

Understanding and predicting habitat for wildlife conservation: the case of Canada lynx at the range periphery

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Abstract. Ecologists and managers are motivated to predict the distribution of animals across landscapes as well as understand the mechanisms giving rise to that distribution. Satisfying this motivation requires an integrated framework that characterizes multi-scale habitat use and selection, as well as builds predictive models such as resource selection functions. However, the assumption of constant habitat use or selection is often made in such analyses, which ignores the possibility that individuals experiencing different conditions might respond differently. Assessing functional responses in habitat use evaluates how animal behavior changes with differing environmental conditions, which has basic and applied utility. Here, we combined these ideas into an integrated process that characterizes habitat relationships, predicts habitat, and assesses behavioral differences with changing environmental conditions. Our species of interest was Canada lynx (*Lynx canadensis*) in the Northern Rocky Mountains, which is a rare and federally threatened forest carnivore. Through our process, we developed multi-scale predictions of lynx distribution and learned that across scales and seasons, lynx use more mature, spruce-fir forests than any other structure stage or species. Intermediate snow depths and the distribution of snowshoe hares (*Lepus americanus*) were the strongest predictors of where lynx selected their home ranges. Within their home ranges, female and male lynx increasingly used advanced regeneration forest structures as they became more available (up to a maximum availability of 40%). These patterns supported the bottom-up mechanisms regulating Canada lynx in that advanced regeneration generally provides the most abundant snowshoe hares, while mature forest is where lynx appear to hunt efficiently. However, lynx exhibited decreasing use of stand initiation structures (up to a maximum availability of 25%). Land managers have an opportunity to promote lynx habitat in the form of advanced regeneration, but are required to go through the stand initiation phase. Thus, managers can apply the relative proportions of forest structure classes along with our response curves to inform landscape actions (e.g., timber harvest) targeted at facilitating the forest mosaic used and selected by Canada lynx. Collectively, the insights gleaned from our approach advance habitat conservation efforts and consequently are of broad utility to applied ecologists and managers.

Key words: functional response; habitat selection; habitat use; *Lynx canadensis*; resource selection function; scale-integrated selection function.

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INTRODUCTION

Ecologists and managers alike are motivated to understand habitat relationships of animals and spatially predict their probability of use (Elith and Leathwick 2009). This is particularly true for species of conservation concern in that the designation of “critical habitat” is required by statutes such as the U.S. Endangered Species Act (ESA) and Canada Species at Risk Act (SARA). Consequently, previous researchers have invested substantial effort to develop spatial maps of habitat (i.e., probability of use) for many species of conservation concern, including caribou (*Rangifer* spp.; Johnson et al. 2004, DeCesare et al. 2012), Amur tigers (*Panthera tigris altaica*; Hebblewhite et al. 2014), brown bears (*Ursus arctos*; Peters et al. 2015), fishers (*Pekania pennanti*; Olson et al. 2014), and golden eagles (*Aquila chrysaetos*; Tack and Fedy 2015). There are many approaches to predict and understand habitat relationships (Elith and Leathwick 2009), but resource selection functions (RSFs; Boyce and McDonald 1999, Manly et al. 2002) are one of the most common methods employed.

Resource selection functions commonly implement a used-available design, whereby the RSF is used to assess differences in habitat covariates at areas used by an animal (as measured by radio-transmitters or global positioning system [GPS] units) and those areas that are likely available for selection (Boyce 2006, Johnson et al. 2006). Generally, this is accomplished by using logistic regression software as a means to maximize the use-availability likelihood (McDonald 2013). A substantial strength of RSFs is that one can use the coefficients derived from a model to generate predictive maps of relative probability of use (Boyce et al. 2002, Johnson et al. 2006), which are commonly presented as habitat maps (Johnson et al. 2004, DeCesare et al. 2012, Hebblewhite et al. 2014). Further, resource selection models are readily implemented and allow ecologists to evaluate habitat selection by animals across spatial and temporal scales by changing measures of availability (Johnson 1980, Boyce 2006, Meyer and Thuiller 2006, DeCesare et al. 2012). Resource selection analyses do, however, exhibit notable limitations for species’ conservation planning.

Here, we address two inherent limitations of resource selection analyses that present

challenges for practitioners wishing to translate results to on-the-ground conservation. First, coefficients characterizing the strength of selection or avoidance for a particular covariate are sensitive to, and indeed conditioned on, how availability is defined (Beyer et al. 2010, Matthiopoulos et al. 2011, Aarts et al. 2013, Northrup et al. 2013). For example, previous simulations have demonstrated that for a situation of constant use, habitat selection can vary widely and even change sign simply based on the definition of availability (Beyer et al. 2010). This is concerning because aligning availability with the perception of an animal or population can be difficult, particularly at the first and second orders of selection (Beyer et al. 2010). The implications of this issue are as follows: (1) selection may not solely reflect the behavior of an animal and (2) inferring the importance of a resource based on the strength of selection or avoidance is tenuous (Beyer et al. 2010, Kertson and Marzluff 2010, Northrup et al. 2013). This is particularly true when examining a subset of Johnson’s (1980) orders of selection (e.g., only assessing third-order selection, which is common) because higher order selection processes may create an abundance of an important resource that appears to be unimportant at lower levels of selection (Anderson et al. 2012). Therefore, we contend that simultaneously assessing multi-scale habitat use and availability, along with habitat selection, would provide a more contextual understanding for practitioners concerning habitat relationships of a particular species. Moreover, habitat use is the direct link between environmental conditions and individual performance (e.g., reproduction, survival) further emphasizing its importance (Gaillard et al. 2010).

The second limitation of resource selection analyses is that RSFs inherently assume that habitat use is a constant function of availability (Myerud and Ims 1998). Many studies, however, have demonstrated biologically relevant shifts in habitat use and selection with changing availability (Myerud and Ims 1998, Hebblewhite and Merrill 2008, Moreau et al. 2012, Tardy et al. 2014, van Beest et al. 2016), which was formally characterized as functional responses in habitat use by Myerud and Ims (1998). Evaluating functional responses provides basic insight into animal behavior as well as facilitates predictions concerning how animals might

alter their behavior when experiencing spatio-temporal changes in environmental conditions (McLoughlin et al. 2010). These insights have strong applied implications as well because ecologists can inform the direction of landscape-altering actions, which ultimately change the availability of resources. Advancing the understanding of animal behavior and providing tangible recommendations to land managers is essential for animal conservation and the recovery of endangered species (McLoughlin et al. 2010, Moreau et al. 2012). Functional responses in habitat use can assist both pursuits.

There are many analytical approaches for modeling functional responses. Mysterud and Ims (1998) initially proposed assessing functional responses by characterizing how relative habitat use changed across relative availability, but more recently studies generally evaluate relationships between habitat selection and availability (Moreau et al. 2012, Tardy et al. 2014, van Beest et al. 2016). Inferring behavioral mechanisms, however, could be difficult when using selection because habitat selection can decrease with increasing availability despite an animal's habitat use remaining constant (see Figs. 1 and 2 in Beyer et al. 2010 and Aarts et al. 2013, respectively). Thus, consistent with the foundational study (Mysterud and Ims 1998), we focused on habitat use to advance the application of functional responses as valuable tools for conservation planning.

In this paper, we characterize an analytical process to assist applied ecologists in translating the results from studies of habitat relationships to on-the-ground conservation. We applied our approach to Canada lynx (*Lynx canadensis*) in the Northern Rocky Mountains (hereafter Northern Rockies), USA. The Canada lynx is a rare, elusive, and federally threatened forest carnivore in the contiguous United States (USFWS 2000). The first step in our process was to characterize habitat use and selection at two spatial scales (second and third orders) and across seasons (i.e., winter and summer) by summarizing habitat use and availability (i.e., outside a RSF framework). This allowed us to assess spatio-temporal differences in habitat use, availability, and selection separately rather than relying only on selection coefficients derived from a RSF, which are conditioned on the definition of availability. Next, under the motivation of parsimony and prediction, we built

RSFs at the second and third orders to (1) evaluate multivariate resource selection and (2) provide single-scale and scale-integrated (DeCesare et al. 2012) predictions of Canada lynx habitat. These spatial predictions represent the habitat maps that are useful for land managers when making decisions. Lastly, we formally challenged the assumption of constant habitat use by implementing a novel approach for assessing functional responses (see *Methods: Functional response analysis*). Our technique for evaluating and visually displaying functional responses facilitated resource-specific insight concerning how Canada lynx altered their behavior with changing availability, which consequently generated concrete suggestions for land managers. More broadly, our collective analytical process illustrated a multi-step approach to achieve a common motivation in applied ecology, which is to (1) advance the understanding of animal-habitat relationships and (2) develop spatial predictions of habitat.

METHODS

Study area

This study took place in the Northern Rockies of northwestern Montana, USA, within the known distribution of Canada lynx (e.g., Squires et al. 2013; Fig. 1). This area covers approximately 3.6 million ha, follows natural topographic and vegetative boundaries, and is mostly composed of public lands (i.e., ~80%) with tribal and private lands making up the remaining. Across this gradient in ownership, there are differing levels of human use and resource extraction permitted; for instance, multiple wilderness areas and Glacier National Park occur within our study area. In addition, this area is ecologically unique within the contiguous United States in that the carnivore community remains intact (e.g., grizzly and black bears [*Ursus arctos* and *Ursus americanus*, respectively], cougars [*Puma concolor*], gray wolves [*Canis lupus*], wolverines [*Gulo gulo*], coyotes [*Canis latrans*], bobcats [*Lynx rufus*], and Canada lynx are all present). Moreover, our study area exhibits a diversity of forest structure types and species compositions (i.e., mostly mixed-conifer stands across structure stages; Appendix S1) and ranges from 220 to nearly 3400 m in elevation capturing

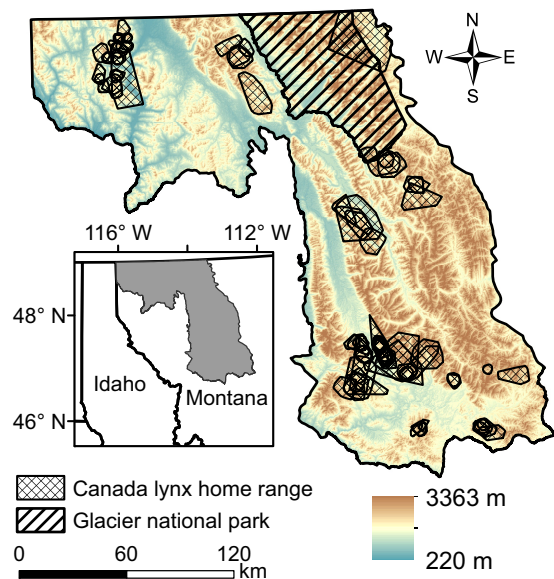


Fig. 1. Our Canada lynx (*Lynx canadensis*) study area in western Montana, USA. The background gradient indicates elevation (m).

a gradient in snow depths (elevation-snow depth $r = 0.72$). The mixed-conifer forests within our study area were mostly composed of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) in lower elevations, and lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) at higher elevations. Forest structure types range from stand initiation stages to mature stands.

