estimate elk use at regional scales.
- Our models and approaches can inform management (e.g., manipulating landscapes through actions such as silviculture and road management) to improve elk nutrition, habitat use, distributions, and performance.

ACKNOWLEDGMENTS

The success of the Westside elk modeling project was due in large part to the generous sharing of elk telemetry data from many sources, data collected prior to our efforts and for other reasons. We thank the following people and organizations for providing data for our meta-analysis: Muckleshoot Indian Tribe (D. Vales), Coquille Indian Tribe (M. Pope), Lower Elwha Klallam Tribe (K. Sager-Fradkin), Makah Indian Tribe (R. McCoy), Quileute Tribe (F. Geyer), Sauk-Suiattle Tribe (C. Danilson), and Washington Department of Fish and Wildlife (S. Harris). In particular the availability of abundant, high-quality data from the Muckleshoot Indian Tribe was instrumental in our project's success. We are also grateful for constructive feedback offered by the Westside model beta testers: K. Aluzas, J. Belcher, C. Chandler, J. Chapman, R. Davis, F. Dobler, J. Doerr, A. Duff, J. Hadwen, J. Hobson, C. McDonald, B. Mecklem, A. Miller, L. Renan, and S. Weber. Financial and logistical support for beta-testing were provided by R. Alvarado, W. Otani, and T. Thompson. We also appreciate helpful insights from other Westside model users: A. Geary, M. Gebben, E. Merrill, K. Proffitt, L. Shipley, and A. Yost. We thank R. Davis, L. McDonald, H. Sawyer, P. Singleton, and S. McCorquodale for fruitful discussions about our modeling process. B. Galleher, M. Gregory, R. Kennedy, J. Ohmann, and H. M. Roberts offered guidance on use of gradient nearest neighbor vegetation data, and D. Bernard provided GIS layers from the Forest Service. We thank P. James, D. Keenan, S. Paz, J. Plumage, and D. Schrenk of the Mt. Baker-Snoqualmie National Forest for providing data and guidance for the example model applications in the White River and Snoqualmie areas. T. DeMeo and C. McCain provided insights on abundance of elk forage species in Westside sites. We thank A. Gonzalez, B. Brown, M. Fallon, S. Frazier, S. Klump, J. Lehmkuhl, J. Murray, S. Seaberg, and J. Stangell for editing road layers used in our models, J. Ottman for document formatting, A. Cox for expert editorial support, B. Hoenes for sharing maps from Washington elk herds, and D. Edge and D. Sanchez for their assistance with elk modeling workshops. R. Juarez and L. Veilleux provided translations of the abstract. H. Sawyer provided useful review of an earlier draft of the manuscript, and thoughtful comments by Editor E. Hellgren, M. Hebblewhite, T. Hobbs, and an anonymous reviewer led to major and substantive improvements in the manuscript.

LITERATURE CITED

Adams, D. C., J. Gurevitch, and M. S. Rosenberg. 1997. Resampling tests for meta-analysis of ecological data. Ecology 78:1277–1283.

Adams, D. M., and G. S. Latta. 2007. Timber trends on private lands in western Oregon and Washington: a new look. Western Journal of Applied Forestry 22:8–14.

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076–1088.

Alaback, P. B., and F. R. Herman. 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. Canadian Journal of Forest Research 18:1522–1530.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 63:502–513.

Austin, D. D., P. J. Urness, and L. C. Fierri. 1983. Spring livestock grazing affects crested wheatgrass regrowth and winter use by mule deer. Journal of Range Management 36:589–593.

Averett, J. P., B. A. Endress, M. M. Rowland, B. J. Naylor, and M. J. Wisdom. 2017. Wild ungulate herbivory suppresses deciduous woody plant establishment following salmonid stream restoration. Forest Ecology and Management 391:135–144.

Babin, J.-S., D. Fortin, J. F. Wilmshurst, and M.-E. Fortin. 2011. Energy gains predict the distribution of plains bison across populations and ecosystems. Ecology 92:240–252.

Barbknecht, A. E., W. S. Fairbanks, J. D. Rogerson, E. J. Maichak, B. M. Scurlock, and L. L. Meadows. 2011. Elk parturition site selection at local and landscape scales. Journal of Wildlife Management 75:646–654.

Beck, J. L., J. M. Peek, and E. K. Strand. 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. Journal of Wildlife Management 70:283–294.

Benkobi, L., M. A. Rumble, G. C. Brundige, and J. J. Millspaugh. 2004. Refinement of the Arc-Habcap model to predict habitat effectiveness for elk. U.S. Forest Service Research Paper RMRS-RP-51, Fort Collins, Colorado, USA.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? American Naturalist 180:407–424.

Boonstra, R. 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. Functional Ecology 27:11–23.

Borenstein, M., L. V. Hedges, J. P. T. Higgins, and H. R. Rothstein. 2009. Introduction to meta-analysis. First edition. Wiley, West Sussex, United Kingdom.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421–431.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:1–20.

Bronson, F. H., and J. M. Manning. 1991. The energetic regulation of ovulation: a realistic role for body fat. Biology of Reproduction 44:945–950.

Brunt, K., and C. Ray. 1986. Seasonal range habitat suitability index models for Vancouver Island Roosevelt elk. Technical Report, Ministry of Environment Wildlife Branch, Campbell River, British Columbia, Canada.

Brunt, K. R., D. Q. Becker, and J. A. Youds. 1989. Vancouver Island Roosevelt elk/intensive forestry interactions: Phase I (1981-1986). Job Completion Report IWIFR-33. British Columbia Ministry of the Environment and Ministry of Forestry, Victoria, British Columbia, Canada.

Bunnell, F. L., and D. J. Vales. 1990. Comparison of methods for estimating forest overstory cover: differences among techniques. Canadian Journal of Forestry Research 20:101–107.

Bunnell, S. D., M. L. Wolfe, M. W. Brunson, and D. E. Potter. 2002. Recreational use of elk. Pages 701–748. *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cameron, A. C., and P. K. Trivedi. 1998. Regression analysis of count data. Cambridge University Press, New York, New York, USA.

Caughley, G. 1979. What is this thing called carrying capacity? Pages 1–8. *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior and management. University of Wyoming Press, Laramie, USA.

Christensen, A. G., L. J. Lyon, and J. W. Unsworth. 1993. Elk management in the Northern Region: considerations in forest plan updates or revisions. U.S. Department of Agriculture, Forest Service, Intermountain Research Station General Technical Report INT-303, Ogden, Utah, USA.

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012*a*. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society B 279:4407–4416.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012*b*. Effects of humans on behavior of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7(11):e50611. https://doi.org/10.1371/journal.pone.0050611.

Clark, D. A. 2014. Implications of cougar prey selection and demography on population dynamics of elk in northeast Oregon. Dissertation, Oregon State University, Corvallis, USA.

Clark, D. A., G. A. Davidson, B. K. Johnson, and R. G. Anthony. 2014. Cougar kill rates and prey selection in a multiple-prey system in northeast Oregon. Journal of Wildlife Management 78:1161–1176.

Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.

Coe, P. K., B. K. Johnson, J. W. Kern, S. L. Findholt, J. G. Kie, and M. J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. Journal of Range Management 54:A51–A76.

Coe, P. K., B. K. Johnson, M. J. Wisdom, J. G. Cook, M. Vavra, and R. M. Nielson. 2011. Validation of elk resource selection models with spatially independent data. Journal of Wildlife Management 75:159–170.

Coffin, A. W. 2007. From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transport Geography 15:396–406.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115–1126.

Cole, E. K., M. D. Pope, and R. G. Anthony. 2004. Influence of road management on diurnal habitat use of Roosevelt elk. Northwest Science 78:313–321.

Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. Journal of Wildlife Management 47:646–663.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management 65:926–940.

Cook, J. G., R. C. Cook, R. Davis, and L. L. Irwin. 2016. Nutritional ecology of elk during summer and autumn in the Pacific Northwest. Wildlife Monographs 195.

Cook, J. G., R. C. Cook, R. W. Davis, M. M. Rowland, R. M. Nielson, M. J. Wisdom, J. M. Hafer, and L. L. Irwin. 2018. Development and evaluation of a landscape nutrition model for elk in western Oregon and Washington. Pages 13–30 *in* Rowland, M. M., M. J. Wisdom, R. M. Nielson, J. G. Cook, R. C. Cook, B. K. Johnson, P. K. Coe, J. M. Hafer, B. J. Naylor, D. J. Vales, R. G. Anthony, E. K. Cole, C. D. Danilson, R. W. Davis, F. Geyer, S. Harris, L. L. Irwin, R. McCoy, M. D. Pope, K. Sager-Fradkin, and M. Vavra. Modeling elk nutrition and habitat use in western Oregon and Washington. Wildlife Monographs 199:1–69.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. DelCurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155.

Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. Journal of Wildlife Management 60:528–541.

Cook, J. G., T. W. Stutzman, C. W. Bowers, K. A. Brenner, and L. L. Irwin. 1995. Spherical densiometers produce biased estimates of forest canopy cover. Wildlife Society Bulletin 23:711–717.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management 65:988–997.

Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. McCorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, S. L. Murphie, K. A. Schoenercker, and P. J. Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. Journal of Wildlife Management 74:880–896.

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. McCorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184.

Coughenour, M. B., and R. J. Singer. 1996. Yellowstone elk population responses to fire—a comparison of landscape carrying capacity and spatial–dynamic ecosystem modeling approaches. Proceedings of the Biennial Conference on the Greater Yellowstone Ecosystem 2:169–179.

Creel, S., D. Christianson, S. Lily, and J. A. Winnie, Jr. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:960.

Cushman, S. A., K. S. McKelvey, C. H. Flather, and K. McGarigal. 2008. Do forest community types provide a sufficient basis to evaluate biological diversity? Frontiers in Ecology and Environment 6:13–17.

Dale, B. W., L. G. Adams, W. B. Collins, K. Joly, P. Valkenburg, and R. Tobey. 2008. Stochastic and compensatory effects limit persistence of variation in body mass of young caribou. Journal of Mammalogy 89:1130–1135.

Dalton, M. M., K. D. Dello, L. Hawkins, P. W. Mote, and D. E. Rupp. 2017. The third Oregon climate assessment report. Oregon Climate Change Research Institute, College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, USA.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33:140–158.

Davidson, G. A., B. K. Johnson, J. H. Noyes, B. L. Dick, and M. J. Wisdom. 2012. Effect of archer density on elk pregnancy rates and conception dates. Journal of Wildlife Management 76:1676–1685.

DeVore, R. M., M. J. Butler, M. C. Wallace, S. L. Liley, A. A. Mertz, S. E. Sesnie, and P. S. Gipson. 2016. Elk resource selection patterns in a semiarid riparian corridor. Journal of Wildlife Management 80:479–489.

DeYoung, C. A., T. E. Fulbright, D. G. Hewitt, D. B. Wester, and D. A. Draeger. 2018. Linking white-tailed deer density, nutrition, and vegetation in a stochastic environment. Wildlife Monographs:in press.

Doerr, J. 2016. Analysis of Westside elk model for changes in DDE under Willamette Forest Plan. U.S. Forest Service, Willamette National Forest, Blue River, Oregon, USA. https://www.fs.fed.us/pnw/research/elk/pdfs/WillametteNF_WestsideNutritionModel_ForestPlan.pdf.

Durner, G. M., D. C. Douglas, R. M. Nielson, S. C. Amstrup, T. L. McDonald, I. Stirling, M. Mauritzen, E. W. Born, Ø. Wiig, E. DeWeaver, M. C. Serreze, S. E. Belikov, M. M. Holland, J. Maslanik, J. Aars, D. A. Bailey, and A. E. Derocher. 2009. Predicting 21st-century polar bear habitat distribution from global climate models. Ecological Monographs 79:25–58.

Edge, W. D., C. L. Marcum, and S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. Journal of Wildlife Management 51:844–851.

Edge, W. D., S. L. Olson-Edge, and L. L. Irwin. 1990. Planning for wildlife in national forests: elk and mule deer habitats as an example. Wildlife Society Bulletin 18:87–98.

Ewald, M., C. Dupke, M. Heurich, J. Müller, and B. Reineking. 2014. LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. Forests 5:1374–1390.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society B 365: 2233–2244.

Fortin, D., R. Courtois, P. Etcheverry, C. Dussault, and A. Gingras. 2008. Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. Journal of Applied Ecology 45:1392–1400.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B 365:2187–2200.

Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing roads networks. Journal of Applied Ecology 45:1504–1513.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20:273–287.

Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41: 201–212.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, USA.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. American Naturalist 138:478–498.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecological Systems 31:367–393.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B 365:2255–2265.

Garroutte, E. L., A. J. Hansen, and R. L. Lawrence. 2016. Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the Greater Yellowstone Ecosystem. Remote Sensing 8:404–411.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 91–154 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Geary, A. B., E. H. Merrill, J. G. Cook, R. C. Cook, and L. L. Irwin. 2017. Elk nutritional resources: herbicides, herbivory and forest succession at Mount St. Helens. Forest Ecology and Management 401:242–254.

Gerhart, K. L., R. G. White, R. D. Cameron, D. E. Russell, and D. Van de Wetering. 1997. Pregnancy rate as an indicator of nutritional status in *Rangifer*: implications of lactational infertility. Rangifer 17:21–24.

Goldstein, M. I., A. J. Poe, L. H. Suring, R. M. Nielson, and T. L. McDonald. 2010. Brown bear den habitat and winter recreation in south-central Alaska. Journal of Wildlife Management 74:35–42.

Griffin, K. A, M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. Journal of Animal Ecology 80:1246–1257.

Guldemond, R., and R. Van Aarde. 2008. A meta-analysis of the impact of African elephants on savanna vegetation. Journal of Wildlife Management 72:892–899.

Hagar, J. C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: a review. Forest Ecology and Management 246:108–122.

Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37:816–830.

Hall, F. C., L. W. Brewer, J. F. Franklin, and R. L. Warner. 1985. Plant communities and stand conditions. Pages 19–31 *in* E. R. Brown, editor. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 1 – chapter narratives. U.S. Forest Service Publication R6-F&WL-192-1985. U.S. Government Printing Office, Washington, D.C., USA.

Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173–182.

Hamann, A., T. Wang, D. L. Spittlehouse, and T. Q. Murdock. 2013. A comprehensive, high-resolution database of historical and projected climate surfaces for western North America. Bulletin of the American Meteorological Society 94:1307–1309.

Hanley, T. A. 1983. Black-tailed deer, elk, and forest edge in a western Cascades watershed. Journal of Wildlife Management 47:237–242.

Hanley, T. A., R. L. Deal, and E. H. Orlikowska. 2006. Relations between red alder composition and understory vegetation in young mixed forests of southeast Alaska. Canadian Journal of Forest Research 36:738–748.

