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Winter recreation and Canada lynx: reducing conflict through niche partitioning

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Abstract. Outdoor recreationists are important advocates for wildlife on public lands. However, balancing potential impacts associated with increased human disturbance with the conservation of sensitive species is a central issue facing ecologists and land managers alike, especially for dispersed winter recreation due to its disproportionate impact to wildlife. We studied how dispersed winter recreation (outside developed ski areas) impacted a reintroduced meso-carnivore, Canada lynx (*Lynx canadensis*), at the southern periphery of the species' range in the southern Rocky Mountains. On a voluntary basis, we distributed global positioning system (GPS) units to winter recreationists and documented 2143 spatial movement tracks of recreationists engaged in motorized and nonmotorized winter sports for a total cumulative distance of 56,000 km from 2010 to 2013. We also deployed GPS radio collars on adult Canada lynx that were resident in the mountainous topography that attracted high levels of dispersed winter recreation. We documented that resource-selection models (RSFs) for Canada lynx were significantly improved when selection patterns of winter recreationists were included in best-performing models. Canada lynx and winter recreationists partitioned environmental gradients in ways that reduced the potential for recreation-related disturbance. Although the inclusion of recreation improved the RSF model for Canada lynx, environmental covariates explained most variation in resource use. The environmental gradients that most separated areas selected by Canada lynx from those used by recreationists were forest canopy closure, road density, and slope. Canada lynx also exhibited a functional response of increased avoidance of areas selected by motorized winter recreationists (snowmobiling off-trail, hybrid snowmobile) compared with either no functional response (hybrid ski) or selection for (backcountry skiing) areas suitable for nonmotorized winter recreation. We conclude with a discussion of implications associated with providing winter recreation balanced with the conservation of Canada lynx.

Key words: backcountry skiing; Colorado; dispersed recreation; functional response; habitat selection; heliskiing; *Lynx canadensis*; outdoor recreation; resource-selection functions; snowmobiling; winter recreation.

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Introduction

There is growing urgency to conserve natural ecosystems given their intrinsic ecological values and services they provide to human well-being (Millennium Ecosystem Assessment 2005). The stewardship of these ever-declining natural landscapes requires in-depth understandings of how human interactions relate to the distribution, persistence, and abundance of sensitive species (Knick et al. 2003, Brennan and Kuvlesky 2005, Hethcoat and Chalfoun 2015). It is especially important to identify how human–wildlife interactions relate to nature-based, outdoor recreation given the worldwide increase in participation across approximately three quarters of nations sampled (Balmford et al. 2009). Nature-based recreation has grown rapidly over recent decades in close juxtaposition to environments that support highly charismatic and sensitive wildlife (Larson et al. 2016). Thus, land managers are increasingly in the difficult position of imposing regulations on the activities of outdoor recreationists in an attempt to mitigate the impacts of human disturbance on sensitive wildlife and ecosystem processes, while acknowledging that outdoor recreationists help provide the political and economic voices necessary to conserve natural landscapes and the species they support (Pyle 2003).

In 2015, public lands managed by the U.S. Department of the Interior, such as national parks, national wildlife refuges, and national monuments, attracted an estimated 443 million recreational visits that provided $45 billion in economic output and 396,000 jobs nationwide (U.S. Department of Interior 2016). Although winter recreation has declined in the United States between 1999 and 2009 (except snowboarding; White et al. 2016), snow-based recreation has higher documented impacts to wildlife compared with other outdoor activities (Sato et al. 2013, Larson et al. 2016). Winter sports are particularly invasive to sensitive wildlife due to the noise and speed associated with snowmobilers and backcountry skiers (i.e., off-piste skiers; Braunisch et al. 2011). Winter impacts to wildlife are intensified by the high energetic costs of traveling in deep snow (Neumann et al. 2010), increased difficulty to forage or avoid predators (Bonnot et al. 2013, Richard and Côté 2016), elevated responses in stress-induced corticosteroid (Arlettaz et al. 2007, 2015, Tablado and Jenni 2017), and high concentrations of wildlife on wintering areas. Developed winter recreation at resorts can also impact wildlife through habitat fragmentation associated with recreation infrastructure (e.g., ski lifts, lodges, and ski runs; Coppes et al. 2017*b*, Slauson et al. 2017).