Canada lynx spatial data and sampling framework

Between 1998 and 2015, we captured Canada lynx during winter using a combination of box (Kolbe et al. 2003) and foothold traps as well as foot snares, all of which were approved by the Institutional Animal Care and Use Committee (University of Montana IACUC permits 4-2008 and TE053737-1). Animals were fitted with very high frequency (VHF) radio-collars (Advanced Telemetry Systems, Isanti, Minnesota, USA), some of which also included Argos platform transmitter terminals (Sirtrack, Havelock North, New Zealand) or store-on-board GPS units (Lotek Wireless, Newmarket, Ontario, Canada). We located individuals with VHF collars every 1–2 weeks using

aerial telemetry, and we programmed GPS collars to collect a location every 30 min for 24 h every other day for 6–8 months. For animals with Argos collars, we attempted to acquire a location twice a day for the lifetime of the collar. We only used Argos locations of classes 1, 2, and 3 (i.e., 20% of total), which have reported precisions of 500–1500 m, 250–500 m, and <250 m, respectively (CLS America 2011). Spatial accuracy of VHF and GPS locations averaged 27–45 m (VHF) and 30 m (GPS) as reported by Squires et al. (2010, 2013), respectively, and GPS collars successfully collected locations in 86% of attempts.

We ensured all lynx exhibited space use consistent with an established home range (e.g., a central location of use) and removed animals with <20 locations. We performed further screening within our GPS data because we only used GPS locations for our fine-scale models of resource selection (i.e., third order of selection; Johnson 1980). We removed animals with <3 weeks of GPS data, as well as implemented the methods of Bjørneraas et al. (2010) to remove 187 error-induced spikes (~0.1% of the data). After these filtering procedures, our total dataset consisted of 166,064 locations (median = 1887 locations/individual, range = 20–7714 locations/individual) for 86 unique individuals (38 females, 48 males). These data were unevenly distributed across Argos (four individuals, 547 locations), VHF (16 individuals, 905 locations), and GPS (66 individuals, 164,612 locations) as well as across time periods (i.e., 2209 locations during 1998–2004, 88,030 locations during 2005–2010, and 75,825 locations during 2011–2015).

We developed RSFs for Canada lynx at the landscape and home range scale, which correspond to Johnson's (1980) second and third orders of selection, respectively. At the second order, we used our entire dataset to build annual or multi-annual home ranges (i.e., 95% minimum convex polygon; MCP) for every individual (Fig. 1). We used 95% MCPs because our intent was not to precisely estimate home range sizes, but rather to capture an approximate home range at the second order while liberally sampling availability at the third order (Hebblewhite and Merrill 2008, Moreau et al. 2012). These 86 home ranges characterized lynx resource use. We sampled available resources by randomly allocating 1000 circular home ranges across our study area

that were equal in area to the median lynx home range (55 km²).

At the third order of selection, we used only our GPS data that we separated into two seasons, winter (November–March) and summer (April–October). For each season, we constructed individual home ranges (i.e., 95% MCP), which resulted in 64 and 60 individuals sampled in winter and summer, respectively. We used individual locations within 95% MCPs (winter = 60,036 locations, summer = 96,291 locations) to sample resource use by Canada lynx (winter: median = 722 locations/individual, range = 113–2972; summer: median = 1433 locations/individual, range = 61–4474). We sampled availability for each individual by randomly allocating

locations (ratio = 1:1 for used and available locations) in both winter and summer home ranges. To build our home ranges for Canada lynx, we used the `adehabitatHR` package (Calenge 2006) in program R (R Core Team 2016) and we used standard tools in ArcGIS (ESRI 2011) to build our samples of availability.

Resource variables

We characterized our study area using a targeted suite of biotic and abiotic covariates that we expected to influence resource use and selection by Canada lynx (Table 1). We characterized abiotic characteristics using topographic metrics including (1) topographic roughness (Jenness 2004), (2) heat load index (McCune and Keon

Table 1. Resource variables used in analyses of habitat use, habitat selection, and functional responses for Canada lynx (*Lynx canadensis*) in western Montana, USA.

Variable	Units	Base resolution (m ²)	Order	Resolution (m ²)	Reference
Cover					
PICO canopy cover	%	30	Both	100, 500	Savage et al. (2015)
PIEN-ABLA canopy cover	%	30	Both	250, 250	Savage et al. (2015)
LAOC canopy cover	%	30	Both	250, 250	Savage et al. (2015)
PSME canopy cover	%	30	Both	100, 100	Savage et al. (2015)
Horizontal cover	%	30	Both	250, 250	Holbrook et al. (2017)
Forest structure					
Proportion of sparse forest	Proportion	30	Both	250, 250	Savage and Lawrence (2017)
Proportion of stand initiation forest	Proportion	30	Both	250, 500	Savage and Lawrence (2017)
Proportion of advanced regenerating forest	Proportion	30	Both	500, 250	Savage and Lawrence (2017)
Proportion of mature forest	Proportion	30	Both	100, 100	Savage and Lawrence (2017)
Climate					
Mean snow depth on 1 April 2005–2013†	m	1000	2	—	NOHRSC (2004)
Topography					
Roughness	Index	30	Both	500, 500	Jenness (2004)
Heat load index	Index	30	3	250, 250	McCune and Keon (2002)
Topographic position index	Index	30	3	500, 250	Guisan et al. (1999)
Prey					
Snowshoe hare occupancy‡	Probability	Multi-scale	Both	NA, NA	Holbrook et al. (2017)
Snowshoe hare intensity of use‡	Pellets/Krebs plot	Multi-scale	Both	NA, NA	Holbrook et al. (2017)

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes; RSF, resource selection function. Covariate codes PICO, PIEN-ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively. "Order" indicates whether the covariate was used for RSFs at the second order (2), third order (3), or both (both). "Resolution" indicates the scale for a particular covariate that was selected based on lowest AIC_c during winter (W) and summer (S), respectively, which was subsequently used in RSFs at the third order.

† Mean snow depth was not included in our third-order RSF models because the resolution (1000 m²) was too coarse.

‡ Snowshoe hare occupancy or intensity of use across multiple scales was not assessed because they were multi-scale composites (Holbrook et al. 2017).

2002), and (3) topographic position index (Guisan et al. 1999). Our heat load index and topographic position index represented hot-dry to cool-moist areas and relative concavity or convexity, respectively. We expected Canada lynx to be associated with cool-moist areas in the context of concave topographic locations (e.g., basins vs. ridges; Squires et al. 2008). In addition, we incorporated spatially explicit data on snow depth because Canada lynx are evolutionarily adapted for success in snowy conditions (Murray and Boutin 1991), and snow depth and extent are sensitive to changes in temperature (Barnett et al. 2005). We gathered snow depth data from the Snow Data Assimilation System (SNODAS) within the National Operational Hydrologic Remote Sensing Center (NOHRSC 2004). Previous analyses indicated a strong association between SNODAS-derived estimates of snow depth and field measurements in the forested ecosystems of the Northern Rockies (Clow et al. 2012). We downloaded 1 April snow depth for 2005–2013 and averaged across years to produce a relatively stable mean estimate for our study area. At the second order of selection, we expected a parabolic relationship between snow depth and Canada lynx resource use because lynx occupy subalpine environments (vs. high elevation alpine areas with deeper snow, and low elevation areas with little snow) in our study area. All abiotic metrics were calculated within ArcGIS (ESRI 2011) using standard tools, DEM Surface Tools for ArcGIS (Jenness 2013), or Geomorphometric and Gradient Metrics Toolbox (Evans et al. 2014).

To characterize forest composition and structure, we used a set of covariates developed specifically for the distribution of lynx in the Northern Rockies. Savage et al. (2015) developed and independently validated predictions of canopy cover for five conifer species during 2013: lodgepole pine, Engelmann spruce, subalpine fir, western larch, and Douglas-fir. Previous work in the Northern and Southern Rockies indicated a positive relationship between Canada lynx and their primary prey (i.e., snowshoe hare; *Lepus americanus*), and spruce-fir habitats (Squires et al. 2010, Berg et al. 2012, Ivan et al. 2014, Holbrook et al. 2017); thus, we combined our maps of subalpine fir and Engelmann spruce into a spruce-fir canopy cover map. In addition, Holbrook et al.

(2017) developed and evaluated a map characterizing horizontal cover during 2013, which is strongly associated with habitat use and kill site locations of Canada lynx (Squires et al. 2008, 2010) as well as high densities of snowshoe hares (Holbrook et al. 2017). We expected a positive relationship between horizontal cover and habitat use by Canada lynx.

Additionally, we used recently developed maps characterizing forest structural classes (Savage and Lawrence 2017). Forest structure mapping used manual interpretation of National Agriculture Imaging Program aerial imagery for reference data to classify 2013 Landsat 8 OLI/TIRS imagery. Classification was accomplished by separating structure classes hierarchically by class similarity and sequentially testing a range of machine-learning algorithms to determine the best predicting models. Classification results were further refined using a time series of forest structure and applying a series of rules to improve the accuracy of the final classification. Overall classification accuracy for the forest structure map was 80%, with most error occurring between open stands and other sparse stands. Thus, structural classes used for our analysis included (1) sparse forests, (2) stand initiation, (3) advanced regeneration, and (4) mature forests (see Table 2 and Appendix S1).

To further validate and define these predicted classes of forest structure, we performed an independent assessment with field-derived data. We used subplot (~170 m²) data for 574 locations collected by the United States Forest Service's Forest Inventory and Analysis (FIA) program during 2005–2012. We spatially overlapped these field data with predicted structural classes and calculated median values of structural metrics including basal area-weighted diameter at breast height (dbh), canopy cover, tree density, and tree height (Table 2; Appendix S1). This validation provided two functions: (1) a biological assessment of our structural classes at our study area extent (Appendix S1: Fig. S1) and (2) an important crosswalk to land managers tasked with managing forests and lynx habitat (Table 2; Appendix S1: Fig. S2). Results from this assessment confirmed that structure classes represented distinct forest conditions and that they captured gradients we expected to be important to Canada lynx (e.g., tree size, canopy cover, stem density). Based on

Table 2. Descriptions of forest structure classes using metrics from the USDA Forest Service Forest Inventory and Analysis program within modeled structure classes in Canada lynx (*Lynx canadensis*) habitat as defined by our RSF (i.e., score of 6–10 from our winter scale-integrated model) in western Montana, USA.