Hanley, T. A., D. E. Spalinger, K. J. Mock, O. L. Weaver, and G. M. Harris. 2012. Forage resource evaluation system for habitat—deer: an interactive deer habitat model. U.S. Forest Service General Technical Report PNW-GTR-858, Portland, Oregon, USA.

Harder, J. D., and R. L. Kirkpatrick. 1994. Physiological methods in wildlife research. Pages 275–306 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Harju, S. M., M. R. Dzialak, R. G. Osborn, L. D. Hayden-Wing, and J. B. Winstead. 2011. Conservation planning using resource selection models: altered selection in the presence of human activity changes spatial prediction of resource use. Animal Conservation 14:502–511.

Harper, J. A. 1987. Ecology and management of Roosevelt elk in Oregon. Oregon Department of Fish and Wildlife, Portland, USA.

Haufler, J. B. 1994. An ecological framework for forest planning for forest health. Journal of Sustainable Forestry 2:307–316.

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. Journal of Animal Ecology 74:226–233.

Hebblewhite, M. 2006. Linking predation risk and forage to ungulate population dynamics. Dissertation, University of Alberta, Edmonton, Canada.

Hebblewhite, M., and D. T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B 365:2303–2312.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage-maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135–2144.

Henderson, J. A., R. D. Lesher, D. H. Peter, and D. C. Shaw. 1992. Field guide to the forested plant associations of the Mt. Baker–Snoqualmie National Forest. R6–ECOL–TP–028–91. U.S. Forest Service, Pacific Northwest Region, Portland, Oregon, USA.

Hershey, D. M., and T. A. Leege. 1982. Elk movements and habitat use on a managed forest in north-central Idaho. Idaho Department of Fish and Game Wildlife Bulletin 10, Boise, USA.

Hester, A. J., L. Edenius, R. M. Buttenshchøn, and A. T. Kuiters. 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry 73:381–391.

Hett, J., R. Taber, J. Long, and J. Schoen. 1978. Forest management policies and elk summer carrying capacity in the *Abies amabilis* forest, western Washington. Environmental Management 2:561–566.

Heydlauff, A. L., P. R. Krausman, W. W. Shaw, and S. E. Marsh. 2006. Perceptions regarding elk in northern Arizona. Wildlife Society Bulletin 34:27–35.

Hilbe, J. M. 2008. Negative binomial regression. Cambridge University Press, New York, New York, USA.

Hjeljord, O., and T. Histol. 1999. Range-body mass interactions of a northern ungulate-a test of hypothesis. Oecologia 119:326–339.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Hobbs, N. T. 2003. Challenges and opportunities in integrating ecological knowledge across scales. Forest Ecology and Management 18:223–238.

Hobbs, N. T., D. L., Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy- and nitrogen-based estimates of elk winter-range carrying capacity. Journal of Wildlife Management 46:12–21.

Hobbs, N. T., and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management 49:814–822.

Hosmer, D. W. Jr., S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression. Third edition. John Wiley and Sons, Hoboken, New Jersey, USA.

Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. Macmillan, New York, New York, USA.

Hurley, M. A., M. Hebblewhite, J.-M. Gaillard, S. Dray, K. A. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. Philosophical Transactions of the Royal Society B 369:1–15.

Hurley, M. A., and G. A. Sargeant. 1991. Effects of hunting and land management on elk habitat use, movement patterns, and mortality in western Montana. Pages 94–98 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers. Proceedings of elk vulnerability symposium. Montana State University, Bozeman, USA.

Hutchins, N. R. 2006. Diet, nutrition, and reproductive success of Roosevelt elk in managed forests of the Olympic Peninsula, Washington. Thesis, Humboldt State University, Arcata, California, USA.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Illius, A. W., and I. J. Gordon. 1999. Scaling up from functional response to numerical response in vertebrate herbivores. Pages 397–497 *in* H. Olff, V. K. Brown, and R. H. Drent, editors. Herbivores: between predators and plants. Blackwell Science, Oxford, United Kingdom.

Jenkins, K., and E. Starkey. 1996. Simulating secondary succession of elk forage values in a managed forest landscape, western Washington. Environmental Management 20:715–724.

Johnson, B. K., A. A. Ager, J. H. Noyes, and N. J. Cimon. 2005. Elk and mule deer responses to variation in hunting pressure. Pages 127–138 *in* M. J. Wisdom, technical editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Allen Press, Lawrence, Kansas, USA.

Johnson, B. K., P. K. Coe, and R. L. Green. 2013. Abiotic, bottom-up, and top-down influences on recruitment of Rocky Mountain elk in Oregon: a retrospective analysis. Journal of Wildlife Management 77:102–116.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64:685–697.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia 127:590–602.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, D. H. 2001. Validating and evaluating models. Chapter 7 *in* T. M. Shenk and A. B. Franklin, editors. Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, D.C., USA.

Johnson, D. H. 2002. The importance of replication in wildlife research. Journal of Wildlife Management 66:919–932.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 126–168 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Kie, J. G., A. A. Ager, and R. T. Bowyer. 2005. Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. Landscape Ecology 20:289–300.

Kohlmann, S. G. 1999. Adaptive fetal sex allocation in elk: evidence and implications. Journal of Wildlife Management 63:1109–1117.

Leege, T. A. 1984. Guidelines for evaluating and managing summer elk habitat in northern Idaho. Idaho Department of Fish and Game Bulletin 9, Boise, USA.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology 82:1183–1191.

Levins, R. 1966. The strategy of model building in population biology. American Scientist 54:421–431.

Lone, K., L. E. Loe, T. Gobakken, J. D. C. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos 123:641–651.

Long, R. A., J. L. Rachlow, and J. G. Kie. 2008. Effects of season and scale on response of elk and mule deer to habitat manipulation. Journal of Wildlife Management 72:113–1142.

Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry 79:658–660.

Lyon, L. J., and A. G. Christensen. 2002. Elk and land management. Pages 557–581 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

Lyon, L. J., T. N. Lonner, J. P. Weigand, C. L. Marcum, W. D. Edge, J. D. Jones, D. W. McCleerey, and L. L. Hicks. 1985. Coordinating elk and timber management: Final report of the Montana Cooperative Elk-Logging Study. Montana Department of Fish, Wildlife, and Parks, Helena, USA.

Manly, B. F. J. 2006. Randomization, bootstrap and Monte Carlo methods in biology. Third edition. CRC Press, Boca Raton, Florida, USA.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691–1707.

McArt, S. H., D. E. Spalinger, W. B. Collins, E. R. Schoen, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology 90:1400–1411.

McCabe, R. E. 2002. Elk and Indians: then again. Pages 121–198 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

McCorquodale, S. M. 2003. Sex-specific movements and habitat use by elk in the Cascade Range of Washington. Journal of Wildlife Management 67:729–741.

McCorquodale, S., S. Knapp, M. Davison, J. Bohannon, C. Danilson, and C. Madsen. 2012. A population assessment for the North Cascades elk herd, 2006–2011. Washington Department of Fish and Wildlife, Olympia, USA.

McDonald, T. L., B. F. J. Manly, R. M. Nielson, and L. V. Diller. 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. Journal of Wildlife Management 70:375–383.

McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. Pages 105–142 *in* P. Zarembka, editor. Frontiers in econometrics. Academic Press, New York, New York, USA.

Meisingset, E. L., L. E. Loe, O. Brekkum, B. Van Moorter, and A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77:181–191.

Merrill, E. H. 1987. Habitat ecology and population dynamics of Mount St. Helens elk. Dissertation, University of Washington, Seattle, USA.

Merrill, E. H. 1994. Summer foraging ecology of wapiti (*Cervus elaphus roosevelti*) in the Mount St. Helens blast zone. Canadian Journal of Zoology 72:303–311.

Merrill, E. H., A. Callahan-Olson, K. J. Raedeke, R. D. Taber, and R. J. Anderson. 1995. Elk (*Cervus elaphus roosevelti*) dietary composition and quality in the Mount St. Helens blast zone. Northwest Science 69:9–18.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013*a*. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013*b*. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecological Letters 16:1023–1030.

Millspaugh, J. J., R. M. Nielson, L. L. McDonald, J. M. Marzluff, R. A. Gitzen, C. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.

Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. Ecology 78:505–521.

Monteith, K. L., R. W. Klaver, K. R. Hersey, A. A. Holland, T. P. Thomas, and M. J. Kauffman. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia 178:1137–1148.

Montgomery, R. A., G. J. Roloff, and J. J. Millspaugh. 2012. Variation in elk response to roads by season, sex, and road type. Journal of Wildlife Management 77:313–325.

Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. Biometrika 37:17–23.

Morris, L. R., K. M. Proffitt, and J. K. Blackburn. 2016. Mapping resource selection functions in wildlife studies: concerns and recommendations. Applied Geography 76:173–183.

Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationships studies. Journal of Wildlife Management 65:613–623.

Morrison, M. L. 2012. The habitat sampling and analysis paradigm has limited value in animal conservation: a prequel. Journal of Wildlife Management 76:438–450.

Morrison, M. L., B. Marcot, and W. Mannan. 2012. Wildlife-habitat relationships: concepts and applications. Third edition. Island Press, Washington, D.C., USA.

Mote, P., A. K. Snover, S. Capalbo, S. D. Eigenbrode, P. Glick, J. Littell, R. Raymondi, and S. Reeder. 2014. Chapter 21 (Northwest). Pages 487–513 *in* J. M. Melillo, T. Richmond, and G. W. Yohe, editors. Climate change impacts in the United States: the third national climate assessment. U.S. Global Change Research Program, Washington, D.C., USA. https://doi.org/10.7930/J04Q7RWX.

Mowrer, H. T., and R. G. Congalton, editors. 2000. Quantifying spatial uncertainty in natural resources: theory and applications for GIS and remote sensing. Sleeping Bear Press, Chelsea, Michigan, USA.

Muhly, T. B., M. Alexander, M. S. Boyce, R. Creasey, M. Hebblewhite, D. Paton, J. A. Pitt, and M. Musiani. 2010. Differential risk effects of wolves on wild versus domestic prey have consequences for conservation. Oikos 119:1243–1254.

Muhly, T. B., M. Hebblewhite, D. Paton, J. A. Pitt, M. S. Boyce, and M. Musiani. 2013. Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. PLoS ONE 8(5):e64311. https://doi.org/10.1371/journal.pone.0064311.

Murtaugh, P. A. 2007. Simplicity and complexity in ecological data analysis. Ecology 88:56–62.

National Research Council. 1984. Nutrient requirements of beef cattle. Sixth edition. National Academy Press, Washington, D.C., USA.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management 73:328–338.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition. McGraw-Hill, Boston, Massachusetts, USA.

Nielson, R. M., B. F. J. Manly, L. L. McDonald, H. Sawyer, and T. L. McDonald. 2009. Estimating habitat selection when GPS fix success is less than 100%. Ecology 90:2956–2962.

Nielson, R. M., and H. Sawyer. 2013. Estimating resource selection with count data. Ecology and Evolution 3:2233–2240.

Noyes, J. H., R. G. Sasser, B. K. Johnson, L. D. Bryant, and B. Alexander. 1997. Accuracy of pregnancy detection by serum protein (PSPB) in elk. Wildlife Society Bulletin 25:695–698.

Olsen-Rutz, K. M., and P. J. Urness. 1987. Comparability of foraging behavior and diet selection of tractable and wild mule deer. Utah Department of Natural Resources, Publication 88-3, Salt Lake City, USA.

Oregon Department of Fish and Wildlife. 2003. Oregon's elk management plan. Oregon Department of Fish and Wildlife, Portland, USA.

Oregon Department of Fish and Wildlife. 2005. Oregon's mule deer and elk management objectives. Oregon Department of Fish and Wildlife, Salem, USA.

Oregon Department of Fish and Wildlife. 2010. Oregon wolf conservation and management plan. Oregon Department of Fish and Wildlife, Salem, USA.

Oregon Department of Fish and Wildlife. 2018. Oregon wolf conservation and management 2017 annual report. Oregon Department of Fish and Wildlife, Salem, USA.

Owen-Smith, R. N. 2002. Adaptive herbivore ecology: from resources to populations in variable environments. Cambridge University Press, Cambridge, United Kingdom.

Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildlife Monographs 143.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Patterson, B. R., and V. A. Power. 2002. Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. Oecologia 130:62–71.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B 363:2369–2375.

Power, M. 1993. The predictive validation of ecological and environmental models. Ecological Modelling 68:33–50.

Proffitt, K. M., J. L. Grigg, R. A. Garrott, K. L. Hamlin, J. Cunningham, J. A. Gude, and C. Jourdannais. 2010. Changes in elk resource selection and distributions associated with a late-season elk hunt. Journal of Wildlife Management 74:210–218.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73:345–356.

Proffitt, K. M., J. A. Gude, K. L. Hamlin, and M. A. Messer. 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. Journal of Wildlife Management 77:514–524.

Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. Ecological Applications 26:2156–2174.

Ramsey, F. L., and D. W. Schafer. 2012. The statistical sleuth: a course in methods of data analysis. Third edition. Brooks/Cole, Boston, Massachusetts, USA.

Rearden, S. N., R. G. Anthony, and B. K. Johnson 2011. Birth-site selection and predation risk of Rocky Mountain elk. Journal of Mammalogy 92:1118–1126.

Riney, T. A. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*) with special reference to New Zealand. New Zealand Journal of Science and Technology 36:429–463.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. J. Baker, C. C. Schwartz, and W. W. Mautz. 1987*a*. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98–107.

Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987*b*. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology 68:1601–1615.

Rolandsen, C. M., E. J. Solberg, B.-E. Sæther, B. V. Moortor, I. Herfindal, and K. Jørnerass. 2017. On fitness and partial migration in a large herbivore – migratory moose have higher reproductive performance than residents. Oikos 126:547–555.

Roloff, G. J. 1998. Habitat potential model for Rocky Mountain elk. Pages 158–175 *in* Proceedings of the 1997 Deer/Elk Workshop. Arizona Game and Fish Department, 21–23 May 1997, Rio Rico, Arizona, USA.

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for elk. Journal of Wildlife Management 65:899–914.

Rowland, M. M., J. M. Hafer, B. J. Naylor, P. K. Coe, M. J. Wisdom, J. G. Cook, R. C. Cook, R. M. Nielson, and B. K. Johnson. 2013. User guidelines for application, summary, and interpretation of Westside elk nutrition and habitat use models. Draft version 2.0. U.S. Forest Service, Pacific Northwest Research Station, La Grande, Oregon, USA. http://www.fs.fed.us/pnw/research/elk/data/WestsideElkModelInstructions_31Jan2013_v2.pdf.