Outdoor recreation generally causes negative impacts to wildlife across taxa (Sato et al. 2013, Larson et al. 2016). As a result, balancing recreation-related disturbance to sensitive species and the social and economic costs of regulations to recreationists is a major land management challenge. This conflict heightens the need for scientists to carefully frame and interpret research results in ways that are transparent to land managers and the general public. This challenge is particularly daunting because a unifying framework is lacking regarding how species or species guilds are impacted by outdoor recreation (Tablado and Jenni 2017). The high variability in species' responses to recreation is due to the many modulating factors affecting impacts such as type and duration of recreation (e.g., number of participants, noise levels, and movement speeds), spatiotemporal context of disturbance (e.g., time of day, habitat relationships, and distance), and the physiological responses (see Tablado and Jenni 2017 for review). In addition, different responses to recreation are due to the array of metrics used to define putative impacts (e.g., physiology, vital rates, movement, and habitat displacement). The complexity and nonlinearity of how species interact with recreation makes it difficult to predict population-level responses, which can obfuscate relationships between wildlife and outdoor recreation (Tablado and Jenni 2017).

Resource-selection functions (RSF) provide a useful tool that can relate patterns of resource use for species to changes in the availability of environmental cues, such as increased recreation (Boyce et al. 2002, Manly et al. 2002). Understandings of resource use may be improved when human use is incorporated into the underlying resource-selection modeling (Meager et al. 2012, Hebblewhite et al. 2014). A mechanism for this improvement may be that disturbance from outdoor recreation creates a "landscape of fear," analogous to prey species minimizing risk through modifications of habitat choice (Gill et al. 1996, Laundré et al. 2001). Understanding how recreation impacts habitat choice and demography of carnivores is particularly pressing given their heightened conservation risk (Ripple et al. 2014). However, carnivores are challenging to study given their low densities, large home ranges, secretive habits, and the variation of within-species responses to human disturbance dependent on landscape context (Knopff et al. 2014, Heinemeyer et al. 2019). Yet, despite these challenges, carnivore conservation requires a clear understanding of how disturbance from outdoor recreation may alter resource selection, movements, or access to required habitats in ways that threaten population persistence.

In this paper, we quantified how resource-selection patterns (Lele et al. 2013) of Canada lynx, a federally listed carnivore in the contiguous United States under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2000), differed from those of winter recreationists. Previous research demonstrated concentrated winter recreation associated with developed ski areas negatively affected Canada lynx (Olson et al. 2018). Here, we considered how dispersed winter recreation (winter activities conducted outside of developed ski areas) influenced resource-use patterns of Canada lynx (*Lynx canadensis;* hereafter interchangeably lynx) at the species' southern range periphery. Canada lynx provide a worthy case species to study recreation impacts due to their specific patterns of resource selection (Squires et al. 2010, Ivan and Shenk 2016) within the same high-snow environments sought by winter recreationists. Similar to northern populations (Canada and Alaska), lynx at the southern range periphery depend almost exclusively on snowshoe hare (*Lepus americanus*) for prey during winter (Squires and Ruggiero 2007, Ivan and Shenk 2016). The Canada lynx we studied were reintroduced two decades ago to Colorado, United States, with second-generation kittens producing kittens of their own (Devineau et al. 2010). The reintroduced population expanded across western Colorado within a region that also supports some of the highest levels of winter recreation in North America. The ski industry in Colorado generates billions of dollars annually to regional economies and supports a robust community of winter recreationists that participate in dispersed winter activities that include snowmobiling, snowshoeing, cross-country/skate skiing, and backcountry skiing. The close juxtaposition of occupied lynx habitat to the same terrain sought by recreationists heightened the need to understand whether winter recreation on this landscape excluded Canada lynx from necessary resources.