Structural class	General description
Sparse	Mixed-conifer stands (Appendix S1) that are sparsely stocked (naturally) or mechanically thinned, which tend to be younger (i.e., ~10–20 yr old) but can occur at any age. Sparse stands exhibited a median basal area-weighted dbh of 6 inches or 16 cm (IQR = 0–11 inches or 0–27 cm), 28% canopy cover (IQR = 8–49%), and a median estimated tree height of 34 ft or 10 m (IQR = 1–52 ft or 0.31–16 m). Median basal area of sparse stands was 40 ft ² /acre or 9 m ² /ha (IQR = 1–101 ft ² /acre or 0.23–23 m ² /ha), while tree density for trees larger than 5 inches (12.7 cm) was 48 trees/acre or 119 trees/ha (IQR = 0–144 trees/acre or 0–357 trees/ha). Tree density for trees <5 inches (12.7 cm) was 900 trees/acre or 2223 trees/ha (IQR = 0–3000 trees/acre or 0–7410 trees/ha)
Stand initiation	Stands that have few trees and an open canopy, and are a result of recent (e.g., ≤5 yr) disturbance (forest harvest or severe fire). Stand initiation exhibited a median basal area-weighted dbh of 0 inches and cm (IQR = 0–8 inches or 0–20 cm), 8% canopy cover (IQR = 0–36%), and a median estimated tree height of 1 foot or 0.31 m (IQR = 0–50 ft or 0–16 m). Median basal area of stand initiation was 0 ft ² /acre or 0 m ² /ha (IQR = 0–55 ft ² /acre or 0–13 m ² /ha), while tree density for trees larger than 5 inches (12.7 cm) was 0 trees/acre and trees/ha (IQR = 0–75 trees/acre or 0–186 trees/ha). Tree density for trees <5 inches (12.7 cm) was 0 trees/acre and trees/ha (IQR = 0–2249 trees/acre or 0–5557 trees/ha)
Advanced regeneration	Early–mid-seral stands of age ~25–40 yr with a mixed species composition, but spruce-fir tends to occur the most frequently (Appendix S1). Advanced regeneration exhibited a median basal area-weighted dbh of 8 inches or 20 cm (IQR = 5–10 inches or 14–27 cm); however, of the 51 plots examined 70% of them were classified at size classes between 5 and 15 inches (12.7–38 cm). Advanced regeneration exhibited median canopy cover of 45% (IQR = 30–70%), median tree height of 51 ft or 16 m (IQR = 34–64 ft or 10–20 m), and median basal area of 89 ft ² /acre or 20 m ² /ha (IQR = 39–124 ft ² /acre or 9–28 m ² /ha). Tree density for trees larger than 5 inches (12.7 cm) was 167 trees/acre or 416 trees/ha (IQR = 72–289 trees/acre or 178–714 trees/ha). Tree density for trees <5 inches (12.7 cm) was 900 trees/acre or 2223 trees/ha (IQR = 150–2549 trees/acre or 370–6298 trees/ha)
Mature	Mid-seral stands of age ≥40 yr arranged in a multi-storied structure with a mixed species composition, but spruce-fir tends to occur twice as much as any other species (Appendix S1). Mature exhibited a median basal area-weighted dbh of 10 inches or 25 cm (IQR = 7–14 inches or 18–35 cm). However, of the 194 plots examined 45% were classified at size classes between 5 and 10 inches (12.7–25.4 cm), 25% at size classes between 10 and 15 inches (25.4–38 cm), and 21% of them were classified at size classes between 15 and 25 inches (38–64 cm). Mature exhibited median canopy cover of 56% (IQR = 40–70%), median tree height of 65 ft or 20 m (IQR = 53–88 ft or 16–27 m), and median basal area of 140 ft ² /acre or 32 m ² /ha (IQR = 91–209 ft ² /acre or 21–48 m ² /ha). Tree density for trees larger than 5 inches (12.7 cm) was 217 trees/acre or 535 trees/ha (IQR = 144–331 trees/acre or 357–818 trees/ha). Tree density for trees <5 inches (12.7 cm) was 1500 trees/acre or 3705 trees/ha (IQR = 300–4200 trees/acre or 741–10,374 trees/ha)

Notes: RSF, resource selection function. Forest inventory data were collected during 2005–2012, and the total sample size was 366 subplots (subplots = ~170 m²), which included 194, 51, 34, and 87 classified as mature, advanced regeneration, stand initiation, and sparse, respectively. English and metric units are presented. Abbreviations IQR and dbh indicate the interquartile range and diameter at breast height, respectively. The calculation for basal area-weighted dbh was as follows: $\Sigma(\text{tree basal area} \times \text{dbh})/\text{total basal area}$.

previous analyses of habitat selection and fitness–habitat relationships (Squires et al. 2008, 2010, McCann and Moen 2011, Simons-Legaard et al. 2013, Kosterman 2014), we expected a positive association between Canada lynx and structural classes exhibiting dense trees and closed canopies (e.g., mature and advanced regeneration). In contrast, we expected a negative effect of the open classes (e.g., sparse and stand initiation) on lynx habitat use and selection. Given the strong association between lynx and forest structure, we expected to observe behavioral shifts in habitat use by lynx with changing availabilities of forest structure (i.e., functional responses).

Finally, we developed maps of predicted snowshoe hare occupancy (classification error = 25%)

and intensity of use (root-mean-square error = 4.22) across the distribution of lynx in the Northern Rockies (Holbrook et al. 2017). These maps characterized a composite for dense forests with high horizontal cover that occurred in intermediate snow depths (see Holbrook et al. 2017 for additional details). We used these data within our analytical process to characterize potential prey resources for Canada lynx. We expected a positive effect of these metrics on lynx habitat use and predicted that snowshoe hare occupancy would likely be a parsimonious predictor for mapping habitat of Canada lynx. In addition, we expected to observe a functional response in habitat use for both snowshoe hare occupancy and intensity of use (i.e., more disproportionate use at low values

of availability vs. high values) because of the strong predator–prey relationship between Canada lynx and snowshoe hares.

Summarizing habitat use, availability, and selection

We sampled and analyzed our resource variables differently at the second and third orders for our initial assessment of habitat use and selection. We calculated the mean value of covariates (see Table 1 for covariates used) within used ($n = 86$) and available ($n = 1000$) home ranges at the second order using the Geospatial Modelling Environment (Beyer 2012). At the third order, we attributed covariate values (Table 1) for used and available locations at the 100 m² resolution using standard tools in ArcGIS (ESRI 2011). We then calculated the mean of covariates at used and available locations for every lynx and subsequently averaged across animals ($n = 64$ for winter and 60 for summer) to estimate mean ($\pm 95\%$ confidence intervals [CIs]) use and availability. To calculate means and 95% CIs, we used the package Rmisc (Hope 2013) in program R (R Core Team 2016).

Development of RSF models

We then built RSFs at the second and third orders using fixed- and mixed-effects logistic regression (e.g., logit link) software, respectively, to understand multivariate resource selection by Canada lynx as well as develop spatial predictions of lynx habitat. We used a fixed-effects model at the second order because our design was not at the individual level; that is, we assessed differences in use and availability across home ranges of lynx. We weighted available : used observations in our second-order RSF at 0.086:1 to balance sample sizes between used and available home ranges that was reflective of our 86 lynx. Our second-order model took the structure:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i) \quad (1)$$

where β_i is the RSF coefficient for covariate i , x_i is the vector of covariate i , and $w(x)$ is the predicted relative probability of use (Boyce et al. 2002).

We built third-order RSFs (i.e., random intercept for lynx) at the seasonal home range level during winter and summer. We used a mixed-effects model at the third order because our

design was at the individual level, whereby the random effect accounted for (1) unbalanced sampling among lynx and (2) repeated measures (i.e., locations) within lynx (Gillies et al. 2006). Our general third-order RSF structure was as follows:

$$w(x) = \exp(\beta_1 x_{1j} + \beta_2 x_{2j} + \dots + \beta_i x_{ij} + \gamma_{0j}) \quad (2)$$

where β_i is the population-level (i.e., marginal) RSF coefficient for covariate i , x_{ij} is the vector of covariate i for individual j , γ_{0j} is the random intercept associated with the j th animal, and $w(x)$ is the same as in Eq. 1. For both our second- and third-order RSF, we standardized covariates (i.e., $(x_i - \bar{x})/SD$) and assessed support for quadratic terms to allow for curvilinear relationships. We observed quadratic effects for only mean snow depth and proportion of advanced regeneration forest in our second-order and our summer third-order RSFs, respectively. In addition, we implemented preliminary analyses to identify the most predictive scale (i.e., 100, 250, and 500 m²; see Table 1) for each covariate included in our third-order RSFs. We then assessed collinearity among all covariates among the suite being considered at both scales (Table 1) and removed those that were contributing to high correlations ($|r| > 0.60$; Appendix S2). When two covariates were correlated, we selected the covariate that was predicted to be more closely associated with Canada lynx ecology based on previous work.

With our set of reduced covariates and curvilinear relationships, as well as our motivation to develop parsimonious and predictive RSFs for habitat mapping, we implemented a model selection procedure to exhaustively search for the most predictive RSF using Akaike's information criterion, corrected for sample sizes (AIC_c; Hebblewhite et al. 2014). We developed a global model for both our second- and third-order RSFs and evaluated all potential subsets. However, because of issues with computational time for our mixed-effects RSFs, we initially searched all potential subsets using only fixed effects at the third order. We then selected the top 100 models, introduced the random intercept for individual lynx (i.e., Eq. 2), and selected the top model based on AIC_c. For all RSF modeling, when several nested models received similar support ($\Delta AIC_c < 2$), we

applied the principle of parsimony and selected the model containing the fewest parameters (Burnham and Anderson 2002). To assess the relative importance of each covariate (i.e., could be a linear or quadratic relationship) in our top models, we iteratively removed each covariate and documented the ΔAIC_c .

We evaluated the robustness of our second- and third-order RSFs using k -fold cross-validation (Boyce et al. 2002). We used two-fold and 10-fold cross-validation for our second- and third-order RSFs, respectively, by randomly dividing the number of lynx home ranges or locations into k -subsets of equal size and re-estimating the β coefficients of our best model. We then generated predicted values for the available sample at the appropriate order of selection from each subset, merged them into 10 equal-area bins characterizing low to high relative probability of use, and used Spearman rank correlations (r_s) to assess the association between the bins and the mean (i.e., across folds) frequency of home ranges or locations within each bin. A strong Spearman rank correlation coefficient indicates a robust model (Boyce et al. 2002). For all RSF modeling, we used the lme4 (Bates et al. 2015), MuMIn (Barton 2015), and AICcmodavg (Mazerolle 2016) package in program R (R Core Team 2016).