Rowland, M. M., R. M. Nielson, M. J. Wisdom, P. K. Coe, J. G. Cook, J. M. Hafer, B. K. Johnson, B. R. Naylor, R. C. Cook, M. Vavra, D. J. Vales, R. G. Anthony, E. K. Cole, C. D. Danilson, F. Geyer, R. McCoy, M. D. Pope, and K. Sager-Fradkin. 2018. Linking nutrition with landscape features in a regional habitat use model for elk in western Oregon and Washington. Pages 31–49 *in* Rowland, M. M., M. J. Wisdom, R. M. Nielson, J. G. Cook, R. C. Cook, B. K. Johnson, P. K. Coe, J. M. Hafer, B. J. Naylor, D. J. Vales, R. G. Anthony, E. K. Cole, C. D. Danilson, R. W. Davis, F. Geyer, S. Harris, L. L. Irwin, R. McCoy, M. D. Pope, K. Sager-Fradkin, and M. Vavra. Modeling elk nutrition and habitat use in western Oregon and Washington. Wildlife Monographs 199:1–69.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672–684.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and M. A. Penninger. 2005. Effects of roads on elk: implications for management in forested ecosystems. Pages 42–52 *in* M. J. Wisdom, technical editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Allen Press, Lawrence, Kansas, USA.

Rykiel, E. J. Jr. 1996. Testing ecological models: the meaning of validation. Ecological Modelling 90:229–244.

SAS Institute. 1988. SAS/STAT user's guide. Release 6.03. SAS Institute, Cary, North Carolina, USA.

Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. Journal of Wildlife Management 71:868–874.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

Schoenecker, K. A., F. J. Singer, L. C. Zeigenfuss, D. Binkley, and R. S. C. Menezes. 2004. Effects of elk herbivory on vegetation and nitrogen processes. Journal of Wildlife Management 68:837–849.

Searle, K. R., N. T. Hobbs, and I. J. Gordon. 2007. It's the "foodscape," not the landscape: using foraging behavior to make functional assessments of landscape condition. Israel Journal of Ecology and Evolution 53:297–316.

Shao, G., and J. Wu. 2008. On the accuracy of landscape pattern analysis using remote sensing data. Landscape Ecology 23:505–515.

Shifley, S. R., C. D. Rittenhouse, and J. J. Millspaugh. 2009. Validation of landscape-scale decision support models that predict vegetation and wildlife dynamics. Pages 415–448 *in* J. J. Millspaugh and F. R. Thompson, III, editors. Models for planning wildlife conservation in large landscapes. Elsevier, New York, New York, USA.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Sinclair, A. R. E., and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society B 357:1221–1231.

Skogland, T. 1991. What are the effects of predators on large ungulate populations? Oikos 61:401–411.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–536 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

Smith, J. L. 1980. Reproductive rates, age structure, and management of Roosevelt elk in Washington's Olympic Mountains. Pages 67–111 *in* Proceedings of the Western States Elk Workshop. Western Association of Fish and Wildlife Agencies and British Columbia Fish and Wildlife Branch, 27–28 February 1980, Cranbrook, British Columbia, Canada.

Spalinger, D. E., S. M. Cooper, D. Martin, and L. A. Shipley. 1997. Is social learning an important influence on foraging behavior in white-tailed deer? Journal of Wildlife Management 61:611–621.

Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist 140:325–321.

Spies, T. A., K. N. Johnson, K. M. Burnett, J. L. Ohmann, B. C. McComb, G. H. Reeves, P. Bettinger, J. D. Kline, and B. Garber-Yonts. 2007. Cumulative ecological and socioeconomic effects of forest policies in coastal Oregon. Ecological Applications 17:5–17.

Sporting Conservation Council. 2007. Federal Advisory Committee letter to the Secretaries of Agriculture and Interior, United States Government. Letter on file. U.S. Forest Service, Pacific Northwest Research Station, La Grande, Oregon, USA.

Stage, A. R. 1976. An expression for the effect of aspect, slope, and habitat type on tree growth. Forest Science 22:457–460.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159–2173.

Starr, H. 2013. Analyzing the influence of Interstate 90 on elk home range establishment and resource selection. Thesis, The Evergreen State College, Olympia, Washington, USA.

Stern, M. J., D. J. Blahna, L. K. Cerveny, and M. J. Mortimer. 2009. Visions of success and achievement in recreation-related USDA Forest Service NEPA processes. Environmental Impact Assessment Review 29:220–228.

Storlie, J. T. 2006. Movements and habitat use of female Roosevelt elk in relation to human disturbance on the Hoko and Dickey Game Management Units, Washington. Thesis, Humboldt State University, Arcata, California, USA.

Stussy, R. J. 1993. The effects of forage improvement practices on Roosevelt elk in the Oregon Coast range. Thesis, Oregon State University, Corvallis, USA.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:97–125.

Swanson, M. E., N. M. Studevant, J. L. Campbell, and D. C. Donato. 2014. Biological associates of early-seral pre-forest in the Pacific Northwest. Forest Ecology and Management 324:160–171.

Thomas, J. W., H. Black, Jr., R. J. Scherzinger, and R. J. Pedersen. 1979. Deer and elk. Pages 104–127 *in* J. W. Thomas, editor. Wildlife habitats in the managed forests, the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture Handbook Number 553, U.S. Government Printing Office, Washington, D.C., USA.

Thomas, J. W., J. F. Franklin, J. Gordon, and K. N. Johnson. 2005. The Northwest Forest Plan: origins, components, implementation experience, and suggestions for change. Conservation Biology 20:257–287.

Thomas, J. W., D. A. Leckenby, M. Henjum, R. J. Pedersen, and L. D. Bryant. 1988. Habitat-effectiveness index for elk on Blue Mountain winter ranges. U.S. Forest Service General Technical Report PNW-GTR-218, Portland, Oregon, USA.

Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. Ecological Applications 9:864–879.

Thompson, M. J., and R. E. Henderson. 1998. Elk habituation as a credibility challenge for wildlife professionals. Wildlife Society Bulletin 26:477–483.

Tomkeiwicz, S. N., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behavior and ecological research. Philosophical Transactions of the Royal Society B 365:2163–2176.

Toweill, D. E., and J. W. Thomas. 2002. The future of elk and elk management. Pages 793–841 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

Trainer, C. E. 1971. The relationship of physical condition and fertility of female Roosevelt elk. Thesis, Oregon State University, Corvallis, USA.

Unsworth, J. W., L. Kuck, E. O. Garton, and B. R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest. Journal of Wildlife Management 62:1255–1263.

U.S. Department of Agriculture [USDA] Forest Service. 2001*a*. Final supplemental environmental impact statement for the Huckleberry land exchange. USDA Forest Service, Mount Baker-Snoqualmie National Forest, Mountlake Terrace, Washington, USA.

U.S. Department of Agriculture [USDA] Forest Service. 1990. Gifford Pinchot National Forest Land and Resource Management Plan, Final Environmental Impact Statement. USDA Forest Service, Gifford Pinchot National Forest, Vancouver, Washington, USA.

U.S. Department of Agriculture [USDA] Forest Service. 2001*b*. Huckleberry land exchange, record of decision and forest plan amendment 16. USDA Forest Service Pacific Northwest Region, Mount Baker-Snoqualmie National Forest, Mountlake Terrace, Washington, USA.

U.S. Department of Agriculture [USDA] Forest Service. 2012*a*. Notice of Decision, Upper White River Vegetation and Restoration Project. USDA Forest Service Pacific Northwest Region, Mount Baker-Snoqualmie National Forest, Mountlake Terrace, Washington, USA.

U.S. Department of Agriculture [USDA] Forest Service. 2012*b*. Upper White River Vegetation and Restoration Project Environmental Assessment. USDA Forest Service Pacific Northwest Region, Mount Baker-Snoqualmie National Forest, Mountlake Terrace, Washington, USA.

U.S. Department of Agriculture [USDA] Forest Service and U.S. Department of the Interior [USDI] Bureau of Land Management. 1994*a*. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. USDA Forest Service, Portland, Oregon, and USDI Bureau of Land Management, Moscow, Idaho, USA.

U.S. Department of Agriculture [USDA] Forest Service and U.S. Department of the Interior [USDI] Bureau of Land Management. 1994*b*. Record of Decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl and standards and guidelines for management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. USDA Forest Service, Portland, Oregon, and USDI Bureau of Land Management, Moscow, ID, USA.

Vales, D. J., M. P. Middleton, and M. McDaniel. 2017. A nutrition-based approach for elk habitat management on intensively managed forestlands. Journal of Forestry 115:406–415.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer-Verlag, New York, New York, USA.

Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91–108 *in* L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122–127.

Walter, W. D., M. J. Lavelle, J. W. Fischer, T. L. Johnson, S. E. Hygnstrom, and K. C. VerCauteren. 2011. Management of damage by elk (*Cervus elaphus*) in North America: a review. Wildlife Research 37:630–646.

Walters, C. 1986. Adaptive management of renewable resources. Macmillan, New York, New York, USA.

Wand, M. P., and M. C. Jones. 1994. Kernel smoothing. CRC Press, Boca Raton, Florida, USA.

Wang, G., N. T. Hobbs, F. J. Singer, D. S. Ojima, and B. C. Lubow. 2002. Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado, USA. Climatic Change 54:205–223.

Washington Department of Fish and Wildlife. 2002*a*. North Cascade (Nooksack) elk herd plan. Wildlife Program, Washington Department of Fish and Wildlife, Olympia, USA.

Washington Department of Fish and Wildlife. 2002*b*. North Rainier elk herd plan. Wildlife Program, Washington Department of Fish and Wildlife, Olympia, USA.

Washington Department of Fish and Wildlife. 2002*c*. South Rainier elk herd plan. Wildlife Program, Washington Department of Fish and Wildlife, Olympia, USA.

Washington Department of Fish and Wildlife. 2004. Olympic elk herd plan. Wildlife Program, Washington Department of Fish and Wildlife, Olympia, USA.

Washington Department of Fish and Wildlife. 2008. 2009–2015 game management plan. Washington Department of Fish and Wildlife, Olympia, USA.

Washington Department of Fish and Wildlife. 2013. 2013 Game status and trend report. Wildlife Program, Washington Department of Fish and Wildlife, Olympia, USA.

Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service. 2017. Washington gray wolf conservation and management 2016 annual report. Washington Department of Fish and Wildlife, Colville, USA.

Weisburg, P. J., and R. J. Swanson. 2003. Regional synchronicity in fire regimes in western Oregon and Washington, USA. Forest Ecology and Management 172:17–28.

White, K. R., G. M. Koehler, B. T. Maletzke, and R. B. Wieglus. 2011*a*. Differential prey use by male and female cougars in Washington. Journal of Wildlife Management 75:1115–1120.

White, P. J., R. A. Garrott, K. L. Hamlin, R. C. Cook, J. G. Cook, and J. A. Cunningham. 2011*b*. Body condition and pregnancy in Northern Yellowstone elk—evidence for predation risk effects? Ecological Applications 21:3–8.

White, P. J., K. M. Proffitt, and T. O. Lemke. 2012. Changes in elk distribution and group sizes after wolf restoration. American Midland Naturalist 167:174–187.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377–384.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parrish. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management 48:1285–1301.

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2005*a*. Effects of off-road recreation on mule deer and elk. Pages 53–66 *in* M. J. Wisdom, technical editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Allen Press, Lawrence, Kansas, USA.

Wisdom, M. J., L. R. Bright, C. G. Carey, W. W. Hines, R. J. Pedersen, D. A. Smithey, J. W. Thomas, and G. W. Witmer. 1986. A model to evaluate elk habitat in western Oregon. U.S. Forest Service Pacific Northwest Region, USDI Bureau of Land Management, and Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

Wisdom, M. J., N. J. Cimon, B. K. Johnson, E. O. Garton, and J. W. Thomas. 2005*b*. Spatial partitioning by mule deer and elk in relation to traffic. Pages 67–80 *in* M. J. Wisdom, technical editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Allen Press, Lawrence, Kansas, USA.

Wisdom, M. J., and J. G. Cook. 2000. North American elk. Pages 694–735 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Wisdom, M. J., J. G. Cook, M. M. Rowland, and J. H. Noyes. 1993. Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. U.S. Forest Service General Technical Report PNW-GTR-311, Portland, Oregon, USA.

Wisdom, M. J., M. M. Rowland, R. M. Nielson, J. C. Cook, B. K. Johnson, P. K. Coe, R. C. Cook, D. J. Vales, and M. Vavra. 2018*a*. Modeling to evaluate elk habitat: contemporary approaches for western Oregon and Washington. Pages 8–12 *in* Rowland, M. M., M. J. Wisdom, R. M. Nielson, J. G. Cook, R. C. Cook, B. K. Johnson, P. K. Coe, J. M. Hafer, B. J. Naylor, D. J. Vales, R. G. Anthony, E. K. Cole, C. D. Danilson, R. W. Davis, F. Geyer, S. Harris, L. L. Irwin, R. McCoy, M. D. Pope, K. Sager-Fradkin, and M. Vavra. Modeling elk nutrition and habitat use in western Oregon and Washington. Wildlife Monographs 199:1–69.

Wisdom, M. J., M. M. Rowland, R. M. Nielson, J. G. Cook, B. K. Johnson, J. M. Hafer, R. C. Cook, P. K. Coe, D. J. Vales, B. J. Naylor, and M. Vavra. 2018*b*. Nutrition and habitat use models for elk management in western Oregon and Washington. Pages 50–62 *in* Rowland, M. M., M. J. Wisdom, R. M. Nielson, J. G. Cook, R. C. Cook, B. K. Johnson, P. K. Coe, J. M. Hafer, B. J. Naylor, D. J. Vales, R. G. Anthony, E. K. Cole, C. D. Danilson, R. W. Davis, F. Geyer, S. Harris, L. L. Irwin, R. McCoy, M. D. Pope, K. Sager-Fradkin, and M. Vavra. Modeling elk nutrition and habitat use in western Oregon and Washington. Wildlife Monographs 199:1–69.

Wisdom, M. J., and J. W. Thomas. 1996. Elk. Pages 157–181 *in* P. R. Krausman, editor. Rangeland wildlife. Society for Range Management, Denver, Colorado, USA.

Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006. Understanding ungulate herbivory-episodic disturbance effects: knowledge gaps and management needs. Wildlife Society Bulletin 34:283–292.

Witmer, G. W. 1981. Roosevelt elk habitat use in the Oregon Coast Range. Thesis, Oregon State University, Corvallis, USA.

Witmer, G. W., and D. S. deCalesta. 1985. Effect of forest roads on habitat use by Roosevelt elk. Northwest Science 59:122–125.

Witmer, G. W., M. Wisdom, E. P. Harshman, R. J. Anderson, C. Carey, M. P. Kuttel, I. D. Luman, J. A. Rochelle, R. W. Scharpf, and D. A. Smithey. 1985. Deer and elk. Pages 41–55 *in* E. R. Brown, editor. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 1 – chapter narratives. U.S. Forest Service Publication R6-F&WL-192-1985. U.S. Government Printing Office, Washington, D.C., USA.