We captured and instrumented Canada lynx with GPS radio collars in areas with high levels of dispersed winter recreation. Concurrently, we asked winter recreationists to carry GPS units so we could evaluate the movements of humans across landscapes with a similar spatial resolution as for lynx. We used RSF models for different modes of winter recreation (e.g., snowmobilers and backcountry skiers) on the same study area from Olson et al. (2017), as additional covariates for selection models we built for Canada lynx. We also evaluated the resource-use patterns of Canada lynx to winter recreationists using a novel application of generalized linear mixed models (GLMMs; Gillies et al. 2006, Bolker et al. 2009) with interaction terms similar to Wiens et al. (2014) and through functional-response models that considered nonlinear lynx-recreation relationships (Hebblewhite and Merrill 2008, Moreau et al. 2012, Holbrook et al. 2017). We hypothesized that Canada lynx would select environmental characteristics more similar to backcountry skiers than motorized recreationists. This rationale was based on the recognition that Canada lynx and their primary prey, snowshoe hares, select areas of high horizontal cover (Squires and Ruggiero 2007, Berg et al. 2012, Thornton et al. 2012, Ivan and Shenk 2016) that is less likely to exclude backcountry skiers compared with motorized recreationists traveling at high speeds (Olson et al. 2017). Thus, we believed that Canada lynx would select resources in ways that segregated their use areas spatially from motorized recreation given the species' association with dense forest cover.

Methods

Study area

Our study area consisted of two broad regions in the southern Rocky Mountains of western Colorado, USA. The northernmost study area was located on the White River National Forest, in the Mosquito Range, near Vail and Leadville, Colorado (approximate centroid coordinates 106.30° W, 39.45° N; Fig. 1). This included the Vail Pass Winter Recreation Area that hosts very high levels of motorized and nonmotorized winter recreationists with maintained trails supported by a fee-payment structure from over 35,000 dispersed users per season (Miller et al. 2017). The southernmost study area was in the San Juan Mountains, on the Uncompahgre and San Juan National Forests, near the towns

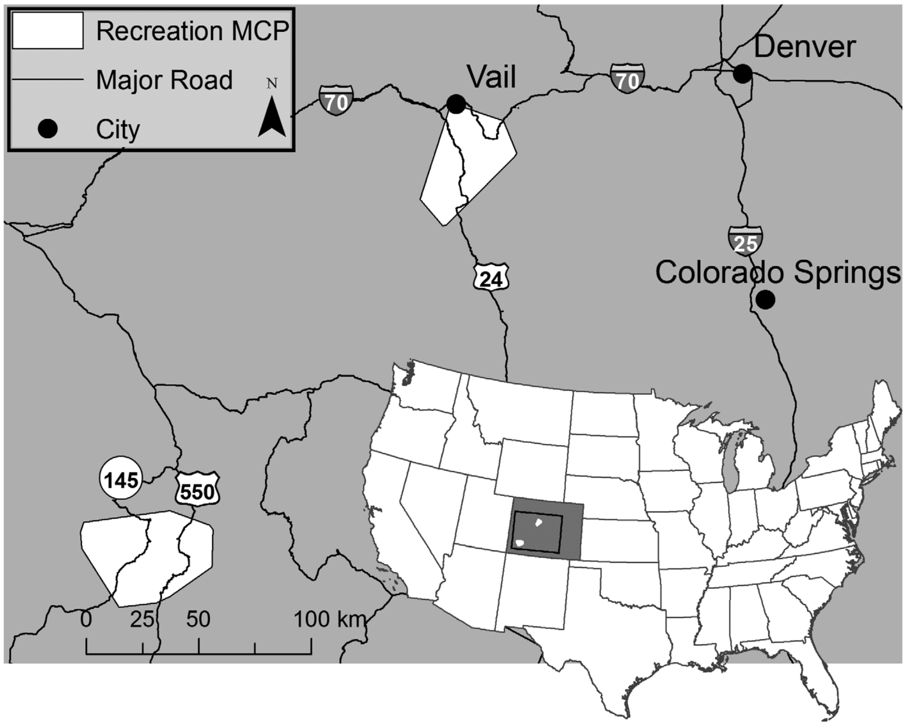

Fig. 1. Locations of the two study areas in the southern Rocky Mountains of western Colorado, USA, where Canada lynx (*Lynx canadensis*) and winter recreation were studied. White polygons indicate the footprint of all types of recreation. Inset shows the location of the study areas in Colorado and in relation to the United States.

of Silverton, Telluride, and Ophir, Colorado (107.88° W, 37.82° N). Recreation in the San Juan study area was mostly backcountry ski and snowboard use with more limited areas of concentrated snowmobile activity. The San Juan Mountain range was the core area that Colorado Parks and Wildlife (then the Colorado Division of Wildlife) reintroduced lynx between 1999 and 2006 (Devineau et al. 2010). Our study areas included both public (70.5%) and private lands (29.5%) with recreationists having open access to most of the federal ownerships.