Habitat mapping and validation across the study area

By sampling home ranges and locations at the second and third orders, respectively, we preserved the conditional nature of habitat selection (sensu Johnson 1980), which allowed us to combine our predictions into scale-integrated habitat maps (DeCesare et al. 2012). We generated population-level RSFs at the second and third orders and across two seasons (winter and summer). We used the population-level β coefficients from Eqs. 1 and 2 to map the relative probability of use ($w(x)$) for Canada lynx across our study area (i.e., second order) at a 30 m² resolution, which generated five habitat maps. Because we summarized our resource variables to used and available home ranges for our second-order analysis, we averaged our second-order predictions using a neighborhood equal to the median home range size for our lynx (55 km²). To generate our scale-integrated habitat maps, we multiplied our second-order derived map by our two

third-order derived maps, which characterized the scale-integrated relative probability of use for Canada lynx during winter and summer. The scale-integrated maps integrate habitat relationships from the second and third orders into a single map, which has been demonstrated to be more predictive of habitat use than a single-order map (DeCesare et al. 2012). For all five maps, we sampled the predicted values using 100,000 random locations to characterize the distribution of predictions and reclassified the predicted values into 10 ordinal categories of equal area (i.e., using quantiles), which characterized low (i.e., 1) to high (i.e., 10) relative probability of use for Canada lynx.

To evaluate the ability of our probability maps (i.e., habitat maps) to predict frequency of use by lynx and inform conservation planning, we used 1919 lynx validation locations that were withheld from our primary analyses. Of the 1919 locations, 920 were collected during the winter (from 20 individuals) and 999 were collected during the summer (from 22 individuals). These locations were generally collected during years (i.e., 75% \leq 2005) and via platforms (i.e., 75% via Argos and VHF) that were independent of our training data, which were primarily collected via the GPS platform (99%) and after 2005 (82%). We assessed how the relative frequency of use measured by Canada lynx locations correlated (i.e., using Spearman rank correlation coefficients; Boyce et al. 2002) with our predicted categories of relative probability of use. This assessment was different than the k -fold cross-validation aforementioned in that it (1) used independent lynx locations (vs. subsets of the training data), (2) was applied only at the study area level (k -fold was at both the second- and third-order domains of availability) and (3) provided a model assessment that we believed was most relevant to conservation planning.

Finally, we developed an approach to empirically identify a binary cut-point for our continuous habitat maps indicating low and high probability of use by Canada lynx as a tool for conservation planning. We applied the concept of Boyce et al. (2002), but rather than assessing the relationship between our equal-area bins and the frequency of use, we assessed how the cumulative percentage of use was distributed across our bins. In other words, we assessed how many

equal-area bins (i.e., 1–10) were needed to capture a given percentage (e.g., 90%) of Canada lynx use. Not only did this provide a cut-point for deciding low and high probability of use that is central to conservation planning, but it also provided a simple means of assessing the relative mapping efficiency of each study area habitat map. In our case, the map that captures 90% of lynx use with the fewest number of bins indicates the most efficient map, that is, capturing the most use for the smallest amount of area. We used standard tools in ArcGIS (ESRI 2011) and program R (R Core Team 2016) for habitat mapping and assessment.

Functional response analysis

Our approach to modeling functional responses was a composite from previous studies in that we first characterized habitat use and availability for each individual by calculating a mean value (similar to Hansen et al. 2009, Matthiopoulos et al. 2011, Laforge et al. 2016) for all biotic covariates. We focused on biotic covariates because land managers could presumably change their availabilities (vs. abiotic covariates such as slope, elevation, or aspect). We then built linear, second-degree polynomial, and third-degree polynomial models (e.g., Pellerin et al. 2010) to test for functional responses in absolute habitat use for male and female lynx:

$$y_{1ij} = \beta_{0j} + \beta_{1j}(a_{1ij}) \quad (3)$$

$$y_{1ij} = \beta_{0j} + \beta_{1j}(a_{1ij}) + \beta_{2j}(a_{1ij}^2) \quad (4)$$

$$y_{1ij} = \beta_{0j} + \beta_{1j}(a_{1ij}) + \beta_{2j}(a_{1ij}^2) + \beta_{3j}(a_{1ij}^3) \quad (5)$$

where y_{1ij} = predicted value of covariate 1 at used areas for lynx i during season j , β_{0j} = y -intercept for lynx during season j , β_{1-3} = regression coefficients for lynx during season j , and a_{1ij} = mean values of covariate 1 at available locations for lynx i during season j . We assessed the relative fit of each model to our data using a likelihood-ratio test ($\alpha \leq 0.05$), wherein we retained lower order polynomials when testing for higher order polynomials. We used standard diagnostics (e.g., residual plots) to evaluate the appropriateness of our most supported model. Support for a curvilinear model (i.e., Eqs. 4 or 5) indicated a functional response in habitat use, which we could then

assess by plotting the relationships and associated 90% CIs. As mentioned in Mysterud and Ims (1998), disproportionate habitat use can occur in some parts of the range of availability and not in others. If a linear model was supported (i.e., Eq. 3), statistical deviations from proportional habitat use (proportional use: $\beta_0 = 0$, $\beta_1 = 1$) indicated additive use and consistent selection ($\beta_0 > 0$, $\beta_1 = 1$), additive use and consistent avoidance ($\beta_0 < 0$, $\beta_1 = 1$), or a functional response ($\beta_1 \neq 1$). Other combinations of β_0 and β_1 provide additional insights as well; for instance, increasing or decreasing habitat use (i.e., $\beta_0 \geq 0$, $\beta_1 > 1$ and $\beta_0 \leq 0$, $\beta_1 < 1$, respectively) relative to random expectation.

We applied our approach to assess how habitat use by Canada lynx might change in the face of changing environments (i.e., changing availabilities). This analysis occurred at the third order of selection, and we separated the data by season (winter and summer) and sex (females and males). Preliminary plotting of the data indicated a substantial outlier and influential observation, which we elected to remove for subsequent analysis (i.e., female 174). We focused our analysis on the following covariates: species-specific estimates of canopy cover, estimated horizontal cover, proportion of forest structural classes, and predicted snowshoe hare occupancy and intensity of use (see Table 1 for variable descriptions). We conducted all analyses of functional responses in program R (R Core Team 2016).

RESULTS

Habitat use, availability, and selection

Canada lynx demonstrated use of mixed-conifer forests and a mosaic of forest structural stages (Fig. 2), suggesting use of predominately mid-late seral conditions. Within this context, lynx selected (i.e., use greater than availability in Fig. 2) canopies composed of spruce-fir and lodgepole pine, but spruce-fir was used more than any other species (Fig. 2). In terms of forest structure, lynx selected mature and advanced regenerating forest, but mature forest was used twice as much as any other forest structure class (Fig. 2). The mature class was composed of early to mid-seral forests that included a diversity of tree sizes (e.g., 45% were 12.7–25.4 cm in diameter, 25% were 25.4–38 cm, and 21% were 38–64 cm; see

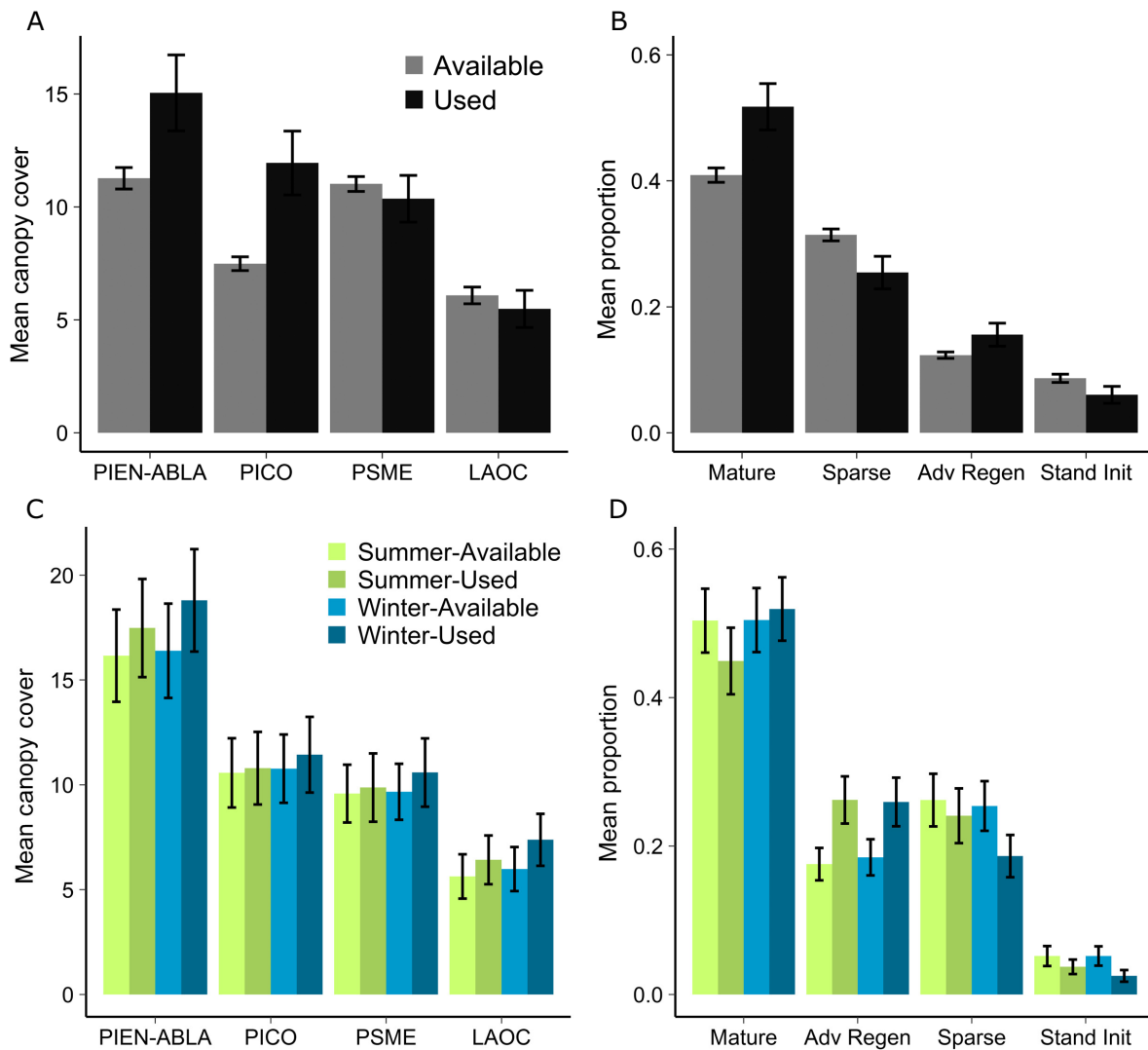


Fig. 2. Mean ($\pm 95\%$ confidence intervals) canopy cover by species and proportion of forest structural classes at the second order (A, B) and third order (C, D) of selection for Canada lynx (*Lynx canadensis*) in western Montana, USA. Covariate codes PICO, PIEN, ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively. In addition, Adv Regen and Stand Init indicate advanced regenerating and stand initiation forest structures, respectively.

Table 2 for all forest metrics). Sparse forest and stand initiation were generally avoided (Fig. 2).

Furthermore, lynx exhibited spatial and seasonal variation in resource selection for specific variables related to forest composition and structure. Lynx used about the same amount of lodgepole pine and Douglas-fir canopy cover, but lodgepole pine was strongly selected at the second order (Fig. 2; Appendix S3: Table S1).