Yarrow, G. K. 1979. Comparison of tame and wild deer food habits. Thesis, Mississippi State University, Starkville, USA.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators of ungulates in North America. Ursus 17:95–108.

Zar, J. H. 2010. Biostatistical analysis. Fifth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this monograph at the publisher's website.

Forest Ecology and Management 411 (2018) 223–233

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Elk responses to trail-based recreation on public forests

Michael J. Wisdom[a,*], Haiganoush K. Preisler[b], Leslie M. Naylor[c,1], Robert G. Anthony[d,2], Bruce K. Johnson[e], Mary M. Rowland[a]

[a] USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA
[b] USDA Forest Service, Pacific Southwest Research Station, 800 Buchanan Street West Annex, Albany, CA 94710, USA
[c] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA
[d] Oregon Cooperative Fish & Wildlife Research Unit, Department of Fisheries & Wildlife, Oregon State University, Corvallis, OR 97331, USA
[e] Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA

ARTICLE INFO

Keywords:
All-terrain vehicles
ATV riding
Elk
Forest roads
Hiking
Horseback riding
Mountain biking
Motorized traffic
Off-highway vehicles
Public forests
Recreation
Recreation trails
Road avoidance
Roads

ABSTRACT

Trail-based recreation is a popular use of public forests in the United States, and four types are common: all-terrain vehicle (ATV) riding, mountain biking, hiking, and horseback riding. Effects on wildlife, however, are controversial and often a topic of land use debates. Accordingly, we studied trail-based recreation effects on elk (*Cervus canadensis*), a wide-ranging North American ungulate highly sought for hunting and viewing on public forests, but that is sensitive to human activities, particularly to motorized traffic on forest roads. We hypothesized that elk would respond to trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. We evaluated elk responses using a manipulative landscape experiment in a 1453-ha enclosure on public forest in northeast Oregon. A given type of recreation was randomly selected and implemented twice daily along 32 km of designated recreation trails over a five-day period, followed by a nine-day control period of no human activity. Paired treatment and control replicates were repeated three times per year for each recreation type during spring-fall, 2003–2004. During treatments, locations of elk and recreationists were simultaneously collected with telemetry units. Elk locations also were collected during control periods. Elk avoided the trails during recreation treatments, shifting distribution farther out of view and to areas farthest from trails. Elk shifted distribution back toward trails during control periods of no human activity. Elk avoided recreationists in real time, with mean minimum separation distances from humans that varied from 558 to 879 m among the four treatments, 2–4 times farther than elk distances from trails during recreation. Separation distances maintained by elk from recreationists also were 3–5 times farther than mean distances at which elk could be viewed from trails. Distances between elk and recreationists were highest during ATV riding, lowest and similar during hiking and horseback riding, and intermediate during mountain biking. Our results support the hypothesis that elk avoid trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. Forest managers can use results to help optimize trade-offs between competing objectives for trail-based recreation and wildlife species like elk that are sensitive to human activities on public forests.

1. Introduction

Trail-based recreation is common on public forests in the United States, and four types are especially popular: all-terrain vehicle (ATV) riding, mountain biking, hiking, and horseback riding (Cordell, 2012). ATV riding, in particular, has increased rapidly. The number of off-highway vehicle (OHV) riders reached 36 million in the early 2000s (Cordell, 2012), and is projected to increase ∼30–60% (to 62–75 million participants) by 2060 (Bowker et al., 2012). Increasing ATV use has prompted concerns about effects on wildlife (Proescholdt, 2007; Tarr et al., 2010; Webb and Wilshire, 2012), which include distribution shifts of populations away from trails; increased flight responses, movement rates and energetic costs; reduced foraging times; and reduced carrying capacity from cumulative effects (Havlick, 2002; Brillinger et al., 2004, 2011; Wisdom et al., 2004a; Preisler et al., 2006, 2013; Naylor et al., 2009; Ciuti et al., 2012).

---

[*] Corresponding author.

E-mail addresses: mwisdom@fs.fed.us (M.J. Wisdom), hpreisler@fs.fed.us (H.K. Preisler), lesnaylor@ctuir.org (L.M. Naylor), bruce.k.johnson1@state.or.us (B.K. Johnson), mrowland@fs.fed.us (M.M. Rowland).

[1] Current address: Confederated Tribes of the Umatilla Indian Reservation, Department of Natural Resources, Agricultural Service Center, Room 2, 10507 North McAlister Road, Island City, OR 97850, USA.

[2] Deceased.

https://doi.org/10.1016/j.foreco.2018.01.032
Received 29 November 2017; Received in revised form 19 January 2018; Accepted 19 January 2018

Mountain biking, hiking, and horseback riding also are popular uses of public lands in the United States (Cordell, 2012), and all three activities are among those projected to increase most in per capita participation by 2060 (Bowker et al., 2012). Mountain biking, in particular, is growing rapidly, with an increase in users of 22% from 2006 to 2015 (The Outdoor Foundation, 2016). In 2006, cycling (road and mountain biking) was the fourth-most popular recreational activity in the United States, behind fishing, camping, and running (Cordell, 2012); mountain biking had > 820 million user days in 2008 (Cordell, 2012).

In contrast to ATV riding, non-motorized forms of trail-based recreation often are considered benign by recreationists (Taylor and Knight, 2003a; Larson et al., 2016), but current knowledge indicates otherwise (Green and Higginbottom, 2000; Leung and Marion, 2000; Newsome and Moore, 2008; Naylor et al., 2009; Ciuti et al., 2012; Larson et al., 2016; Hennings and Soll, 2017). Effects on wildlife are similar to those of ATV riding (e.g., population displacement away from trails, Larson et al., 2016), but ATVs likely have more pronounced negative effects because of high levels of speed and noise and thus affect more area per unit time (Lovich and Bainbridge, 1999; Wisdom et al., 2004a; Proescholdt, 2007; Naylor et al., 2009; Ciuti et al., 2012; Preisler et al., 2013). Motorized uses like ATV riding thus are more likely to have a greater impact than non-motorized recreation on wide-ranging mammals whose large home ranges put them in more frequent contact with the larger ranges and spatial influence of motorized riders (Wisdom et al., 2004a; Ciuti et al., 2012; Beyer et al., 2013).

Concerns about ATV use and the more general effects of motorized traffic on wildlife and other natural resources prompted the USDA Forest Service to revise its policy regarding motorized travel management on National Forests in 2005. A new regulation that year required that all roads, trails, and areas open to motorized use be formally designated to better manage vehicle traffic and prevent resource damage (USDA Forest Service, 2004; Federal Register, 2005; Adams and McCool, 2009). This change in policy acknowledged a variety of negative effects from unmanaged motorized uses, especially OHVs, whose numbers had been increasing steadily on National Forests (Cordell, 2005; Federal Register, 2005). Similar changes in policy have occurred on state-managed forests in response to negative effects of OHVs (Asah et al., 2012a, 2012b).

Despite the changes in public forest policy that occurred over a decade ago, current knowledge of both motorized and non-motorized recreation is not well-developed regarding the extent and intensity of effects at most spatial and temporal scales meaningful to wildlife populations (Gutzwiller et al., 2017). Wisdom et al. (2004a), Preisler et al. (2006, 2013), and Naylor et al. (2009) addressed some of these knowledge voids with their ungulate research in northeast Oregon, United States, and Ciuti et al. (2012) conducted a similar study in Alberta, Canada. Replication elsewhere and for many wildlife species, however, is lacking. Knowledge voids have likely contributed to ongoing public debate about recreational uses on public forests, particularly ATV riding (Asah et al., 2012a, 2012b). Public comments on National Forest travel management plans have been diverse and contentious (Yankoviak, 2005; Thompson, 2007), reflecting strong societal views in the face of limited knowledge and perceptions of overly restrictive federal policies (Adams and McCool, 2009).

In response to these issues, we studied effects of trail-based recreation on elk (*Cervus canadensis*), a wide-ranging North American ungulate highly sought for hunting and viewing on public forests, but that is sensitive to human activities, particularly to motorized traffic on forest roads (e.g., Lyon, 1983; Cole et al., 1997, 2004; Rowland et al., 2000, 2004; Frair et al., 2008; Montgomery et al., 2012, 2013; Prokopenko et al., 2016). We hypothesized that populations of elk would avoid trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests during non-hunting periods of late spring through early fall. We further hypothesized that avoidance would occur at distances that allow elk to stay out of view of recreationists, and that avoidance would be strongest in response to motorized recreation (ATV riding).

We tested our hypotheses by evaluating behavioral responses of elk to trail-based recreation using a manipulative landscape experiment in a 1453-ha enclosure on public forest in northeast Oregon. We had 2 objectives: (1) to document the degree of elk avoidance of trails during each recreation activity, compared to control periods of no activity; and (2) to evaluate direct, real-time responses of elk to recreationists during each type of recreation. We estimated distances between elk and the trails during recreation activities, and in real time between elk and recreationists based on simultaneous collection of telemetry locations of animals and humans. We provided context for interpreting results by estimating the distances at which elk could be viewed from the trails, per our hypothesis that avoidance occurs at distances that allow elk to hide from view. We also characterized differences in spatial distributions of elk during each type of recreation treatment versus paired control periods when no humans were present.

Research was conducted with approval and guidance by the Starkey Institutional Animal Care and Use Committee (IACUC 92-F-0004), as required by the United States Animal Welfare Act of 1985. We followed protocols established by the IACUC for conducting ungulate research at the Starkey Experimental Forest and Range (Wisdom et al., 1993).

2. Materials and methods

2.1. Study area

Research was conducted from April-October 2003–2004 at the USDA Forest Service Starkey Experimental Forest and Range (Starkey), 35 km southwest of La Grande in northeast Oregon, USA (Fig. 1A). In 1987, approximately 10,125 ha of elk summer range within Starkey were enclosed with a 2.4 m (8-foot) elk-proof fence for long-term ungulate research (Rowland et al., 1997; Wisdom, 2005). Our study was conducted in the 1453-ha Northeast Study Area (Fig. 1A), which is separated from Starkey's other study areas by elk-proof fence (Wisdom et al., 2005). The Northeast Study Area is further subdivided by elk-proof fence into 2 pastures, East (842 ha) and West (610 ha) (Stewart et al., 2005). Approximately 98 elk occupied the East Pasture (69 adult females, 16 calves, and 13 adult males) and 25 occupied the West Pasture (18 adult females, 2 calves, and 5 adult males). Elk were last hunted in the study area in 1996 as part of a rifle hunt of males to evaluate their responses to motorized versus non-motorized hunting access (Wisdom et al., 2004b). Our research did not include hunting and focused on the non-hunting periods of late spring through early fall.

Approximately 70% of the area was forested, arranged in a mosaic of patches interspersed with thin-soiled grasslands. Forested areas were composed of dry or mixed conifer types common to the interior western United States (Wisdom et al., 2005). Dominant tree species included Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*). Approximately 50% of the forest types underwent commercial timber harvest from 1992 to 1994 that included clearcutting, seed tree, and shelterwood prescriptions applied as small (1–22 ha) harvest units interspersed with untreated stands (Wisdom et al., 2004b). Regeneration cuts established a mosaic of open and closed forest structural conditions, interspersed with the less common open grasslands (Wisdom, 2004b). Rowland et al.,(1997), Stewart et al. (2005), Wisdom (2005), and Naylor et al. (2009) provide details about the study area and past research.

2.2. Data collection

2.2.1. Recreation treatments and locations of recreationists

We implemented ATV riding, mountain biking, hiking, and horseback riding as four separate types of recreation treatments to which elk responses were evaluated during spring-fall, 2003–2004. A given

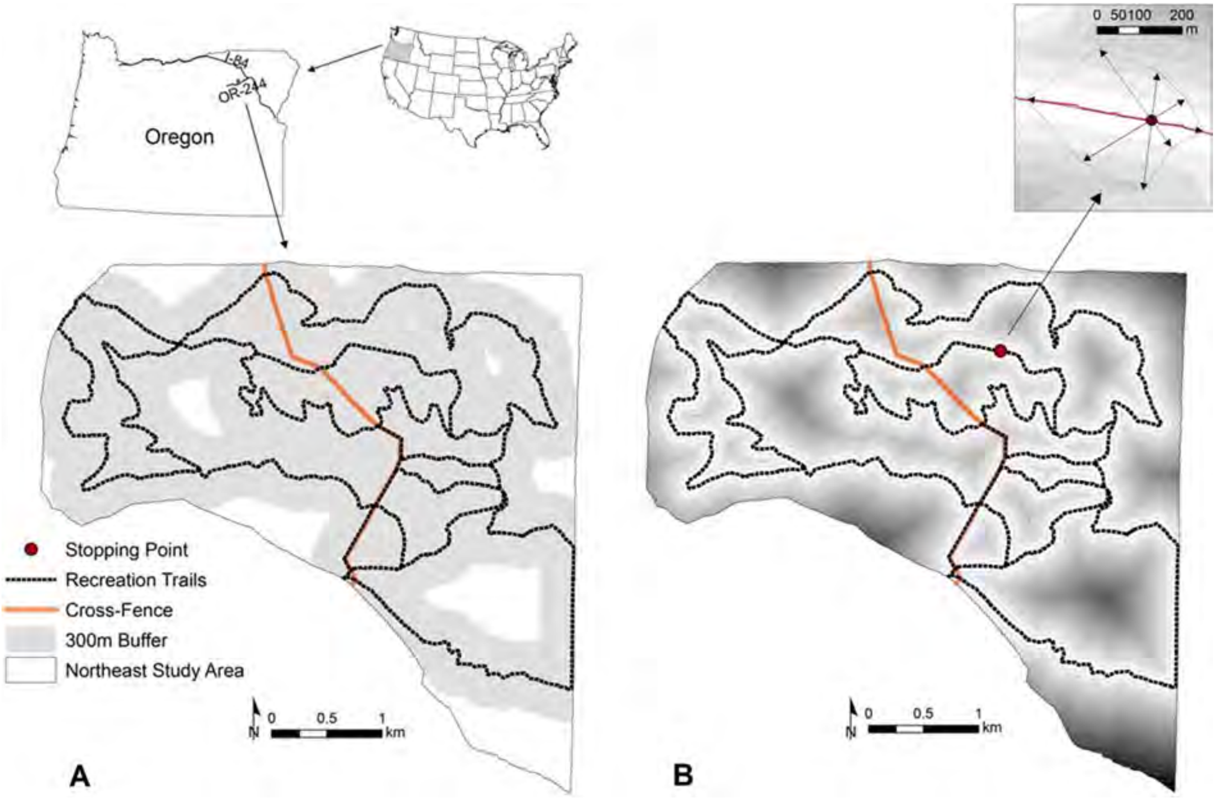


Fig. 1. Location of the 1453-ha Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA, with 32 km of recreation trails on which four recreation treatments were evaluated during 2003–2004 (A). Viewing distances were estimated in eight cardinal directions at sampling points every 0.2 km along trails (upper right, B), and 50-m distance intervals from the trails were mapped to estimate the percentage of study area in relation to viewing distances and elk locations (B).

treatment type was implemented over a five-day period, followed by nine days of control, during which no human activity occurred in the study area. Each pair of treatment and control replicates was applied three times/year for each of the four types of recreation (12 total treatment–control periods annually, 24 for the two years), with the order of treatment type randomly assigned. During each five-day period, the assigned treatment was implemented along 32 km of recreation trails that followed old road beds and trails typically used by recreationists on public forests (Fig. 1A) (Wisdom et al. 2004a). An initial two-week control period was implemented each year before treatments began.