The topography of study areas was typical of the southern Rocky Mountains with steep mountain valleys and high peaks with an elevation range of approximately 2000–4300 m asl. The high topographic relief produced a mosaic of vegetation patterns that was dominated by montane conifer forests interspersed with meadows and avalanche paths extending up in elevation to alpine tundra. Lynx most frequently occupied the elevation zone between 2500 and 3500 m asl in forest composed primarily of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) in the southern study area and spruce, fir, and Lodgepole pine (*Pinus contorta*) in the northern study area. Aspen (*Populus tremuloides*) was common on disturbed slopes and was intermixed with conifers in mid-seral stands. Willow (*Salix* spp.) occurred in high-elevation meadows and riparian bottomlands. Winters were relatively long with a snow season from November through May (low elevations) and some snow cover persisting into June. Annual snowfall was approximately 380–1000 cm (National Oceanic and Atmospheric Administration 2017).

Canada lynx data collection and processing

In 2010 and 2011, we captured lynx in our northern study area near the Vail Pass Winter Recreation Area where winter track surveys (Squires et al. 2012) and previous work by Colorado Parks and Wildlife had demonstrated lynx presence. In 2012 and 2013, we extended our trapping effort to areas adjacent to Leadville, Colorado, in the northern study area, and to a southern study area in the San Juan Mountains near the towns of Silverton and Telluride, Colorado. We captured lynx in box traps (Kolbe et al. 2003) that we set in travel areas identified by snow tracks; traps were checked every 24 h. We instrumented adult lynx (>3-yr-olds) with Sirtrack store-on-board GPS collars (210–230 g) equipped with a VHF beacon transmitter and a drop-off mechanism. We programmed collars to collect GPS locations every 20 min, 24 h per day in 2010, 2012, and 2013, and at 30-min intervals, every other day in 2011. Consistent with Pépin et al. (2004), we evaluated scale-dependency issues between the two fix rates (i.e., 20 min vs. 30 min) and found that step lengths of lynx were similar (median step length: 30-min duty cycle = 42.0 m, standard deviation [SD] = 260.4; 20-min duty cycle = 40.9 m, SD = 195.2 m) regardless of duty cycle. We conducted lynx capture and handling under the guidelines of Animal Care and Use Permit CDOW-ACUC File #13-2009 and University of Montana International Animal Care and Use Committee (IACUC) permit AUP-062-13MHWB-122013.

The Canada lynx we studied exhibited movements that were consistent with individuals having established home ranges, and we discarded locations from extra-home-range movements (outside the 95% use area) given they may differ from typical resource use (Nicholson et al. 1997). We identified and removed spurious movement "spikes" as those with turning angles between 166° and 194° and movement speeds greater than 3 kph following Bjørneraas et al. (2010) and Hurford (2009). We also restricted our evaluation to seasonal locations taken from January to April to ensure our sample of lynx habitat use corresponded to when winter recreation was most prevalent on our study areas; collars were programmed to automatically drop off after 1 June. We did not correct for potential habitat-induced bias in data acquisition because our GPS mean fix rate was high ($\bar{x}$ = 84%) across lynx (Hebblewhite et al. 2007). We captured 8 lynx (four females and four males) on the northern study area and 10 (five females and five males) on the southern; this sample represented most individual lynx present on study areas based on telemetry and field observation of winter tracks. After filtering procedures, our lynx dataset included 64,135 GPS locations across 18 individuals (nine males and nine females). We captured four lynx in two successive years. These animals did not change their spatial use between years, so we combined their points across years and treated the individual as the sample unit for statistical analyses.

Sampling winter recreationists

We distributed small, lightweight GPS units (Qstarz International, Taipei, Taiwan; model BT-Q1300) to winter recreationists at trailheads, parking lots, and other recreation portals to document their spatial movements (Miller et al. 2017, Olson et al. 2017, Squires et al. 2018). Technicians classified the mode of recreation for participants as snowmobilers, backcountry skiers or snowboarders (hereafter backcountry skier), or hybrid users that included recreationists who used mostly snowmobiles or enclosed snow coaches to gain elevation so they could then ski (or snowboard) the downhill descent; this hybrid mode of recreation is growing rapidly in popularity across the southern Rocky Mountains. Olson et al. (2017) provide detailed explanations of our sampling and analytical methods to characterize winter recreation using GPS telemetry, and provided detailed depictions of resource-selection patterns of winter recreationists by activity across our study areas. In addition to these modes of recreation, we had opportunities to record recreation tracks made by heliskiing, where skiers or snowboarders were ferried to high-elevation slopes by helicopters. However, due to the limited sample size, we restricted our analysis to a brief summary of anecdotal observations for heliskiing.