Canopy cover of western larch, however, was used the least by lynx and was generally used in proportion to availability across scales and seasons (Fig. 2). Moreover, sparse forest was used less than mature forest but more than advanced regenerating forest at the second order (Fig. 2; Appendix S3: Table S1). However, sparse forest was avoided by lynx at the second order as well as at the third order during winter (Fig. 2;

Appendix S3). Advanced regenerating forest and sparse forest were used similarly by lynx at the third order, but advanced regenerating forest was strongly selected by lynx across scales and seasons (Fig. 2; Appendix S3). Stand initiation was used the least by lynx across seasons and scales and was avoided at the second order and the third order during winter (Fig. 2; Appendix S3).

Canada lynx exhibited additional patterns of selection that were generally consistent with our expectations. Lynx selected higher values of horizontal cover at the second order, and higher snowshoe hare occupancy and intensity of use at both the second and third orders (Appendix S3). At the second order, lynx selected deeper snow, but avoided areas of high topographic roughness (Appendix S3: Table S1). Finally, lynx selected basins at the third order during winter (Appendix S3: Table S2).

RSF models

Resource variables within our most predictive and parsimonious RSF models varied based on scale and season. At the second order, our top model contained only three covariates, which included a quadratic relationship with snow depth and a positive effect of snowshoe hare occupancy and canopy cover of lodgepole pine (Table 3). The next four models included one additional parameter and exhibited a ΔAIC_c value of 1.94–2.12 (i.e., they were penalized the maximum AIC can allow for the addition of one parameter), indicating no model uncertainty associated with our second-order RSF. Spearman rank correlations from our two-fold cross-validation indicated a robust model ($r_s = 0.91$, $P < 0.001$).

Table 3. Standardized regression coefficients, standard errors (SE), and P values for our most parsimonious resource selection function for Canada lynx (*Lynx canadensis*) in western Montana, USA, at the second order of selection.

Covariate	β	SE	ΔAIC_c	P
PICO canopy cover	0.63	0.20	4.74	0.002
Snowshoe hare occupancy	1.05	0.26	7.56	<0.001
Snow depth	2.22	0.52	24.23	<0.001
Snow depth ²	-2.18	0.53	<0.001	<0.001

Notes: AIC_c , Akaike's information criterion, corrected for sample sizes. The ΔAIC_c indicates relative weight of each covariate. Covariate code PICO indicates lodgepole pine (*Pinus contorta*).

At the third order during winter, our most parsimonious model included 11 covariates indicating relative probability of use was positively related to canopy cover (across species: lodgepole pine, spruce-fir, western larch, and Douglas-fir), advanced regeneration and mature forests, valley bottoms or basins, and snowshoe hare occupancy (Table 4). We observed negative effects of stand initiation and rough topographies exposed to high heat loads (Table 4). The next closest model (i.e., $\Delta\text{AIC}_c = 1.96$) included all the same variables along with intensity of use by snowshoe hares; thus, we selected the reduced model (i.e., model without intensity of use by snowshoe hares) as our top RSF for winter. The remaining models within our candidate set were $\geq 15 \Delta\text{AIC}_c$ values from our top model, indicating substantial support for our selected model. Spearman rank correlations from the 10-fold cross-validation indicated our model was robust ($r_s = 1$, $P < 0.001$).

Finally, our most parsimonious model at the third order during summer also included 11 covariates, but the patterns were different than in our winter model. The relative probability of use was positively related to canopy cover of lodgepole pine, spruce-fir, and Douglas-fir, as well as occupancy and intensity of use by snowshoe hares (Table 4). However, we documented a negative effect associated with canopy cover of western larch, proportion of mature forest and stand initiation, and rough topographies exposed to high heat loads. We also observed a quadratic relationship (i.e., probability of use was highest at mid-ranges) with advanced regenerating forest. The next closest model ($\Delta\text{AIC}_c = 1.80$) included an additional parameter (i.e., pretending variable; Anderson 2008), and the remaining models exhibited a $\Delta\text{AIC}_c \geq 20$, collectively indicating substantial support for the selection of our top model. Spearman rank correlations from the 10-fold cross-validation indicated a robust model ($r_s = 1$, $P < 0.001$).

Habitat mapping and validation

We used the RSF coefficients from our predictive and parsimonious models (Tables 3, 4), and the appropriately scaled covariates (Table 1), to develop three habitat maps across our study area (Fig. 3). We then integrated these study area-level predictions from our second- and third-order

Table 4. Standardized marginal coefficients, standard errors (SE), and *P* values from our most parsimonious mixed-effects resource selection function for Canada lynx (*Lynx canadensis*) during winter (November–March) and summer (April–October) in western Montana, USA, at the third order of selection.

Covariate	Winter (<i>n</i> = 64 lynx)				Summer (<i>n</i> = 60 lynx)			
	β	SE	ΔAIC_c	<i>P</i>	β	SE	ΔAIC_c	<i>P</i>
PICO canopy cover	0.04	0.01	20.70	<0.001	0.03	0.01	20.20	0.001
PIEN-ABLA canopy cover	0.18	0.01	285.90	<0.001	0.07	0.01	63.00	<0.001
LAOC canopy cover	0.03	0.01	15.30	<0.001	-0.07	0.01	106.70	<0.001
PSME canopy cover	0.27	0.01	988.8	<0.001	0.16	0.01	519.30	<0.001
Proportion stand initiation	-0.07	0.01	81.00	<0.001	-0.06	0.01	118.80	<0.001
Proportion advanced regeneration	0.41	0.01	1953.80	<0.001	0.48	0.01	2396.30	<0.001
Proportion advanced regeneration ²	-	-	-	-	-0.15	0.01	-	<0.001
Proportion mature	0.07	0.01	57.40	<0.001	-0.05	0.01	42.40	<0.001
Topographic roughness	-0.18	0.01	417.60	<0.001	-0.14	0.01	397.70	<0.001
Heat load index	-0.05	0.01	51.40	<0.001	-0.07	0.01	168.40	<0.001
Topographic position index	-0.13	0.01	421.50	<0.001	-	-	-	-
Probability of snowshoe hare occupancy	0.21	0.01	702.10	<0.001	0.11	0.01	231.60	<0.001
Intensity of use by snowshoe hares	-	-	-	-	0.07	0.01	109.50	<0.001

Notes: AIC_c , Akaike's information criterion, corrected for sample sizes. The ΔAIC_c indicates relative weight of each covariate. Covariate codes PICO, PIEN, ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively.

RSFs to provide two additional scale-integrated habitat maps (one each for winter and summer; Fig. 3). Our validation indicated that our models strongly predicted the frequency of lynx use as measured by independent lynx locations: second-order derived map $r_s = 0.94$, $P < 0.001$, third-order (winter) derived map $r_s = 0.85$, $P = 0.003$, third-order (summer) derived map $r_s = 0.87$, $P = 0.003$, winter scale-integrated $r_s = 0.94$, $P < 0.001$, and summer scale-integrated $r_s = 0.99$, $P < 0.001$. However, as expected, our second-order and scale-integrated predictions were the most efficient at characterizing lynx use across our study area (Fig. 4). That is, only 4 and 5 equal-area bins were required to capture 90% of our withheld lynx locations during winter and summer using our scale-integrated and second-order maps, respectively, as compared to 6–7 bins using maps derived from third-order coefficients (Fig. 4).

Functional responses

Our assessment of functional responses in habitat use provided novel insights concerning lynx habitat ecology and thus was an essential component of our analytical process. For instance, we demonstrated that female lynx during the winter not only avoided stand initiation and sparse forest, but that use decreased (relative to random) as stand initiation (gradient = ~0.2–22%) and sparse

forest (gradient = ~10–52%) became more available (Fig. 5, Table 5). In contrast, females exhibited additive use and consistent selection of advanced regenerating forest across the range of availability (~10–40%; Fig. 5, Table 5). Mature forest was used in proportion to its availability (~16–75%; Fig. 5, Table 5), although 66% of female home ranges contained $\geq 50\%$ mature forest. Together, these results demonstrated that female lynx occupy home ranges of mostly mature forest during the winter, and within that context they reduce their use of open structure classes, but additively use advanced regeneration as these structures become more available.

We discovered additional functional responses in habitat use concerning forest structural stages, which in some cases differed by sex. Male lynx exhibited a positive functional response for advanced regenerating forest in that habitat use increased (relative to random) as availability increased during winter and summer (Fig. 6, Table 6). Male and female lynx exhibited decreasing habitat use (relative to random) with increasing stand initiation, and the response appeared to be stronger for females (Fig. 6, Tables 5, 6). This response also indicated that habitat use of stand initiation plateaued at low availabilities and remained similar as the availability increased. Lastly, males during winter demonstrated decreasing habitat use