Treatments were implemented by recreationists who traveled the trails once each morning (0800–1159 h local time) and afternoon (1200–1600 h local time) while carrying global positioning system (GPS) units to record their locations. Coverage of the 32 km of trails on a given morning or afternoon required one group of ATV riders or mountain bikers, two groups of hikers, and three groups of horseback riders because of differences in recreation speeds (Wisdom, unpublished data; see Section 4). Each of the two groups of hikers traversed one-half of the trails, and each of the three groups of horseback riders rode one-third. This design resulted in the same spatial coverage of recreationists on trails, and exposure of elk to recreationists, each morning and afternoon, but with different rates of speed (Naylor, 2006; see Section 4).

Each treatment followed a "tangential" experimental approach in which recreationists did not directly target or pursue elk, but remained along the pre-determined trails (Taylor and Knight, 2003b). Recreationists followed explicit instructions regarding these methods of implementing the treatments. See Naylor et al. (2009) for additional details about design and implementation of the treatments.

GPS units (Trimble 3C, Trimble, Inc.) worn by recreationists collected human locations continuously (every second). Mean spatial error of GPS locations was < 10 m, based on distances measured in ArcGIS (ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, CA) between the plotted locations of recreationists and the geo-referenced location of the recreation trails (Wisdom, unpublished data).

2.2.2. *Telemetry locations of elk*

We used long-range aid to navigation (LORAN-C) and GPS telemetry (Johnson et al., 1998; Hansen and Riggs, 2008) to evaluate responses of 35 telemetered adult female elk to the four types of recreation. Telemetry locations were collected throughout each five-day treatment and paired nine-day control.

Telemetry collars were programmed to obtain one location/telemetered elk every 10 and 30 min under the LORAN-C and GPS systems, respectively, during recreation treatments. The higher relocation schedule of LORAN-C collars was designed to analyze the real-time responses of telemetered elk to the telemetered recreationists. Similar data were collected in 2002 and published earlier (Wisdom et al., 2004a), but with different response variables than considered here. All collars were programmed at 30-min relocation schedules during control periods. Limited battery life of GPS collars and sampling restrictions on the total number of LORAN-C locations that could be collected among all collars at Starkey study areas (Johnson et al., 1998) dictated the 30-min relocation schedule during control periods.

Spatial error of the elk telemetry locations was < 50 m and < 20 m for LORAN-C and GPS telemetry, respectively (Johnson et al., 1998; Hansen and Riggs, 2008). Fix success, defined as the percentage of programmed locations successfully obtained from collars, exceeded 98% for GPS data, indicating no need for bias correction (Frair et al., 2004; Nielson et al., 2009). Fix success for LORAN-C data averaged 65% and was largely associated with unbiased sources of random variation (Johnson et al., 1998). LORAN-C fix success varied slightly by location, however, and was corrected with a spatially-explicit algorithm developed for the study area (Johnson et al., 1998, 2000).

2.2.3. Viewing distances

At the conclusion of the study, we measured the distances at which we estimated an elk could be viewed from the recreation trails (Fig. 1B). Viewing distances provided context for interpreting the distances that elk maintained from the recreation trails and from recreationists during treatments, and for evaluating support for our hypothesis that elk would stay hidden from view of recreationists.

We sampled viewing distances approximately every 0.2 km along the trails, for a total of 231 sampling points. At each sampling point, we used a GPS unit (Trimble Unit TSCe, Trimble, Inc.) to spatially reference the point and used a laser rangefinder (Bushnell™ Yardage Pro 1000) to measure the distance at which we estimated an elk could be viewed. Because elk could be viewed at any possible angle from the trails, we measured distances in the eight cardinal compass directions, with 0 degrees set as straight ahead on the trail at a given sampling point (Fig. 1B).

Viewing distances can be interrupted by topography or vegetation, such that elk can be viewed at closer and farther distances but not in between. Consequently, for each of the eight angles, we measured the distance at which an elk could be viewed to the first point of visual obstruction, referred to as the "near" distance. We also measured the subsequent distance at which an elk could be viewed, beyond the first point of visual obstruction, referred to as the "far" distance. The far distance thus represented the distance at which elk could be viewed without consideration of the near distance obstruction. For a given viewing angle in which there were no obstructed areas between near and far distances, the near and far distances were identical and recorded as the same for both distances. By contrast, near and far distances could be substantially different where dense vegetation or topography obstructed views close to the trails, but open areas could be viewed farther from the trails. Rangefinder estimation errors generally were < 5% of the true distance (Wisdom, unpublished data), similar to published estimates of these technologies as tested in forest environments (Sicking, 1998).

2.3. Data analysis

2.3.1. Viewing distances from trails

We calculated the mean and 95% confidence interval (CI) of the near and the far viewing distances to which elk could be viewed from the recreation trails, considering all distances measured at the sampling points. We used each sampling point as a sample unit and the eight distance measurements/sampling point as subsamples. We averaged the values of the eight near viewing distances measured at each sampling point, and did the same for the eight far viewing distances, to estimate the mean values and 95% CIs.

We also calculated the percentage of near and far viewing distances by 50-m distance intervals away from the recreation trails (Fig. 1B), and the percentage of the study area within these distance categories. We did the same for the percentage of the study area from trails within the maximum viewing distance, estimated to be 300 m. Analyses provided insight about the percentage of the study area in which elk could be viewed from the recreation trails.

2.3.2. Avoidance of trails

We used analysis of variance (ANOVA) with random elk effects (i.e., each telemetered elk as a sample unit) to evaluate differences in mean distances (± 95% CIs) of elk from the nearest trail among the four recreation treatments and paired controls, and further summarized these distances in parallel boxplots with median notches (Chambers et al., 1983; Benjamini, 1988). Mean distances and boxplots of elk from the nearest trail were summarized for each telemetered elk/day/treatment type and control, pooled across like replicates, using observations that were averaged for each morning (0800–1159 h local time) and each afternoon (1200–1600 h local time). This analysis evaluated average responses to treatments across seasons and years, but accounting for diurnal effects (Wisdom et al., 2004a; Naylor et al., 2009). Prior analyses (Wisdom et al., 2004a; Wisdom, unpublished data) also indicated that elk in a given pasture responded to recreation treatments in both pastures, given the adjacency of trails and long distances of elk responses. Calculation of distances thus considered trails in both pastures. Results were further related to the mean near and far viewing distances (± 95% CIs) from trails.

We analyzed the spatial distribution of elk in relation to trails in two additional ways. First, we calculated the percentage of elk locations by 50-m distance intervals from the nearest trail during each treatment type and control, and percentage of near and far viewing distances by the 50-m intervals. Locations were pooled across animals. And second, we estimated and mapped kernel densities of elk locations during each treatment type and control. Kernel densities (Venables and Ripple, 1997) were based on the pooled locations among telemetered elk as an estimate of the stationary distribution of the population (Preisler et al., 2013) during each treatment type and control. We used a random subsample of locations from the recreation treatments equal to the number of locations during the corresponding control periods to estimate kernel densities and produce comparable maps.

Analyses of elk distances and distributions in relation to trails documented the degree of trail avoidance and whether the elk population shifted beyond viewing distances during the recreation treatments, and shifted back toward trails during control periods. If elk were farther from trails than they could be viewed during recreation, this would support our hypothesis that avoidance was related to elk staying hidden from view. Moreover, a shift in elk distributions closer to the trails during control periods, with more locations in view during these periods of no human activity, would further support this hypothesis as a potential cause-effect process.

2.3.3. Avoidance of recreationists

We analyzed the minimum separation distances that elk maintained from recreationists as a measure of how tolerant elk were to the proximity of humans. We first matched the locations of recreationists in time with the LORAN-C telemetry locations of elk (Preisler et al., 2006). LORAN-C elk locations were used because of the higher relocation frequency (every 10 min) compared to the GPS telemetry locations (every 30 min), thus providing a larger set of close matches in time. Each LORAN-C elk location was matched with the location of the nearest group of recreationists closest in time to the elk location, considering all locations of recreationists within a five-minute time window before each elk location. Time-matched locations of elk and recreationists were measured as the shortest Euclidean distance between each (ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, CA).

To calculate the mean and 95% CI for the minimum separation distance/treatment type, we identified the distance of each LORAN-C elk to the nearest group of recreationists during each morning and each afternoon for each of the five days of a treatment replicate. This provided two observations of minimum distance/elk/day/treatment replicate, spanning the three seasons and two years. Minimum separation distances/elk for each morning and afternoon were used as subsamples, and a mean minimum distance of these values calculated for each animal among replicates of each treatment type. We then calculated the mean minimum distance and 95% CI among all LORAN-C telemetered elk (n = 19) across like replicates in the same manner as done for calculating mean distances from trails. We further analyzed the distribution of minimum separation distances of elk with boxplots and median notches by treatment type.

We considered minimum separation distance to be the most direct indicator of the spatial tolerance of elk to recreationists, particularly their tolerance to remain in view. Elk often seek edges close to cover or in cover, presumably for hiding from humans or predators, even during non-hunting periods of spring-fall (Witmer et al., 1985; Johnson et al., 2000; Coe et al., 2011; Harju et al., 2011; Buchanan et al., 2014).

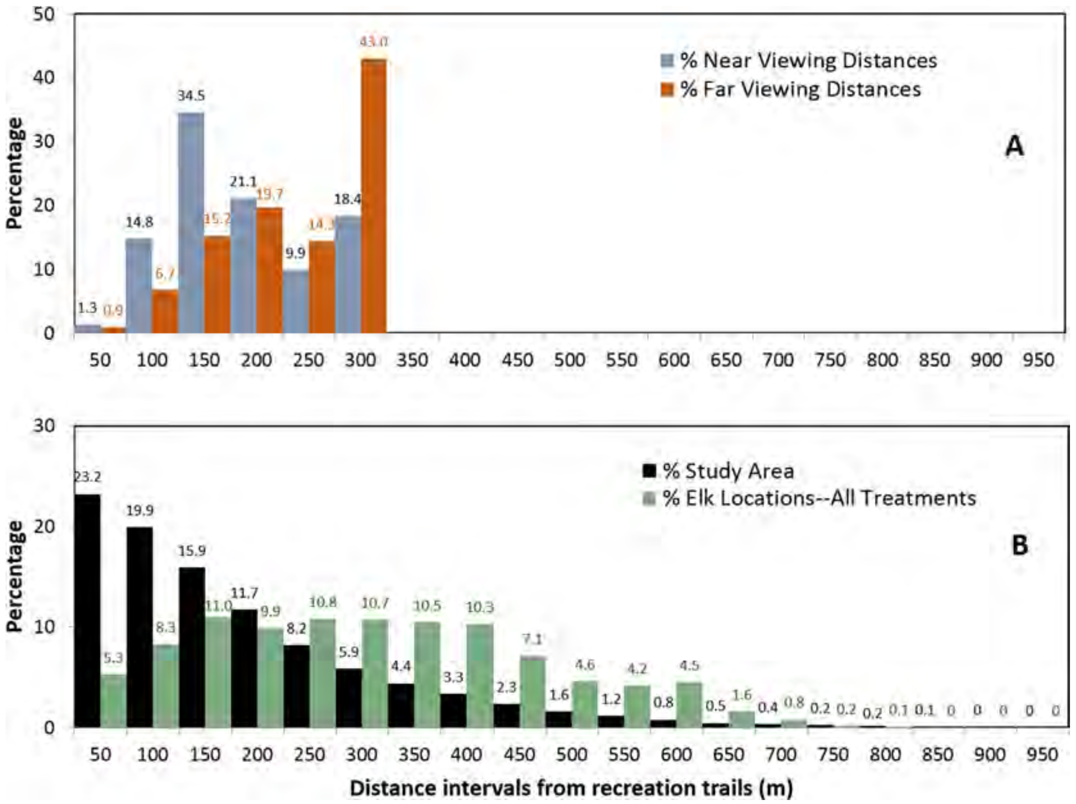


Fig. 2. Percentage of near and far viewing distance values by 50-m distance intervals from the recreation trails (A) in relation to the percentage of the study area and percentage of elk locations by intervals (B), Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Elk locations were from 35 telemetered elk monitored during all-terrain vehicle riding, mountain biking, hiking, and horseback riding, 2003–2004 combined.

Evaluation of separation distances in relation to viewing distances considered elk use of visual obstructions of cover and topography to hide from view as part of avoidance responses.

3. Results

3.1. Viewing distances from trails and area available for elk use

Mean near and far distances to which elk could be viewed from the recreation trails were 172 m and 222 m, respectively (Fig. 2A; Table 1). Over 50% of the study area was within the mean near viewing distance of 172 m, and > 70% was within the mean far viewing distance of 222 m, based on study area percentage by distance intervals from trails (Fig. 2A). Just 15% of the study area exceeded the maximum viewing distance of 300 m that was estimated for near and far viewing distances at 18% and 43% of the sampling points, respectively (Fig. 2A). The percentage of the study area available for elk use by 50-m distance intervals from trails (Fig. 1B, 2A) directly followed the patterns of study area percentage by viewing distance (Fig. 2A).

3.2. Elk avoidance of trails

We found significant differences in elk avoidance of trails among the four recreation treatments and paired controls (ANOVA, $P < .01$). Mean distances of elk from the recreation trails ranged from 239 to 310 m during the four recreation activities (Fig. 3; Table 1). Mean and median distances were significantly farther (non-overlapping 95% CIs and median notches) during ATV riding, mountain biking, and horseback riding than distances of these same telemetered elk during the paired control periods (Fig. 3; Table 1), indicating that elk moved away from the trails during recreation and back toward trails when no humans were present. During hiking, mean and median distances of elk from trails were similar to those during horseback riding, but elk movement back toward trails during the hiking control period was less distinct (Fig. 3), and CIs for the hiking treatment and control periods slightly overlapped (5-m overlap, Table 1).