Resource selection of Canada lynx in recreation landscapes

We developed RSFs to evaluate resource selection of lynx at the home-range scale (third-order selection; Johnson 1980). We sampled resource availability within lynx home ranges at GPS locations ($\bar{x}$ = 2915/individual, range = 433–6412) distributed randomly within a 95% fixed kernel home range delineated using the AdehabitatHR package in R (Calenge 2006); we sampled used-available locations across home ranges at a 1:5 ratio. We used a general linear mixed model with a binomial distribution and a logit link, and included a random intercept for each lynx to account for nonindependence within individuals

(Gillies et al. 2006). Using notation from Boyce et al. (2002), our model of lynx resource selection took the form (Eq. 1):

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

where $\tau(x)$ is the predicted relative probability of use, scaled from 0 to 1, β_i is the population-level coefficient for covariate i, x_{ij} is the value of covariate i for individual j, and γ_{0j} is a random intercept estimated for each individual j. Note the lack of an intercept in the interpretation of the used-available design. In this context, a RSF design based on used-available data yields a relative probability of use (Gillies et al. 2006). Models were estimated using the lme4 package in R (Bates et al. 2015). Consistent with Hosmer et al. (2013), we only considered potential covariates in multivariate RSF models if they performed better than the null with both the linear and quadratic terms considered. We then used the MuMIn package in R to perform all-subsets modeling of retained covariates to calculate multivariate models of resource use (Barton 2015). We prevented correlated terms ($|r| > 0.6$) from being considered in the same model, and ranked candidate models using Akaike's information criterion, corrected for sample sizes (AIC_c).

To test how recreation impacted lynx resource selection compared to environmental characteristics, we refit the top-performing lynx RSF model with the predicted RSF value from each recreation activity (backcountry ski, hybrid ski, hybrid snowmobile, snowmobile on-trail, and snowmobile off-trail) as developed by Olson et al. (2017). Model improvement from added recreation predictions suggested that Canada lynx either selected or avoided habitats that were preferentially used by recreationists. Full methods for the analysis of resource selection for winter recreationists by outdoor activity are presented in Olson et al. (2017). In brief, we used a similar used-available design within the home range of all recreation and compared used GPS locations from recreationists to available locations to create separate RSF models for backcountry skiers, off-trail snowmobiling, on-trail snowmobiling, ski segments of hybrid skiing, and snowmobiled segments of hybrid skiing. Snowmobile tracks were considered on-trail if GPS points were within 15 m on either side of a known road or trail, and off-trail if greater than this distance, and hybrid tracks were separated between the ski and snowmobile phases (Olson et al. 2017). We used a minimum convex polygon of all recreation points combined per study area as a biologically meaningful area to randomly draw available points for RSF analyses. We used the same covariate and model selection procedures for models including winter recreation RSFs as we did for lynx.

Model validation

We evaluated the top-performing lynx RSF model using leave-one-out cross-validation (Matthiopoulos et al. 2011). We withheld each individual lynx's data in turn, refit the top model on the remaining lynx, and used the model-generated coefficients to predict probability of selection of the withheld individual. We binned the RSF scores from the predicted probability surface into 10 equal area bins using percentiles as cutoffs and determined the frequency of withheld lynx locations that fell within each bin. We then calculated a Spearman rank correlation between the frequency of locations within each bin and the bin rank (Boyce et al. 2002). We repeated this process for each withheld lynx and averaged the Spearman correlation over all lynx.