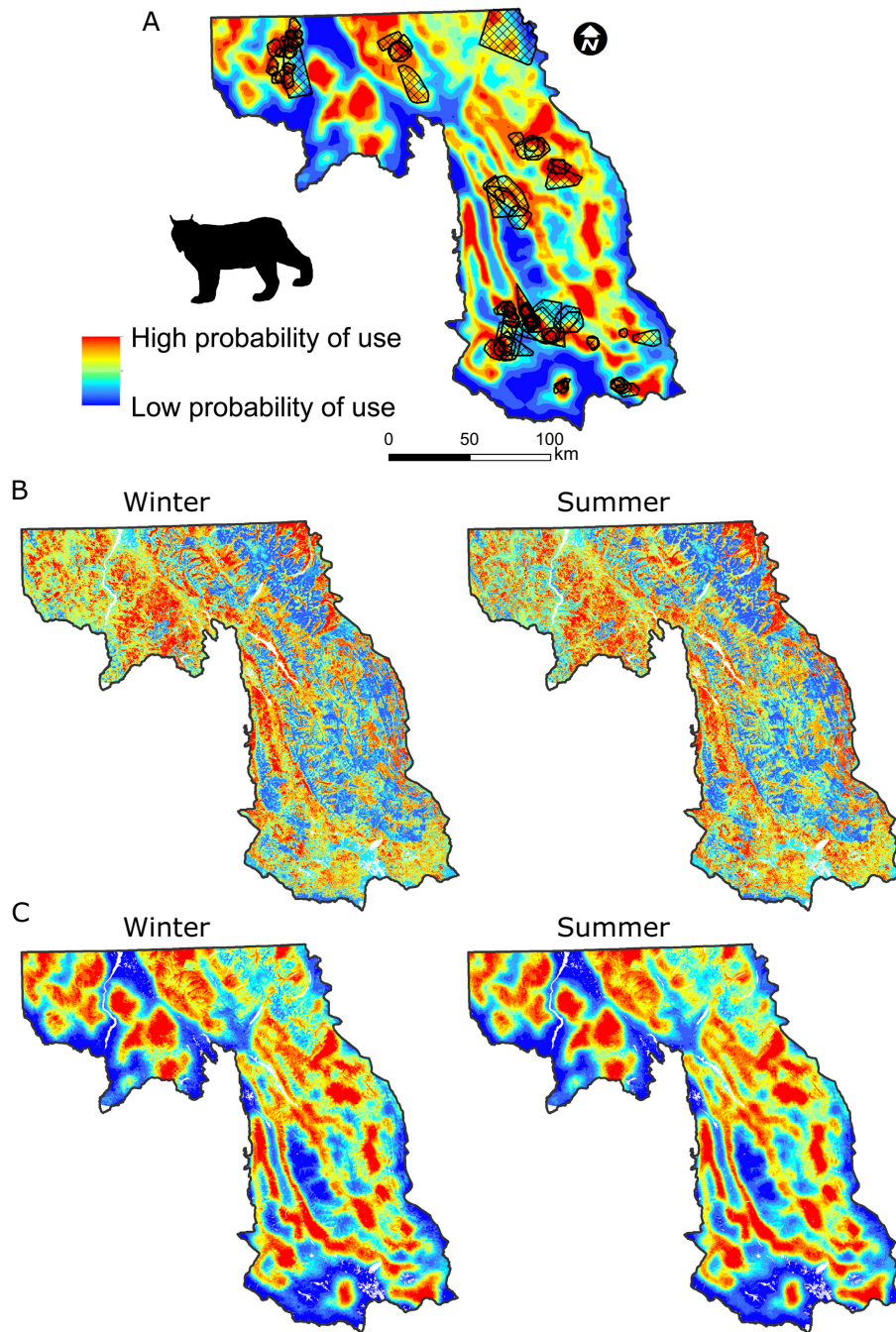


Fig. 3. Predicted probability of use for Canada lynx (*Lynx canadensis*) in western Montana, USA. These maps were generated from our top resource selection functions at the second order (A) and third order (B) of selection. Lynx home ranges are highlighted on our second-order map (hashed polygons in A). We then integrated these maps to develop scale-integrated predictions of use by Canada lynx (C).

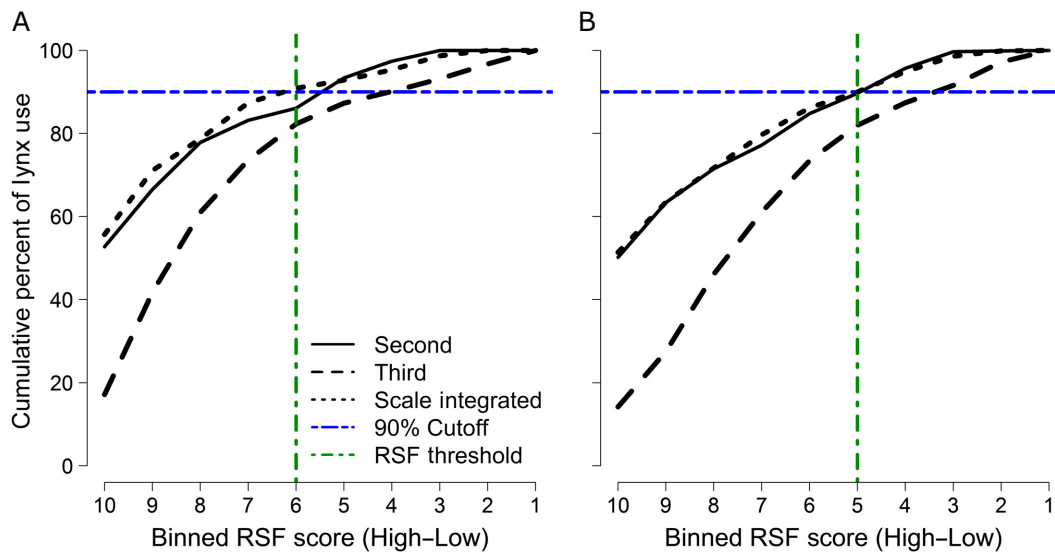


Fig. 4. Cumulative percent of withheld Canada lynx (*Lynx canadensis*) locations across our predicted probabilities of lynx use in western Montana, USA, using our second- and third-order, as well as scale-integrated, resource selection function (RSF) during winter (A; November–March) and summer (B; April–October). The x-axis represents 10 equal-area RSF scores ranging from high to low. The intersection of the “second,” “third,” and “scale-integrated” curves and the horizontal line indicate the RSF score that was required to capture 90% of lynx use. Because the RSF scores are of equal area (Boyce et al. 2002), these figures also illustrated that the scale-integrated RSF mapped more efficiently during winter (A) because it captured the same percent of lynx use over a reduced area (i.e., lower number of equal-area bins). The intersection of the vertical and horizontal lines illustrates an example of where managers could determine habitat vs. non-habitat using an empirically derived threshold from the mapped predictions.

(relative to random) of sparse and mature forest, respectively (Fig. 6, Table 6).

Finally, lynx exhibited functional responses in habitat use for predicted snowshoe hare habitat as well as vegetation cover. We observed a strong functional response for snowshoe hare occupancy and intensity of use for both sexes and across seasons (Fig. 7, Tables 5, 6). This indicated that habitat selection by lynx was strongest at low snowshoe hare availability and that selection decreased in strength as snowshoe hare availability increased (Fig. 7). In addition, females during winter demonstrated avoidance of Douglas-fir canopy cover at low availabilities but proportional use at higher availabilities (Table 5; Appendix S4). Males exhibited increasing habitat use with increasing availability of canopy cover of Douglas-fir during both seasons (Table 6; Appendix S4), as well as with increasing canopy cover of spruce-fir (although a slight decrease toward the maximum value) during winter and

lodgepole pine during summer (Table 6; Appendix S4). Males also demonstrated additive use (and consistent selection) for spruce-fir canopy cover and horizontal cover during the summer, as well as canopy cover of western larch during the winter (Table 6). All other relationships indicated proportional habitat use across sexes and seasons.

DISCUSSION

Translating the advancement of animal–habitat relationships to on-the-ground conservation is difficult and requires an integrated analytical framework. Here, we provided a process that merged the research motivation of understanding and prediction, as well as embraced the intricacies of exploring animal–habitat relationships. By examining habitat use, availability, selection, and functional responses, we were able to improve the current understanding of Canada

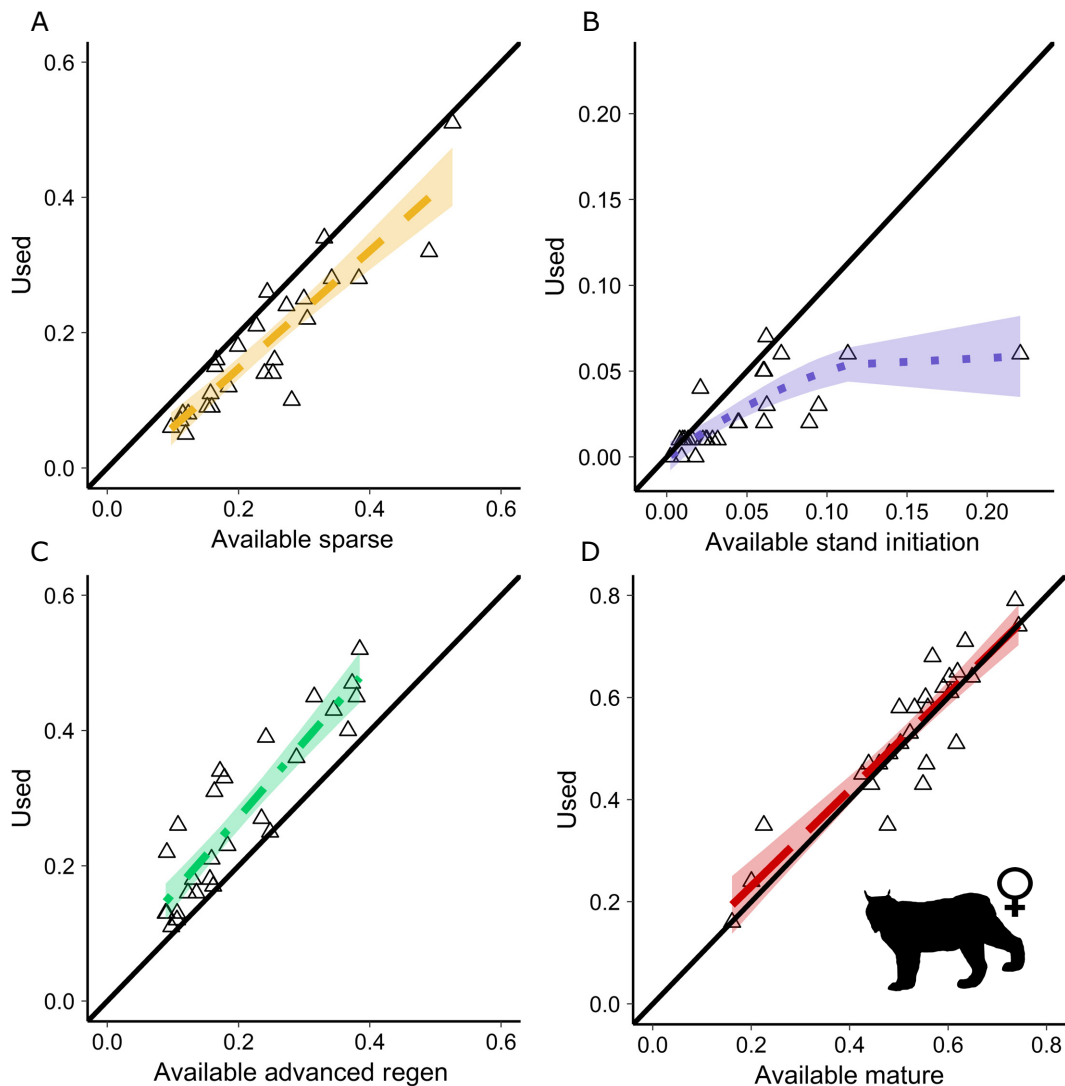


Fig. 5. Predicted relationships characterizing functional responses in habitat use by female Canada lynx (*Lynx canadensis*) during winter in western Montana, USA, across four forest structural stages. The diagonal line indicates random (i.e., proportional) habitat use. Data points indicate 27 female lynx used to develop predicted relationships and confidence bounds are 90% confidence intervals. Panels (A) and (B) indicate decreasing use, while panels (C) and (D) indicate additive use (and consistent selection) and proportional use, respectively. See Table 1 and Appendix S1 for details concerning forest structure classes.

lynx–habitat relationships while also providing maps predictive of lynx use. If we had not implemented all parts of our approach, we might have developed incomplete understandings of lynx–habitat relationships, which would result in incomplete conservation recommendations at best and misleading recommendations at worst. We illustrate this by presenting the following two examples.

We demonstrated that considering multi-scale habitat use and selection is essential when assessing animal–habitat relationships and developing conservation recommendations. Canada lynx in the Northern Rockies use a gradient of forest structures and compositions (Figs. 2, 3), but they use more mature, spruce-fir forest than any other structural stage or species. Contrasting these results with selection coefficients derived from

Table 5. Results from functional response analysis for female Canada lynx (*Lynx canadensis*) during winter (November–March) and summer (April–October) in western Montana, USA.