Shifts of elk away from and back toward trails in the presence versus absence of recreationists were evident in the boxplot distributions (Fig. 3). Shifts also were evident spatially in the kernel densities of elk locations of paired treatment and control periods, shown in Fig. 4 for ATV and horseback riding. Similar spatial differences in kernel densities between treatment and control periods were found during mountain

Table 1
Mean (± 95% CI) near and far distances at which elk could be viewed from recreation trails, and mean distances (± 95% CIs) that elk maintained from nearest trail during all-terrain vehicle riding (ATV), mountain biking (BIKE), hiking (HIKE), and horseback riding (HORSE) treatments (T) and control periods (C), 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA.

Mean viewing distance (m) (N = 231)		Mean distance (m) of elk from nearest trail (N = 35)							
Near	Far	ATV		BIKE		HIKE		HORSE	
		T	C	T	C	T	C	T	C
172 (± 5)	222 (± 5)	311 (± 28)	237 (± 15)	286 (± 26)	197 (± 8)	276 (± 18)	248 (± 15)	240 (± 13)	172 (± 9)

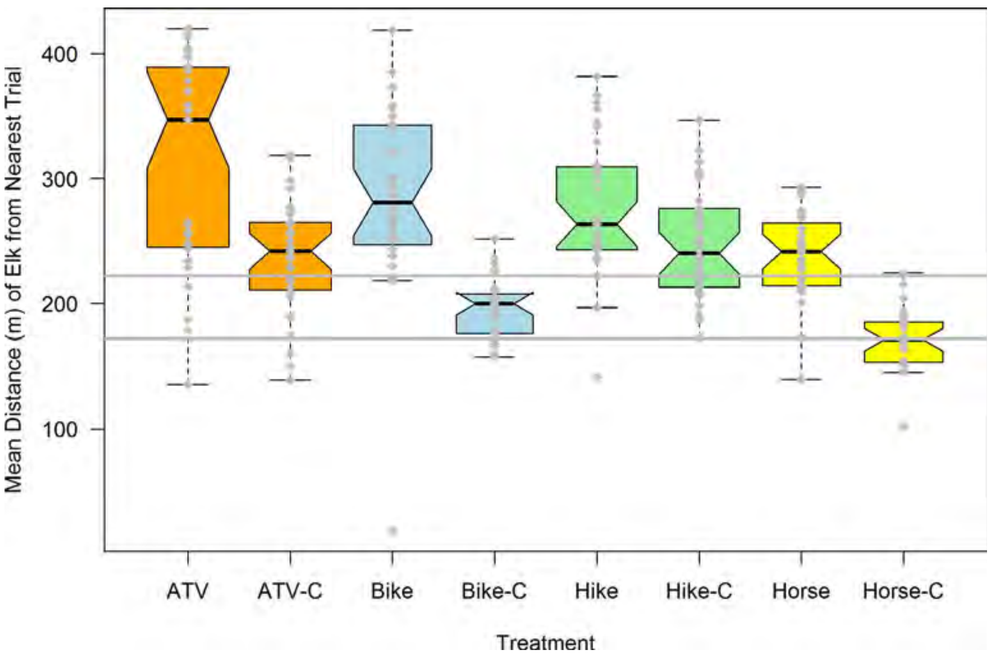


Fig. 3. Parallel boxplots showing the variability among elk (variability within each box) and among treatments (variability between boxes) in mean distances of telemetered elk (n = 35) from the nearest recreation trail during four types of recreation (all-terrain vehicle riding [ATV], mountain biking [Bike], hiking [Hike], horseback riding [Horse]) and corresponding control (C) periods, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Non-overlapping notches provide 'strong evidence' that the two medians differ (Chambers et al. 1983, p. 62; Benjamini, 1988). Silver dots show mean distances of individual elk. The two horizontal grey lines indicate the mean near (172 m) and mean far (222 m) viewing distances from trails.

biking. Shifts away from and back toward trails during the hiking treatment versus control periods were more subtle, as reflected in the small overlap of CIs of mean values (Table 1) and overlapping median notches (Fig. 3).

Mean and median distances of elk from the recreation trails were farther during ATV riding than during the three non-motorized types of recreation (non-overlapping CIs and notches); these distances were not different between mountain biking, hiking, and horseback riding (overlapping CIs and notches, Fig. 3; Table 1). Boxplot distributions, however, indicated an overall trend of strongest avoidance during ATV riding, followed by mountain biking, hiking, and horseback riding (Fig. 3). These trends were supported by the rank order of both mean and median values among the four treatments (Fig. 3; Table 1).

Variability in mean distances among individual elk, however, was highest (least precise) during ATV riding. Lower precision of elk response to ATV riding was evident in the longer boxplot below the median, and high number of individual mean distances farther below the median, compared to other types of recreation (Fig. 3), suggesting that ATV riding elicited either a hiding (stationary) or a flight (active) response (see Section 4). Higher precision was associated with elk responses to horseback riding and hiking, and during all control periods except hiking.

Mean distances of elk from the trails also were farther (non-overlapping CIs) during all four recreation activities than the mean near and far viewing distances (Table 1). The large majority of elk locations were well beyond the mean near and far viewing distances from trails, and 44% of all elk locations during the recreation treatments were beyond the maximum viewing distance of 300 m (Fig. 2B). This pattern was stronger during ATV riding and mountain biking, when 52% and 50% of all elk locations occurred > 300 m from the trails. The pattern was weaker during hiking and horseback riding, when 37% and 25% of elk locations were beyond the maximum viewing distance (Fig. 2B).

Almost one-half (44%) of elk locations occurred on just 15% of the study area farthest from trails and out of view (Fig. 2B). The large majority (85%) of the study area was within the maximum viewing distance of 300 m from the recreation trails, but only 56% of elk locations occurred in these distance intervals (Fig. 2B). These patterns were evident in the kernel densities of treatment versus control periods (Fig. 4).

3.3. Elk avoidance of recreationists

Mean minimum separation distances that elk maintained from recreationists were highest during ATV riding (879 m, ± 68 m), lowest and similar during hiking (547 m, ± 44 m) and horseback riding (558 m, ± 45 m), and intermediate during mountain biking (662 m, ± 53 m). Boxplot distributions and median notches followed this same pattern (Fig. 5): median distances were highest during ATV riding, followed by mountain biking, both of which had non-overlapping notches with each other and with the overlapping notches of hiking and horseback riding. The taller height of the boxplot above the median during ATV riding compared to other types of recreation (Fig. 5) further illustrated the stronger but less precise elk response to motorized recreation.

Separation distances from recreationists were significantly farther than elk distances from trails (non-overlapping CIs with those in Table 1), illustrating the difference in real-time responses of elk to recreationists (five-minute time windows each morning and afternoon) versus the more static responses to trails (8-h time window each day). Specifically, mean minimum distances of elk from recreationists (558–879 m) were 2–4 times farther than mean distances from trails (239–310 m, Table 1) during the same recreation periods. Differences in elk distances from recreationists also were more distinct and consistent (more precise) between the four treatments than those for distances from trails (boxplot variability across treatments in Fig. 3 versus 5), suggesting that the direct responses of elk to recreationists was more predictable than their indirect responses to trails.

Minimum separation distances also were 3–5 times farther than the mean near and far distances of 172 and 222 m at which elk could be viewed from the trails (non-overlapping CIs with those in Table 1), and 2–3 times farther than the maximum viewing distance of 300 m. Over 75% of the minimum distances between elk and recreationists exceeded the maximum viewing distance of 300 m (see boxplot portions above 300 m, Fig. 5), indicating a strong tendency of elk to be hidden from view of recreationists. This percentage of elk distances from recreationists beyond 300 m, estimated for a 5-min time window (Fig. 5), was higher than the estimate of 44% of elk locations beyond 300 m based on the more generic 8-h time window (Fig. 2B). The long "tails" of elk distances extremely far from recreationists (e.g., 1500–4000 m distances, per dotted lines in uppermost part of each boxplot, Fig. 5) were evident during all four recreation activities, indicating avoidance

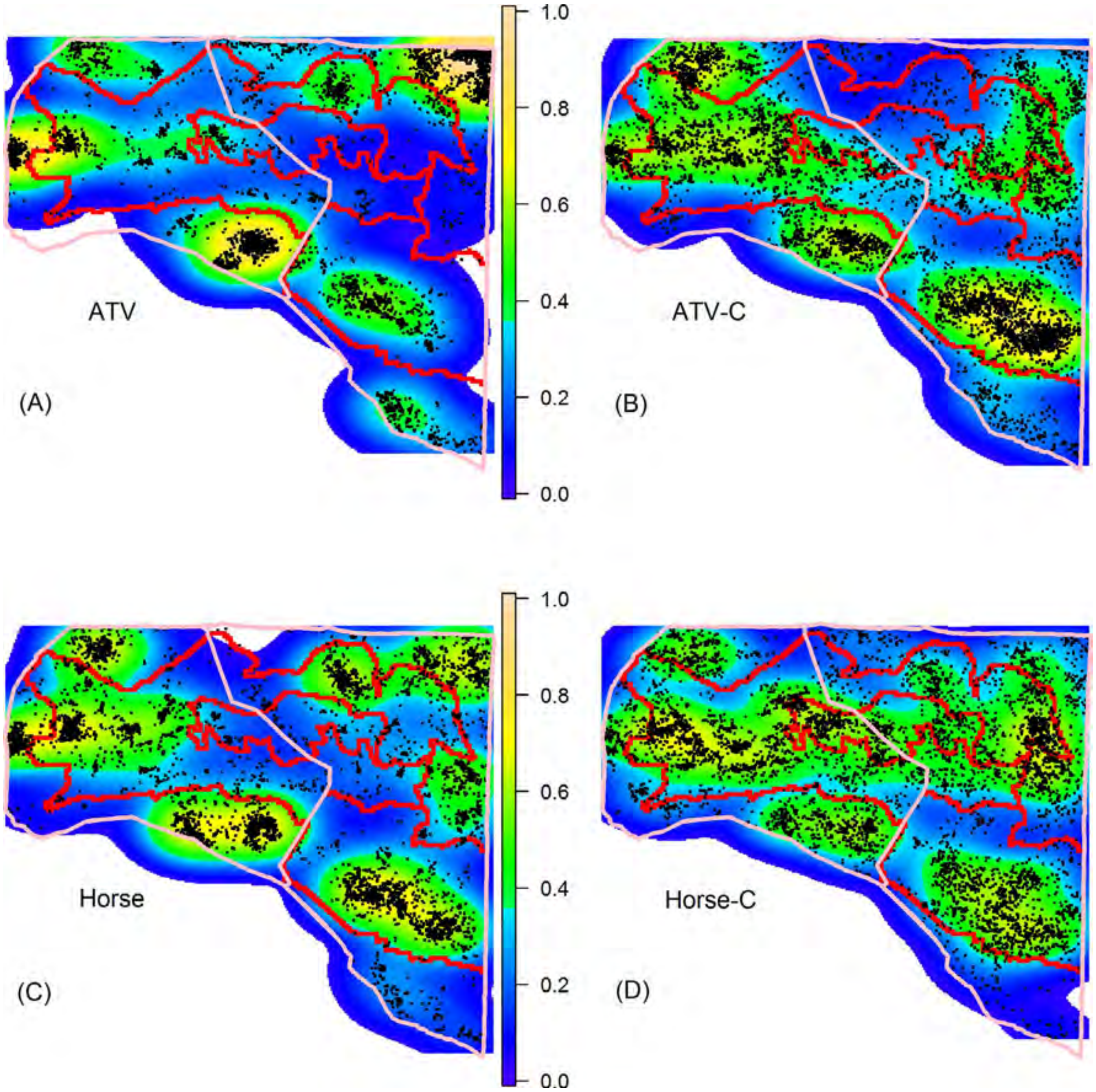


Fig. 4. Locations of 35 elk during ATV riding (ATV, A) and horseback riding (Horse, C) versus corresponding control periods (B and D), superimposed on estimates of the spatial probability distribution of elk locations, estimated as kernel densities, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Probability of use is scaled from 0 to 1, with higher use shown by warmer colors (yellow, then green) and lower use by cooler colors (light blue, then dark blue). Red lines are the recreation trails and pink lines fences. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

responses at distances as far as possible from recreationists.

4. Discussion

4.1. Elk avoidance of recreation trails and recreationists

Our results showed strong avoidance by elk to the recreation trails during each of the four types of recreation. Almost one-half of all elk telemetry locations during the recreation activities occurred on just 15% of the study area farthest from trails. Elk avoidance of recreation trails was strongest during ATV riding. Elk avoidance of trails during mountain biking, hiking and horseback riding was statistically similar but the distribution of elk locations during these three types of recreation indicated that elk shifted farther from trails during mountain biking.

Elk avoidance of trails was calculated as the mean distance of telemetered elk to trails, using data pooled for each animal across treatment and control replicates of each recreation type. Estimates thus represented the "average" distribution of elk in relation to trails during each recreation treatment, and did not account for finer temporal responses, such as potential population shifts away from and back toward trails as recreationists passed by a given area. By contrast, the minimum separation distances that elk maintained from recreationists in real time documented the direct effect of human movement on the species' behavior at five-minute time windows during each recreation treatment. Results showed that elk were quite sensitive to human presence, shifting distributions away from recreationists and farther out of view as the activities moved along the trails. The minimum daily distances maintained by elk from recreationists were notably large (averaging 558–879 m among treatments), indicating a strong spatial intolerance of elk to recreationists and well beyond areas visible from trails. Direct responses of elk to recreationists were stronger and more precise across treatments than their indirect responses to trails.

The pattern of long-distance avoidance by elk to recreationists was supported by real-time documentation of elk fleeing from approaching recreationists that was documented in earlier publications from data collected in our study area (Preisler et al., 2006, 2013). Flight responses of elk to the recreation activities in our study area showed substantially higher probabilities of flight than expected at distances of 500–1000 m (Wisdom et al., 2004a). Minimum separation distances in our study

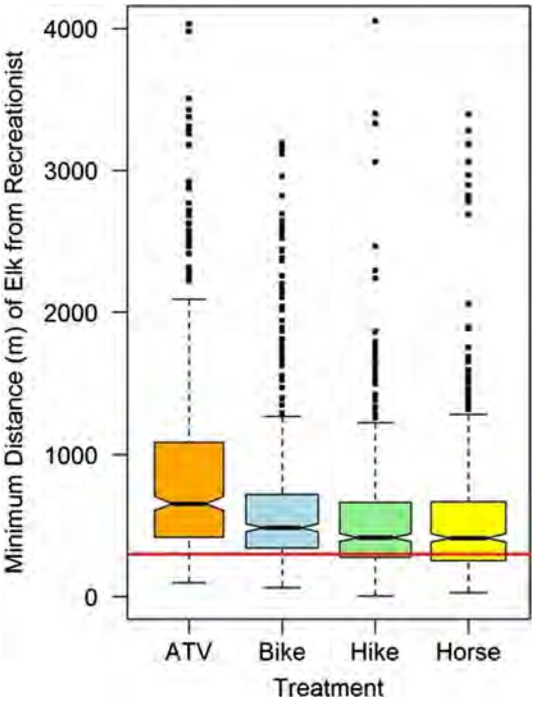


Fig. 5. Parallel boxplots showing the variability among elk (variability within each box) and among treatments (variability between boxes) in minimum separation distances of LORAN-C telemetered elk (n = 19) from recreationists during all-terrain vehicle riding (ATV), mountain biking (Bike), hiking (Hike), and horseback riding Horse, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Minimum distances were evaluated per elk/day, with two values per day (morning and afternoon) per elk. Horizontal red line shows the maximum viewing distance of 300 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

followed a similar pattern to these flight responses, with the latter modeled with 2002 elk telemetry data not used in our analysis (Wisdom et al., 2004a).