Covariate	Winter ($n = 27$ lynx)			Summer ($n = 24$ lynx)		
	β_0 (90% CI)	β_1 (90% CI)	R^2	β_0 (90% CI)	β_1 (90% CI)	R^2
PICO canopy cover	0.61 (–0.53 to 1.76)	0.99 (0.89–1.08)	0.92	0.62 (–0.32 to 1.56)	0.95 (0.87–1.03)	0.95
PIEN-ABLA canopy cover	0.66 (–1.44 to 2.75)	1.07 (0.97–1.18)	0.92	0.00 (–3.42 to 3.42)	1.01 (0.88–1.27)	0.80
LAOC canopy cover	1.29 (–0.57 to 3.14)	1.01 (0.74–1.28)	0.62	0.76 (–0.67 to 2.20)	0.99 (0.79–1.19)	0.77
PSME canopy cover	Second ($P = 0.001$)		0.96†	–0.46 (–2.80 to 1.89)	1.11 (0.88–1.33)	0.77
Horizontal cover	–0.27 (–6.12 to 5.58)	1.03 (0.92–1.13)	0.92	–1.14 (–11.27 to 9.00)	1.05 (0.86–1.23)	0.81
Sparse	–0.03 (–0.06 to 0.01)	0.87 (0.73–1.01)	0.82‡	–0.01 (–0.07 to 0.05)	0.95 (0.75–1.15)	0.76
Stand initiation	Second ($P = 0.010$)		0.61†	Second ($P = 0.026$)		0.60†
Advanced regeneration	0.05 (0.01–0.09)	1.12 (0.94–1.30)	0.82§	0.08 (0.02–0.15)	0.96 (0.60–1.32)	0.49§
Mature	0.04 (–0.04 to 0.12)	0.94 (0.79–1.09)	0.82	0.05 (–0.06 to 0.16)	0.81 (0.61–1.02)	0.68
Hare occupancy	Second ($P = 0.002$)		0.62†	0.35 (0.23–0.46)	0.53 (0.35–0.70)	0.55†
Hare intensity	1.30 (0.42–2.17)	0.69 (0.38–0.99)	0.37†	1.60 (0.81–2.39)	0.56 (0.26–0.86)	0.32†

Notes: CI, confidence interval. If a polynomial model was supported, we indicate the complexity of the model (i.e., second or third degree) and provide the P value of the likelihood-ratio test (χ^2 distribution). If a linear model was supported, we provide the estimated intercept (β_0) and slope (β_1) along with the 90% CI. For all models, we provide the coefficient of determination (R^2). Covariate codes PICO, PIEN, ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively.

† Functional response.

‡ Perhaps biologically significant functional response, although not statistically significant ($\alpha \leq 0.10$).

§ Additive use (and consistent selection).

our most predictive RSFs (i.e., selected based on parsimony) highlighted the potential issues of solely relying on top RSFs for understanding habitat relationships. For instance, neither mature forest nor spruce-fir canopy cover were included in our most parsimonious RSF at the second order, despite the evidence that lynx exhibited selection for both of these resources (i.e., use greater than availability in Fig. 2). Moreover, our RSF models at the third order indicated comparatively weak selection for mature forest and spruce-fir canopy cover (Table 4). In fact, and consistent with previous work (Squires et al. 2010), lynx exhibited avoidance of mature forest in the summer (Table 4). Taken alone, our RSFs might lead one to suggest that Canada lynx are indifferent to the mature forest structure class (as suggested by others; Mowat and Slough 2003) and spruce-fir canopies. However, as previously mentioned, we demonstrated that mature, spruce-fir forests were used more by lynx than any other structure or species (Fig. 2). Because we summarized use and availability separately and across scales, we were able to highlight that (1) mature forests and spruce-fir canopies were highly available across our study area, potentially indicative of first-order selection processes and (2) it was indeed selection for mature, spruce-fir forests at

the second order (i.e., Fig. 2) that generated a context of broad availability at the third order. And by definition, it is difficult to strongly select habitat attributes that are abundant (Beyer et al. 2010, Kertson and Marzluff 2010). This example illustrates that characterizing use and availability prior to identifying predictive and parsimonious RSFs is essential for inferring covariate importance and that scale and availability are central to interpreting selection (as mentioned in Beyer et al. 2010, Matthiopoulos et al. 2011, Aarts et al. 2013, Northrup et al. 2013).

In addition, characterizing functional responses in habitat use allowed us to gain a deeper understanding of lynx–habitat relationships and provide land managers with expected responses under changing environmental conditions. For instance, during the winter (i.e., the most constraining season for lynx; Squires et al. 2010) female and male Canada lynx exhibited increasing and additive use, respectively, for advanced regenerating forest as it became more available (Fig. 6). In contrast, both sexes demonstrated decreasing use of stand initiation and sparse forest (Fig. 6). Placing these responses within their respective availability ranges (i.e., x -axis in Fig. 6) illustrated the magnitude of their effects, as well as indicated they are occurring within a broader

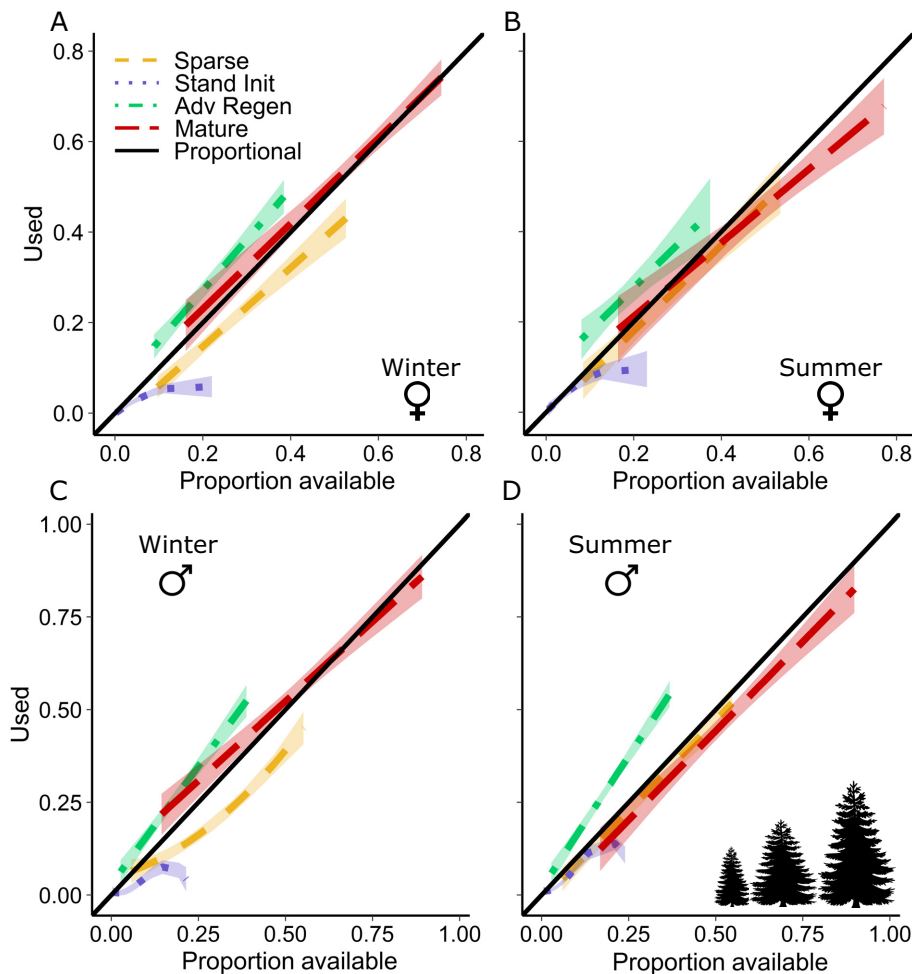


Fig. 6. Predicted relationships characterizing functional responses in habitat use by female (A: winter, and B: summer) and male (C: winter, and D: summer) Canada lynx (*Lynx canadensis*) in western Montana, USA, across four forest structural stages. The diagonal line indicates random (i.e., proportional) habitat use, and confidence bounds are 90% confidence intervals. Data points used to develop predicted relationships are not shown. See Table 1 and Appendix S1 for details concerning forest structure classes.

context of mature forest (Fig. 6). Interpreting functional responses within the appropriate context of availability is essential to avoid extrapolating third-order behavioral responses beyond the bounds set by second-order selection.

Moreover, these patterns capture some of the spatio-temporal issues land managers might consider when implementing landscape-altering actions to enhance lynx habitat. For example, managers might want to implement tools (e.g., timber harvest or fire) that create advanced regeneration in the long term, but recognize they will have to create stand initiation structures in

the short term. To dampen the negative response by lynx in the short term, managers might focus their conservation efforts in areas with relatively low availabilities of existing stand initiation or sparse forest. This example illustrates the applied insights and recommendations one can derive from examining functional responses. Landscape management can benefit greatly from the development of habitat maps (Johnson et al. 2004, Fattebert et al. 2015), but maps capture a spatio-temporal snapshot with no context as to how habitat use or selection might change with changing conditions (Hirzel and Le Lay 2008,

Table 6. Results from functional response analysis for male Canada lynx (*Lynx canadensis*) during winter (November–March) and summer (April–October) in western Montana, USA.

Covariate	Winter ($n = 36$ lynx)			Summer ($n = 35$ lynx)		
	β_0 (90% CI)	β_1 (90% CI)	R^2	β_0 (90% CI)	β_1 (90% CI)	R^2
PICO canopy cover	0.07 (–1.49 to 1.62)	1.05 (0.93–1.17)	0.86	–0.44 (–1.22 to 0.34)	1.07 (1.00–1.13)	0.96†
PIEN-ABLA canopy cover	Second ($P = 0.002$)		0.92†	2.35 (0.73 to 3.97)	0.95 (0.87–1.04)	0.91‡
LAOC canopy cover	1.28 (0.07 to 2.48)	1.03 (0.87–1.19)	0.78‡	0.83 (–0.07 to 1.74)	1.00 (0.87–1.13)	0.83
PSME canopy cover	–1.32 (–2.87 to 0.23)	1.20 (1.07–1.33)	0.88†	–1.02 (–2.26 to 0.22)	1.11 (1.00–1.21)	0.90†
Horizontal cover	3.19 (–2.25 to 8.63)	0.98 (0.88–1.08)	0.89	4.89 (0.71 to 9.06)	0.95 (0.88–1.03)	0.93‡
Sparse	Second ($P = 0.015$)		0.84†	–0.1 (–0.05 to 0.02)	0.97 (0.84–1.11)	0.82
Stand initiation	Third ($P = 0.018$)		0.52†	Third ($P < 0.001$)		0.82†
Advanced regeneration	0.03 (–0.01 to 0.06)	1.28 (1.09–1.46)	0.81†	0.02 (–0.01 to 0.05)	1.42 (1.26–1.59)	0.86†
Mature	0.09 (0.02 to 0.17)	0.86 (0.72–1.00)	0.76†	–0.04 (–0.12 to 0.05)	0.96 (0.81–1.12)	0.77
Hare occupancy	0.32 (0.23 to 0.41)	0.61 (0.48–0.74)	0.64†	Second ($P = 0.015$)		0.78†
Hare intensity	Second ($P = 0.024$)		0.80†	Second ($P = 0.045$)		0.85†

Notes: CI, confidence interval. If a polynomial model was supported, we indicate the complexity of the model (i.e., second or third degree) and provide the P value of the likelihood-ratio test (χ^2 distribution). If a linear model was supported, we provide the estimated intercept (β_0) and slope (β_1) along with the 90% CI. For all models, we provide the coefficient of determination (R^2). Covariate codes PICO, PIEN, ABLA, LAOC, and PSME indicate lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), respectively.