Separation distances maintained by elk from recreationists appear to represent a cause-effect process that we cannot attribute to other factors. We controlled for human access with our design of randomly selecting and implementing one type of recreation activity for a given five-day period, followed by a paired nine-day control period of no human activity. We further controlled for effects of season and year by replicating this design during spring, summer, and fall, and across years. Other factors influencing elk movements may have involved the two main predators of elk in our study area, cougars (*Puma concolor*) and black bears (*Ursus americanus*); however, these predators were constant background factors operating during both treatment and control periods (Wisdom et al., 2005). We know of no other factors beyond the recreation activities that would help explain our results.

4.2. Sensory cues used by elk to avoid recreationists

Long separation distances maintained by elk from recreationists beg the question: what types of sensory cues are elk using to react to humans? Large mammals and many other vertebrates have keen senses of smell, hearing, and sight that have evolved to detect predators (Hunter and Skinner, 1998; Lima and Dill, 1990; Bennett et al., 2009; Wikenros et al., 2015). Elk moved largely out of view during the recreation activities, suggesting visibility was a strong factor in avoidance of trails. However, viewing distances were based on human capacity to see elk, not vice versa. Moreover, ungulates such as elk can easily hear and smell humans at the distances that elk maintained from recreationists (see citations above), suggesting that any combination of sensory cues could have been used.

In addition, visual detection of humans can be impaired by obstructions of vegetation and topography, and auditory and olfactory cues to human presence are affected by wind speed and direction. Olfactory cues also were likely different for each recreation activity: ATVs emit a distinct gasoline odor and horses provide an additional olfactory cue beyond that of humans.

Each recreation activity also was associated with a different level of noise, which clearly affects wildlife (Barber et al., 2009). ATV riding is the loudest of the four recreation activities, with levels as high as 110 dB (Lovich and Bainbridge, 1999), and thus has high noise impact on wildlife (Bowles, 1995, Lovich and Bainbridge, 1999). It is unclear whether any of the other three recreation activities were louder than the others. We are not aware of any comparative research on noise associated with non-motorized forms of trail-based recreation.

Differences in speed of the recreation activities may also have provided additional cues for elk detection of recreationists. The speed of ATVs was > 2 times faster than mountain bikes, and > 4–5 times faster than hikers and horseback riders, respectively, during our study (Wisdom, unpublished data). Our treatment design ensured equal spatial coverage of the trail system by all four recreation treatments, but ATVs covered the trails at a faster rate each morning and afternoon. The higher speed of ATVs, combined with their substantially higher noise, may help explain the stronger avoidance response of elk to ATVs. The higher speed of ATVs might also have limited the reaction time of elk, as shown by some elk maintaining closer distances to trails and possibly hiding during this activity (see Wisdom et al. (2004a) for a related discussion of elk hiding versus flight responses to ATV riding). Given the wide variety of visual, auditory, and olfactory stimuli, different combinations of sensory cues were likely used by elk under varying conditions to detect and respond to recreationists.

4.3. Support for hypotheses on viewing, ATV effects, and forest roads

We identified three hypotheses for our analyses: (1) that elk avoidance would occur at distances that allow animals to stay out of view of recreationists; (2) that avoidance would be strongest in response to motorized recreation (ATV riding); and (3) that elk would respond to trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. We found support for all three hypotheses. Elk avoided trails and recreationists at distances largely beyond human view (hypothesis 1). This result agrees with past studies showing elk use of areas obstructed from view (e.g., Montgomery et al., 2012), sometimes referred to as “hiding cover” for elk (Thomas et al., 1979; Canfield et al., 1986; Lyon, 1987). Elk also use areas of steeper slopes, complex topography, or areas closer to cover-forage edges, presumably as a means of remaining hidden from humans or predators (e.g., Witmer et al., 1985; Thomas et al., 1988; Johnson et al., 2000; Coe et al., 2011; Harju et al., 2011; Buchanan et al., 2014).

Extensive timber harvest occurred on 35% of our study area during the 1990s, which uniformly increased openness of the landscape due to the even distribution of harvested vs. unharvested stand mosaics (Wisdom et al., 2004b). Viewing distances in our study increased in response to the extensive timber harvest and may have increased the distances that elk maintained from recreationists. The influence of silviculture and forest topography on viewing, and the subsequent recreation effects on wildlife sensitive to human presence, agrees with Lyon’s (1987) modeling of forest structure and topography to characterize hiding cover for elk.

Elk avoidance of ATVs also was stronger than to the three types of non-motorized recreation (hypothesis 2). Ciuti et al. (2012) found similar results in a comparative study of ATV riding, mountain biking, hiking, and horseback riding in Alberta, Canada. Other authors have inferred that ATV riding has a stronger effect on wildlife than non-motorized recreation because of higher noise and faster speeds, which influences more area per unit time (Lovich and Bainbridge, 1999; Wisdom et al., 2004a; Proescholdt, 2007; Ciuti et al., 2012; Preisler et al., 2013). However, Larson et al.'s (2016) meta-analysis of recreation effects on wildlife suggested that non-motorized recreation had stronger effects than motorized (but differences were not statistically significant). Additional research is needed to address inconsistencies among studies and to investigate effects of trail-based recreation on fitness of different wildlife species and taxa.

Avoidance responses by elk to the recreation activities also were similar to those documented in relation to forest roads open to motorized traffic (hypothesis 3). Our review of the literature revealed displacement of elk from forest roads open to motorized traffic that often exceeded 0.5–1.5 km. Avoidance responses by elk distance to open roads, or to open road density, have been documented consistently and overwhelmingly by > 30 studies conducted during the past 5 decades in forested areas of western North America. Examples from each decade are Perry and Overly (1977), Lyon (1983), Cole et al. (1997), Rowland et al. (2000), and Prokopenko et al. (2016).

Distance responses by elk to recreationists during our study mirrored the general avoidance distances of 0.5–1.5 km or farther that were documented in many roads studies during non-hunting seasons. Elk sometimes move much longer distances (e.g., > 25 km) from public to private lands during hunting seasons when public forests are highly roaded and lack adequate security for elk to hide from hunters (Proffitt et al., 2013). We did not evaluate the effects of hunting, nor could we evaluate the potential for such longer-distance landscape responses by elk because of the study area enclosure.

Similarities between elk responses to trail-based recreation and forest roads also depend on the specific response variables evaluated and the spatial and temporal scales at which responses are measured. Different studies evaluated elk avoidance over different time periods (seasonal or multiple seasons in a year or multiple years) and spatial extents. Results will vary by sample size and the degree of "averaging" of avoidance effects by time of day, seasons, and years. This variation was obvious in our results. Analysis of elk distances to trails represented an average response over the eight-hour period of all days among all replicates of each treatment type. These avoidance distances were substantially less than the minimum separation distances maintained by elk from recreationists, as measured in five-minute time windows over the same eight-hour days and replicates. Minimum separation distances of elk from recreationists are a more direct measure of elk responses; we consider these results comparable to contemporary finer-scale distance responses of elk to open roads (e.g., Buchanan et al., 2014; Morris et al., 2016; Prokopenko et al., 2016; Ranglack et al., 2017).

4.4. Bias in visual observations of elk

Elk are widely distributed and occupy summer ranges on nearly every National Forest in the western United States (O'Gara and Dundas, 2002). Consequently, the species has been a topic of public comments as part of travel management planning on National Forests. Motorized recreationists often have commented that elk populations do not avoid OHVs because elk are observed while riding. We heard this comment numerous times during meetings we held with recreation stakeholders about our research. Of direct relevance to these public comments was the research by Naylor (2006), who summarized the distances at which elk were directly observed by recreationists during implementation of the recreation treatments in our study area. Elk were observed by recreationists at mean distances of 116–161 m among the four types of treatments (Naylor, 2006). These distances are shorter than or similar to the average near viewing distance of 172 m at which elk could be viewed without visual obstruction.

Telemetered elk, representing a random sample of female elk in our study area, maintained minimum separation distances that were 4–8 times farther from recreationists than the distances estimated by visual observation. Thus, a large percentage of telemetered elk were present beyond the distances at which visual observations were possible, and elk consistently maintained these longer distances during each type of recreation.

Recreationists in our study were able to observe a small portion of the elk population in view of trails, but unable to see the large majority of the elk population that remained hidden from view during recreation activities. Visual observations of elk during recreation thus could not detect the strong avoidance by elk that occurred out of view. This pattern explains the differences between motorized recreationists' comments about elk as part of travel management planning and the responses that we documented with telemetered elk in our study.

Stankowich (2008) summarized results from > 50 studies that reported results of flight distance of wild ungulate species in response to human activities. The majority of reported studies were based on visual observations, but no mention was given in Stankowich (2008) about the potential for bias with the use of visual observations in environments where viewing was substantially limited, or for ungulate species whose response to human presence is to remain out of view. Automated and remotely-sensed technologies are now available that document a variety of animal behaviors and responses to human activities without dependence on human observations (e.g., Cooke et al., 2004; Coulombe et al., 2006; Shepard et al., 2008; Naylor et al., 2009; Suraci et al., 2017).

4.5. Implications

Avoidance by elk to recreation trails and recreationists represents a form of "habitat compression," similar to that described for effects of forest roads open to traffic (Wisdom et al., 2000, Rowland et al., 2004, Buchanan et al., 2014, Prokopenko et al., 2016). Habitat compression in response to human activities is a form of habitat loss for species like elk (Rowland et al., 2004, Frair et al., 2008, Buchanan et al., 2014), considering the potentially large areas not used or used less in the presence of humans, and that otherwise might be selected by a species in the absence of humans. Habitat compression can ultimately lead to large-scale population shifts by elk from public forests to private lands, thus eliminating hunting and viewing opportunities on public lands (Proffitt et al., 2013).

To address these types of effects, forest managers could use our results to evaluate trade-offs between competing objectives for trail-based recreation and wildlife species like elk that are sensitive to human activities on public forests. Although public forests are governed by laws and policies of multiple use, not all areas can be simultaneously co-managed for recreation and recreation-sensitive wildlife. Different land allocations can accommodate such competing uses, but often on different landscapes with clear objectives about which resources are featured. Optimizing land allocations through spatial analyses of trade-offs between competing forest uses (Wang et al., 2004), with the inclusion of human ecology mapping (McLain et al., 2013a, 2013b) and stakeholder engagement (Asah et al., 2012a, 2012b) is a forest planning approach that holds promise in helping address recreation and wildlife conflicts. We suggest that such an approach be considered in co-managing trail-based recreation and sensitive wildlife like elk on public forests.

Author contributions

BJ, LN, RA, and MW conceived, designed, and implemented the research; BJ, HP, LN, MR, and MW analyzed the data and wrote and edited the manuscript.

Acknowledgments

Funding was provided by the Oregon Department of Parks and Recreation, Oregon Department of Fish and Wildlife, and USDA Forest Service Pacific Northwest Region and Pacific Northwest Research Station. Additional support was provided by the USDA Forest Service Pacific Southwest Research Station. Jennifer Hafer and Bridgett Naylor helped prepare figures and summarize results. The authors wish to thank > 50 individuals, particularly Kristen Munday, who implemented the recreation activities for this study.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.01.032.

References

Adams, J.C., McCool, S.F., 2009. Finite recreation opportunities: the Forest Service, the Bureau of Land Management, and off-road vehicle management. Nat. Res. J. 49, 45–116.

Asah, S.T., Bengston, D.N., Wendt, K., DeVaney, L., 2012a. Prognostic framing of stakeholders' subjectivities: a case of all-terrain vehicle management on state public lands. Environ. Manage. 49, 192–206.

Asah, S.T., Bengston, D.N., Wendt, K., Nelson, K.C., 2012b. Diagnostic reframing of intractable environmental problems: case of a contested multiparty public land-use conflict. Environ. Manage. 108, 108–119.

Barber, J.R., Crooks, K.R., Fristrup, K.M., 2009. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180–189.

Benjamini, Y., 1988. Opening the box of a boxplot. Am. Statist. 42, 257–262.

Bennett, V.J., Beard, M., Zollner, P.A., Fernández-Juricic, E., Westphal, L., LeBlanc, C.L., 2009. Understanding wildlife responses to human disturbance through simulation modeling: a management tool. Ecol. Complex. 6, 113–134.

Beyer, H.L., Ung, R., Murray, D.L., Fortin, M.J., 2013. Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density. J. Appl. Ecol. 50, 286–294.

Bowker, J.M., Askew, A.E., Cordell, H.K., Betz, C.J., Zarnoch, S.J., Seymour, L., 2012. Outdoor recreation participation in the United States – projections to 2060. U.S. Forest Service Gen. Tech. Rep. SRS-GTR-160, Asheville, NC, USA.

Bowles, E., 1995. Responses of wildlife to noise. In: Knight, L., Gutzwiller, J. (Eds.), Wildlife and Recreationists. Island Press, Washington DC, USA, pp. 108–156.

Brillinger, D.R., Preisler, H.K., Ager, A.A., Wisdom, M.J., 2004. Stochastic differential equations in the analysis of wildlife motion. 2004 Proceedings, American Statistical Association, Section on Statistics and the Environment, Alexandria, VA, USA: American Statistical Association < https://www.stat.berkeley.edu/users/brill/Papers/jsm2004j.pdf > .

Brillinger, D.R., Preisler, H.K., Wisdom, M.J., 2011. Modelling particles moving in a potential field with pairwise interactions and an application. Brazil. J. Prob. and Stat. 25, 421–436.

Buchanan, C.B., Beck, J.L., Bills, T.E., Miller, S.N., 2014. Seasonal resource selection and distributional response by elk to development of a natural gas field. Rangeland Ecol. Manage. 67, 369–379.

Canfield, J.E., Lyon, L.J., Hillis, J.M., 1986. The influence of viewing angle on elk hiding cover in young timber stands. U.S. Forest Service Research Paper INT-371, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.

Chambers, J.M., Cleveland, W.S., Kleiner, B., Tukey, P.A., 1983. Graphical Methods for Data Analysis. Wadsworth International Group, Belmont, CA, USA.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7, e50611. http://dx.doi.org/10.1371/journal.pone.0050611.

Coe, P.K., Johnson, B.K., Wisdom, M.J., Cook, J.G., Vavra, M., Nielson, R.M., 2011. Validation of elk resource selection models with spatially independent data. J. Wildl. Manage. 75, 159–170.

Cole, E.K., Pope, M.D., Anthony, R.G., 1997. Effects of road management on movement and survival of Roosevelt elk. J. Wildl. Manage. 61, 1115–1126.

Cole, E.K., Pope, M.D., Anthony, R.G., 2004. Influence of road management on diurnal habitat use of Roosevelt elk. Northwest Sci. 78, 313–321.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: a mechanistic approach to ecology. Trends Ecol. Evol. 19, 334–343.

Cordell, K., Betz, J., Green, G., Owens, M., 2005. Off-highway vehicle recreation in the United States, regions and states: A national report from the National Survey on Recreation and the Environment (NSRE). USDA Forest Service Southern Research Station, Athens, GA, USA.

Cordell, H.K., 2012. Outdoor recreation trends and futures: a technical document supporting the Forest Service 2010 RPA Assessment. U.S. Forest Service Gen. Tech. Rep. SRS-GTR-150, Asheville, NC, USA.

Coulombe, M.L., Massé, A., Côté, S.D., 2006. Quantification and accuracy of activity data measured with VHF and GPS telemetry. Wildl. Soc. Bull. 34, 81–92.

Federal Register, 2005. Part IV. Department of Agriculture, Forest Service. 36 CFR Parts 212, 251, and 295. Travel management; designated routes and areas for motor vehicle use; Final Rule, vol. 70. Federal Register, Washington, DC, USA0, pp. 68264–68291.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B., Beyer, H.L., 2004. Removing GPS collar bias in habitat selection studies. J. Appl. Ecol. 41, 201–212.

Frair, J.L., Merrill, E.H., Beyer, H.L., Morales, J.M., 2008. Thresholds in landscape connectivity and mortality risks in response to growing roads networks. J. Appl. Ecol. 45, 1504–1513.

Green, R.J., Higginbottom, K., 2000. The effects of non-consumptive wildlife tourism on free-ranging wildlife: a review. Pacific Cons. Biol 6, 183–197.

Gutzwiller, K.J., D'Antonio, A.L., Monz, C.A., 2017. Wildland recreation disturbance: broad-scale spatial analysis and management. Front. Ecol. Environ. http://dx.doi.org/10.1002/fee.1631.

Hansen, M.C., Riggs, R.A., 2008. Accuracy, precision, and observation rates of global positioning system telemetry collars. J. Wildl. Manage. 72, 518–526.

Harju, S.M., Dzialak, M.R., Osborn, R.G., Hayden-Wing, L.D., Winstead, J.B., 2011. Conservation planning using resource selection models: altered selection in the presence of human activity changes spatial prediction of resource use. Animal Cons. 14, 502–511.

Havlick, D., 2002. No Place Distant: Roads and Motorized Recreation on America's Public Lands. Island Press, Washington D, C., USA.

Hennings, L., Soll, J., 2017. Hiking, mountain biking and equestrian use in natural areas: A recreation ecology literature review. Portland Metro Parks and Nature, 600 NE Grand Avenue, Portland, OR, USA.

Hunter, L.T.B., Skinner, J.D., 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour 135, 195–211.

Johnson, B.K., Ager, A.A., Findholt, S.L., Wisdom, M.J., Marx, D., Kern, J., Bryant, L.D., 1998. Mitigating spatial differences in observation rate of automated telemetry systems. J. Wildl. Manage. 62, 958–967.

Johnson, B.K., Kern, J.W., Wisdom, M.J., Findholt, S.L., Kie, J.G., 2000. Resource selection and spatial separation of mule deer and elk in spring. J. Wildl. Manage. 64, 685–697.

Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLoS ONE 11 (12), e0167259. http://dx.doi.org/10.1371/journal.pone.0167259.

Leung, Y.F., Marion, J.L., 2000. Recreation impacts and management in wilderness: a state-of-knowledge review, in: Cole, N.D., McCool, S.F., Borrie, W.T. O'Loughlin, J. (Comps.), Wilderness science in a time of change conference, Volume 5: Wilderness ecosystems, threats, and management; U.S. Forest Service Rocky Mountain Research Station RMRS-P-15-VOL-5, Ogden, UT, USA, pp 23–48.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lovich, J.E., Bainbridge, D., 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. Environ. Manage. 24, 309–326.

Lyon, L.J., 1983. Road density models describing habitat effectiveness for elk. J. Forestry 81, 592–613.

Lyon, L.J., 1987. HIDE2: Evaluation of elk hiding cover using a personal computer. U.S. Forest Service, Intermountain Research Station, INT-365, Odgen, UT, USA.

McLain, R., Cerveny, L., Besser, D., Banis, D., Biedenweg, K., Todd, A., Kimball-Brown, C., Rohdy, S., 2013a. Mapping human-environment connections on the Olympic Peninsula: an atlas of landscape values. Occas. Pap. Geogr. 7.

McLain, R., Poe, M., Biedenweg, K., Cerveny, K.L., Besser, D., Blahna, D., 2013b. Making sense of human ecology mapping: an overview of approaches to integrating socio-spatial data into environmental planning. Hum. Ecol. 41, 651.

Montgomery, R.A., Roloff, G.J., Millspaugh, J.J., 2012. The importance of visibility when evaluating animal response to roads. Wildl. Biol. 18, 393–405.

Montgomery, R.A., Roloff, G.J., Millspaugh, J.J., 2013. Variation in elk response to roads by season, sex, and road type. J. Wildl. Manage. 77, 313–325.

Morris, L.R., Proffitt, K.M., Asher, V., Blackburn, J.K., 2016. Elk resource selection and implications for anthrax management in Montana. J. Wildl. Manage. 80, 235–244.

Naylor, M., 2006. Behavioral Responses of Rocky Mountain Elk (Cervus elaphus) to Recreational Disturbance. Oregon State University, Corvallis, Oregon, USA M.S. Thesis.

Naylor, L.M., Wisdom, M.J., Anthony, R.G., 2009. Behavioral responses of North American elk to recreational activity. J. Wildl. Manage. 37, 328–338.

Newsome, D., Smith, A., Moore, S.A., 2008. Horse riding in protected areas: a critical review and implications for research and management. Curr. Iss. Tourism 11, 144–166.

Nielson, R.M., Manly, B.F.J., McDonald, L.L., Sawyer, H., McDonald, T.L., 2009. Estimating habitat selection when GPS fix success is less than 100%. Ecol. 90, 2956–2962.

O'Gara, B.W., Dundas, R.G., 2002. Distribution: past and present. In: Toweill, D.E., Thomas, J.W. (Eds.), North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, D.C., USA, pp. 67–119.

Perry, C., Overly, R., 1977. Impact of roads on big game distribution in portions of the Blue Mountains of Washington, 1972–1973. Washington Game Department Technical Bulletin, Olympia, WA, USA.

Preisler, H.K., Ager, A.A., Wisdom, M.J., 2006. Statistical methods for analyzing responses of wildlife to human disturbance. J. Appl. Ecol. 43, 164–172.

Preisler, H.K., Ager, A.A., Wisdom, M.J., 2013. Analyzing animal movement patterns using potential functions. Ecosphere 43, 32. https://doi.org/10.1890./ES12-00286.1.

Proescholdt, K., 2007. Collision Course? Off-Road Vehicle Impacts on Hunting and Fishing. Izaak Walton League of America, Gaithersburg, MD, USA < http://www.iwla.org/docs/default-source/Outdoor-America-articles/off-track-by-kevin-proescholdt.pdf?sfvrsn=2 > (accessed 17.08.03).

Prokopenko, C.M., Boyce, M.S., Avgar, T., 2016. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. J. Appl. Ecol. 54, 470–479.

Proffitt, K.M., Gude, J.A., Hamlin, K.L., Messer, M.A., 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. J. Wildl. Manage. 77, 514–524.

Ranglack, D.H., Proffitt, K.M., Canfield, J.M., Gude, J.A., Rotella, J., Garrott, R.A., 2017. Security areas for elk during archery and rifle hunting seasons. J. Wildl. Manage. 81, 778–791.

Rowland, M.M., Bryant, L., Johnson, B., Noyes, J., Wisdom, M.J., Thomas, J.W., 1997. The Starkey Project: History, Facility and Data Collection Methods for Ungulate Research. U.S. Forest Service Gen. Tech. Rep. PNW-GTR-396, Portland, OR, USA.

Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. J. Wildl. Manage. 64, 672–684.

Rowland, M.M., Wisdom, M.J., Johnson, B.K., Penninger, M.A., 2004. Effects of roads on elk: implications for management in forested ecosystems. Trans. N. Amer. Wildl. Nat. Res. Conf. 69, 491–508.

Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G., Liebsch, N., Albareda, D.A., Halsey, L.G., Gleiss, A., Morgan, D.T., Myers, A.E., Newman, C., Macdonald, D.W., 2008. Identification of animal movement patterns using tri-axial accelerometry. Endang. Species Res. 10, 47–60.

Sicking, L. P. 1998. Rangefinder comparison. USDA Forest Service Technology Development Center Bulletin 9824 1307-SDTDC, San Dimas Technology and Development Center, San Dimas CA, USA < https://www.fs.fed.us/eng/pubs/html/98241307/98241307.html > (accessed 10 November 2017).

Stankowich, T., 2008. Ungulate flight responses to human disturbances: a review and meta-analysis. Biol. Cons. 141, 2159–2173.

Stewart, K.M., Bowyer, R.T., Dick, B.L., Johnson, B.K., Kie, J.G., 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143, 85–93.

Suraci, J.P., Clinchy, M., Mugerwa, B., Delsey, M., Macdonald, D.W., Smith, J.A., Wilmers, C.C., Zanette, L.Y., 2017. A new automated behavioural response system to integrate playback experiments into camera trap studies. Meth. Ecol. Evol. 8, 957–964.

Tarr, N.M., Simons, T.R., Pollock, K.H., 2010. An experimental assessment of vehicle disturbance effects on migratory shorebirds. J. Wildl. Manage. 74, 1176–1183.

Taylor, A.R., Knight, R.L., 2003a. Wildlife responses to recreation and associated visitor perceptions. Ecol. Appl. 13, 951–963.

Taylor, A.R., Knight, R.L., 2003b. Behavioral responses of wildlife to human activity: terminology and methods. Wildl. Soc. Bull. 31, 1263–1271.

Thomas, J. W., Black Jr., H., Scherzinger, R.J., Pedersen, R.J., 1979. Deer and elk. In: Thomas, J.W. (Ed.), Wildlife habitats in the managed forests, the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture Handbook 553, U.S. Government Printing Office, Washington, D.C., USA, pp 104–125.

Thomas, J.W., Leckenby, D.A., Henjum, M., Pedersen, R.J., Bryant, L.D., 1988. Habitat-effetiveness index for elk on Blue Mountain winter ranges. U.S. Forest Service Pacific Northwest Research Station Gen. Tech. Rep. PNW-GTR-218, Portland, OR, USA.

The Outdoor Foundation, 2016. Outdoor Recreation Participation. The Outdoor Foundation, Washington, DC, USA.

Thompson, A., 2007. Management perceptions of off-highway vehicle use on National Forest System lands in Appalachia. West Virginia University, Morgantown WV M.S. Thesis.

USDA Forest Service, 2004. Managing the National Forest System: Great Issues and Great Divisions. U.S. Department of Agriculture, Forest Service report, January 21, 2004, on file, Pacific Northwest Research Station, La Grande, OR, USA.

Venables, W.N., Ripley, B.D., 1997. Modern Applied Statistics with S-PLUS, Second Edition with 1999 Updates. Springer, New York.

Wang, X., Yu, S., Huang, G.H., 2004. Land allocation based on integrated GIS-optimization modeling at a watershed level. Landsc. Urban Plan. 66, 61–74.

Webb, R.H., Wilshire, H.G., 2012. Environmental Effects of Off-Road Vehicles: Impacts and Management in Arid Regions. Springer Science and Business Media, New York, New York.

Wikenros, C., Dries, D.P.J., Kuijper, P.J., Behnke, R., Schmidt, K., 2015. Behavioural responses of ungulates to indirect cues of an ambush predator. Behaviour 152, 1019–1040.

Wisdom M.J., Cook, J.G., Rowland, M.M., Noyes, J.H., 1993. Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. U.S. Forest Service Gen. Tech. Rep. PNW-GTR-311, Portland, Oregon, USA.

Wisdom, M.J., Holthausen, R.S., Wales, B.C., Hargis, C.D., Saab, V.A., Lee, D.C., Hann, W. J., Rich, T.D., Rowland, M.M., Murphy, W.J., Eames, M.A., 2000. Source habitats for terrestrial vertebrates of focus in the Interior Columbia Basin: broad-scale trends and management implications. U.S. Forest Service Pacific Northwest Research Station Gen. Tech. Rep. PNW-GTR-485, Portland, OR. USA.

Wisdom, M.J., Ager, A.A., Preisler, H.K., Cimon, N.J., Johnson, B.K., 2004a. Effects of off-road recreation on mule deer and elk. Trans. N. Amer. Wildl. Nat. Res. Conf. 69, 531–550.

Wisdom, M.J., Johnson, B.K., Vavra, M., Boyd, J.M., Coe, P.K., Kie, J.G., Ager, A.A., Cimon, N.J., 2004b. Cattle and elk responses to intensive timber harvest. Trans. N. Amer. Wildl. Nat. Res. Conf. 69, 727–758.

Wisdom, M.J. (Ed.), 2005. The Starkey Project: A Synthesis of Long-Term Studies of Elk and Mule Deer. Alliance Communications Group Allen Press, Lawrence, KS, USA.

Witmer, G.W., Wisdom, M.J., Harshman, E.P., Anderson, R.J., Carey, C., Kuttel, M.P., Luman, I.D., Rochelle, J.A., Scharpf, R.W., Smithey, D.A., 1985. Deer and elk. In: Brown, E.R. (Ed.), Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington, part 1-chapter narratives. USDA Forest Service Publication R6-F&WL-192-1985. U.S. Government Printing Office, Washington, DC, USA, pp 41–55.

Yankoviak, M., 2005. Off-Road Vehicle Policy on USDA National Forests: Evaluating User Conflicts and Travel Management. University of Montana, Missoula, MT, USA M.S. Thesis.