† Functional response.

‡ Additive use (and consistent selection).

Matthiopoulos et al. 2011, Paton and Matthiopoulos 2016). Functional responses provide a means to assess animal responses to changing environments and as such are essential additions to characterizing habitat relationships (Moreau et al. 2012).

On advancing habitat relationships and conservation of Canada lynx

In this study, we expanded the current understanding of lynx–habitat relationships through our integrated analytical process. This combined analysis provided a refined lens of lynx resource use in the context of landscape pattern and conservation planning. For instance, we confirmed that Canada lynx in the Northern Rockies use a mixture of conifer species and structural stages, but highlighted that selection and use of mature, spruce-fir forests appears to be largely a first- or second-order process (Fig. 2). Additionally, lynx exhibited the strongest selection for intermediate snow depths, predicted snowshoe hare habitat, and lodgepole pine canopy cover at the second order of selection. These results emphasize the sensitivity of lynx to consistent and abundant snow as well as snowshoe hare availability. Previous work in the Northern Rockies has demonstrated that advanced regenerating or

multi-storied forests with a substantial component of lodgepole pine can provide high-quality habitat for snowshoe hares (Holbrook et al. 2017). Additionally, the reliance of snowshoe hares (Zimova et al. 2016) and lynx on snow conditions highlights foreseeable conservation challenges because snow extent and depth are projected to decrease within the Northern Rockies (Klos et al. 2014).

To our knowledge, all previous work on lynx–habitat relationships has implicitly assumed habitat use or selection will remain constant with changing availabilities (Poole et al. 1996, Squires et al. 2010, Simons-Legaard et al. 2013, Montgomery et al. 2014). Our work is the first to challenge that assumption. First, female lynx selected a narrower gradient of forest structures compared to males, and among-female use was most consistent during the most limiting season (i.e., winter $R^2 >$ summer R^2 ; Table 5), whereas males did not display a similar pattern (Table 6). Thus, conservation planning should be focused on the needs of females when developing management plans. Second, both males and females demonstrated selection of predicted snowshoe hare occupancy and use, but selection increased as occupancy and use became less available (Fig. 7). This pattern was expected and consistent with

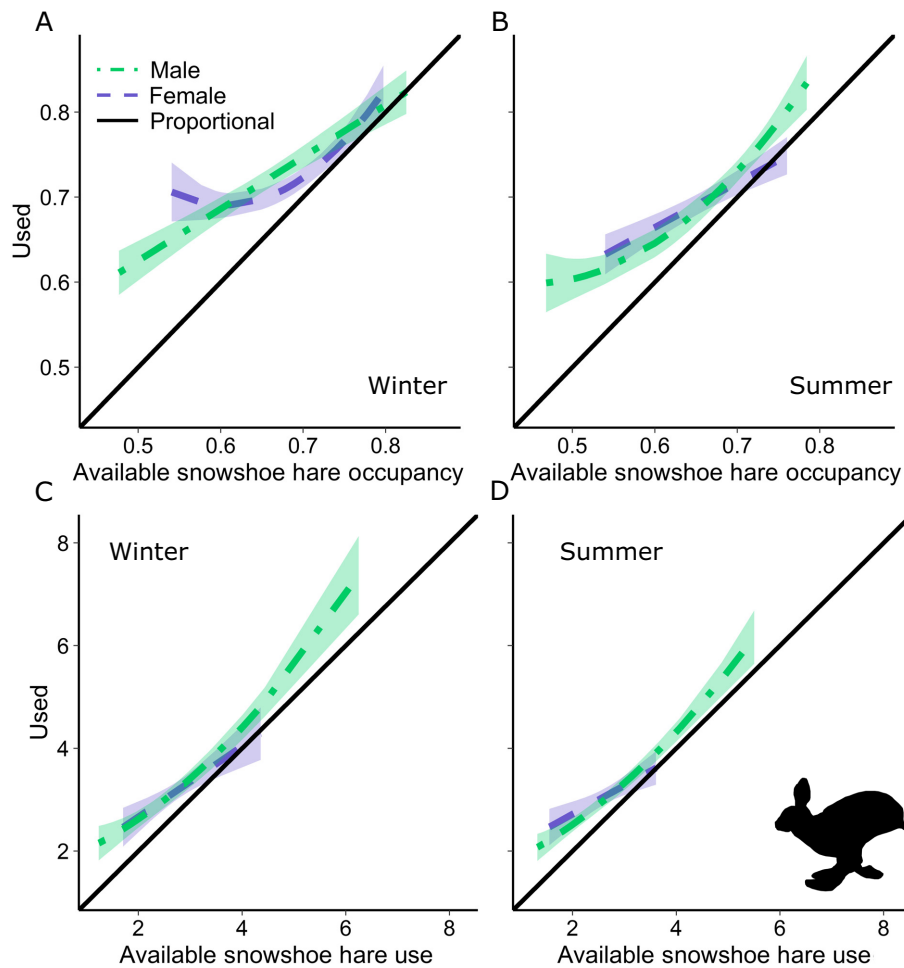


Fig. 7. Predicted relationships characterizing functional responses in habitat use by male and female Canada lynx (*Lynx canadensis*) in western Montana, USA, for snowshoe hare (*Lepus americanus*) occupancy (A: winter, and B: summer) and intensity of use (C: winter, and D: summer). The diagonal line indicates random (i.e., proportional) habitat use, and confidence bounds are 90% confidence intervals. Data points used to develop predicted relationships are not shown. See Table 1 for addition details on snowshoe hare covariates.

Canada lynx specializing on snowshoe hares (Elton and Nicholson 1942, Krebs et al. 2001, Ivan and Shenk 2016). Finally, male lynx demonstrated a positive functional response (increasing use with increasing availability) for advanced regeneration while females demonstrated additive use (Fig. 6). The affinity of lynx to advanced regenerating forest within a home range, coupled with the high use of mature forest (Fig. 3), suggests that Canada lynx spend a significant amount of time at the interface between mature and advanced regenerating forest. This is consistent with the mechanism that advanced

regeneration likely produces the highest snowshoe hare densities (Cheng et al. 2015), but the mature structure class is where hares are most accessible for lynx (Fuller et al. 2007, Ivan and Shenk 2016). This mechanism received demographic support by Kosterman (2014), who demonstrated that female lynx with core areas of highly connected mature forest and intermediate levels of regenerating forests had the highest probability of producing a litter. The integration of resource selection and functional response analyses begins to define the gestalt of landscape mosaics and behaviors that give rise to the

distribution of Canada lynx, which facilitates and informs habitat conservation efforts.

The second motivation for this work was to provide efficient habitat maps for Canada lynx with the goal of assisting land managers in their decision-making processes. Managers of public lands are tasked with making multi-scale decisions in the context of social, biological, and legal complexities and thus require objective and science-based designations of habitat for species listed under the ESA, SARA, or similar statutes. We provided five landscape-level maps characterizing the probability of use by Canada lynx in the Northern Rockies (Fig. 3), all of which were deemed predictive of lynx use (Fig. 4). Although, consistent with DeCesare et al. (2012), our scale-integrated habitat maps appeared to perform best based on validation and mapping efficiency (Fig. 4). We believed this was the case because the second-order map had a much wider range in relative probabilities of use (i.e., more discriminatory) than the third-order map, such that a high prediction from the third order would seldom override the second order except on the low end of the second-order range. Therefore, by integrating the second order with the third order, the scale-integrated map appears to capture the hierarchical nature of habitat selection and generate efficient maps. Finally, by extending the concept of Boyce et al. (2002) we provided a simple, objective, and defensible approach to determine the threshold value of a habitat map (Fig. 4). This will be helpful for land managers if they are required to make decisions in a binary fashion, where a habitat and non-habitat designation is needed.

The application of our habitat maps, or the data characterizing lynx habitat, will depend on the extent and resolution of the management objective. For instance, our second-order and scale-integrated habitat map would be best applied at broad extents (e.g., landscape level). At the project level (e.g., 40 acres or 16 ha), however, the third-order derived maps would likely be the most informative for land managers, but this is conditioned on the project area occurring within lynx habitat as modeled at the broad extent. At fine resolutions (3–10 acres or 1–4 ha), managers will likely need to couple our maps with site visits (and field data described elsewhere; Squires et al. 2010) to develop the most informed decisions concerning Canada lynx habitat.

Similarly, the absolute values of forest structure and composition characterizing lynx habitat (e.g., as in Fig. 2, Table 2; Appendices S1 and S3) should be applied in a relative and general sense. All of our metrics are derived from models with error and characterize resolutions $\geq 100 \text{ m}^2$ (Table 1). Indeed, maps of forest characteristics and animal habitat are useful tools for conservation planning and prioritization (Johnson et al. 2004, DeCesare et al. 2012), but will likely need refinement based on site-specific understandings derived from direct observation.

CONCLUSIONS

Understanding and predicting habitat is essential in animal ecology and management (Elith and Leathwick 2009), particularly for species that are threatened or endangered. Here, we demonstrated an integrated process to understand, prioritize, and predict habitat, which we applied in the case of the federally threatened Canada lynx. Our approach was novel because we characterized habitat use, availability, selection, and functional response across scales, which embraced the multi-scale behavioral process of habitat selection (Johnson 1980, Boyce 2006, Meyer and Thuiller 2006). Although previous work has demonstrated the conditional nature of habitat selection, and the potential issues deriving importance from selection (Beyer et al. 2010, Anderson et al. 2012, Northrup et al. 2013), our work is among the first to highlight the conservation costs of such issues. This is particularly a concern when examining a subset of Johnson's (1980) orders of selection, which is commonly the case. Further, we developed a synthetic approach to characterize functional responses in habitat use, which provided critically important insights into the behavior of Canada lynx. Indeed, assessing functional responses in habitat use can inform both ecologists and managers on the expected responses of animals to changing environmental conditions and thus should become basic tools in applied ecology (Moreau et al. 2012). Successful conservation efforts for most endangered and threatened species require spatial characterizations of habitat and precise understandings of the mechanisms giving rise to those spatial depictions. Our multi-scale and integrated process offers a means to that end.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1939/full>