Environmental variables

We based Canada lynx RSF models on 12 environmental covariates that represented biotic and abiotic gradients across study areas (Table 1). We believed these covariates captured the environmental heterogeneity that would influence movements and resource-use patterns of Canada lynx when traversing landscapes. Topographic covariates that we considered included elevation, aspect, slope, surface ratio (an index of terrain roughness), and topographic position index (TPI, an index of terrain concavity or convexity). We expected that lynx would select more moderate landscape topographies and concave drainages (Squires et al. 2013) compared with winter recreationists. Given that we expected both lynx (Koehler et al. 2008, Squires et al. 2010, Ivan and Shenk 2016) and winter recreationists (Miller

Table 1. Environmental/spatial covariates used to model the movements of Canada lynx (*Lynx canadensis*) and winter recreationists in the southern Rocky Mountains, Colorado, USA, 2010–2013.

Names	Resolution (m)	Source	Description
Dist hwy	Vector/30	State highway layer from CDOT	Euclidean distance to nearest highway
Elevation	30	USGS National Elevation Dataset	Elevation (m)
Canopy cover	30	National Land Cover Database 2011 Tree Canopy	Percent tree canopy cover
Evergreen	30	National Land Cover Database 2011 Land Cover	Evergreen forest
North	30	ArcGIS Aspect Tool, cosine transformation	Index of north-facing aspect
Ann precip	800	PRISM 1980–2010 Precip Normals	Average annual precipitation
Slope	30	ArcGIS Slope Tool	Slope in degrees
Ann temp	800	PRISM 1980–2010 Mean temp Normals	Mean annual temperature
Roughness	30	DEM Surface Tools, JennessEnt	Index of topographic roughness
TPI	30	Land Facet Corridor Tools, JennessEnt	Topographic position index, measure of landscape curvature
Rd density	Vector/30	CPW road layer from all forests, including only forest roads, not highways	Measure of linear distance of roads per unit area, varying scales
Forest Edge	30	NLCD Land Cover Type, deciduous, evergreen, and mixed forest	Measure of length of forest/non-forest edge per unit area, varying scales

Note: Variable name, native resolution of spatial layer, source, and description of environmental attribute are given.

et al. 2017, Olson et al. 2017) to be sensitive to forest structure, we included a percent tree canopy-cover covariate from the National Land Cover Database (NLCD; Homer et al. 2015) as an index to tree density, a land cover layer indicating the presence of evergreen forest, and a measure of the density of forest edge as an index of forest fragmentation (the length of edge between forest/non-forest areas as determined by the NLCD land cover layer in a given neighborhood divided by the area). We included distance to nearest highway and the density of forest roads as indices of human access and development. Finally, we also considered average annual temperature and precipitation from the Prism dataset (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu) as an index to snow depth. We assumed that recreationists and Canada lynx potentially perceived environmental covariates at different spatial scales when making habitat-use decisions. Thus, we used a moving window in ArcMap (Environmental Systems Research Institute 2011, ArcGIS Desktop: Release 10, Redlands, California, USA) to calculate the average of each covariate within a 125, 500, 1250, and 2500 m radius of each location. We standardized all covariates by subtracting the mean and dividing by the SD to allow direct comparison between estimated model coefficients and to facilitate model fitting.

Can Canada lynx and recreationists reduce conflict through landscape partitioning?

We incorporated model interactions within a GLMM framework (Gillies et al. 2006, Bolker et al. 2009) similar to Wiens et al. (2014) to identify how patterns of resource selection by winter recreationists differed (or not) compared with environmental features selected by Canada lynx. Here, we evaluated the hypothesis that Canada lynx may increase (or decrease) the potential for disturbance impacts through their differences in resource selection compared to how winter recreationists may partition landscape features. For this analysis, we randomly selected a 1:1 ratio of available and used points from each recreation track (N = 2116 tracks) and added them to available and used points for lynx to create a single dataset that included an indicator variable coding recreation mode (backcountry skiing, hybrid skiing, hybrid snowmobiling, snowmobiling on-road, snowmobiling off-road), and Canada lynx (a total of 6 factor levels, 5 recreation and 1 lynx). We then estimated the top-performing environmental RSF model for Canada lynx on the combined (lynx and recreation) dataset. We built in an interaction between each covariate in the model and the 6-level factor indicator variable so the model estimated a separate slope and intercept for lynx and each recreation activity (Eq. 2), and included a random effect of recreation track or lynx ID:

$$\tau(x) = \frac{\exp(\alpha + \varphi z_j + \sum_{i=1}^{10} \theta x_i + \sum_{j=1}^{6} \beta_{ij} x_{ij} z_j + \gamma_k + \varepsilon_i)}{1 + \exp(\alpha + \varphi z_j + \sum_{i=1}^{10} \theta x_i + \sum_{j=1}^{6} \beta_{ij} x_{ij} z_j + \gamma_k + \varepsilon_i)} \quad (2)$$

where τ(x) is the estimated relative probability of use, α is the model intercept (which was retained to help interpret the random effects, Gillies et al. 2006), φ is the intercept for each of the *j* levels of the factor variable *z*, θ is the intercept for each of the *i* covariates *x*, β_{ij} are the estimated slopes of the interactions for *j* factor levels *z* interacting with *i* covariates *x*, γ is the random intercept for each of *k* individual tracks or lynx, and ε_i is the error term. We set "lynx" as the factor reference category to allow comparison between the slope and intercept for each recreation activity with all environmental covariates included in the best-fit lynx RSF model. This approach provided a direct estimation of differences or similarities in how lynx and recreation respond to environmental gradients across the covariates that defined lynx resource selection. These balanced use-availability data were modeled assuming a binomial distribution with a logit link function, and the mixed-model degrees of freedom were adjusted using the Kenward–Roger method (Kenward and Roger 1997). We conducted that analysis using SAS PROC GLIMMIX and PROC PLM in version 9.4 of the SAS System for Windows (SAS Institute Inc., Cary, North Carolina, USA).

We then used functional responses to evaluate whether lynx adjusted their resource selection response to recreation depending on its availability. Inherent in resource-selection studies based on use-availability designs is the assumption that selection is constant, such that habitat use is proportional to availability across the range of availability (Mysterud and Ims 1998, Hebblewhite and Merrill 2008, Beyer et al. 2010, Holbrook et al. 2019). However, this assumption is naïve for wildlife in many ecologically relevant situations (Mysterud and Ims 1998, Hebblewhite and Merrill 2008, Moreau et al. 2012), including for Canada lynx (Holbrook et al. 2017). Consistent with Mysterud and Ims (1998) and Holbrook et al. (2019), we modeled functional responses that related recreation-habitat availability (and thus, by proxy, recreation) to used and available points in each lynx's home range. We first calculated the mean RSF predicted value for each lynx at used and available points (each averaged to a neighborhood) for each recreation type (backcountry ski, hybrid ski, hybrid snowmobile, snowmobile off-trail, and snowmobile on-trail). We used a likelihood ratio test to evaluate whether linear, quadratic, and third-degree polynomial models provided the most supported functional response (either higher-order models were supported or the linear slope did not equal zero) of lynx to the various modes of winter recreation (Hosmer et al. 2013).

Results

Resource selection of Canada lynx in recreation landscapes

The best-fitting resource-selection model for Canada lynx was based on 10 spatial covariates and had little model uncertainty; no models were within 2 ΔAIC of the top-performing model (Table 2; Appendix S1: Table S1). Spatial predictions from the best-fitting RSF model delineated the relatively narrow zone of suitable lynx

Table 2. Beta coefficients (β) and standard errors (SE) of covariates from the top-performing resource-selection model for Canada lynx (*Lynx canadensis*) in the southern Rocky Mountains, Colorado, USA, 2010–2013.

Covariates	β	SE
Dist hwy$_{500}$	−0.06	0.01
Elevation$_{125}$	−0.49	0.02
Elevation$^2_{125}$	−0.43	0.01
Forest edge$_{500}$	0.12	0.01
Canopy cover$_{125}$	0.90	0.01
Canopy cover$^2_{125}$	−0.33	0.01
North$_{1250}$	0.03	0.01
Ann precip	0.05	0.01
Rd density$_{500}$	0.15	0.01
Slope$_{2500}$	0.56	0.01
Roughness$_{125}$	−0.26	0.01
TPI$_{500}$	0.04	0.01

Note: TPI, topographic position index. Spatial scales (m) are appended to covariate names in subscript.

habitat that exists in the southern Rocky Mountains, between the alpine and valley bottoms (Fig. 2). The RSF for Canada lynx exhibited very high model fit, with an overall Spearman rank correlation of 0.975 from the leave-one-out cross-validation. Within home ranges, Canada lynx selected areas with greater forest edge (forest patchiness), mid-elevation, higher forest-road

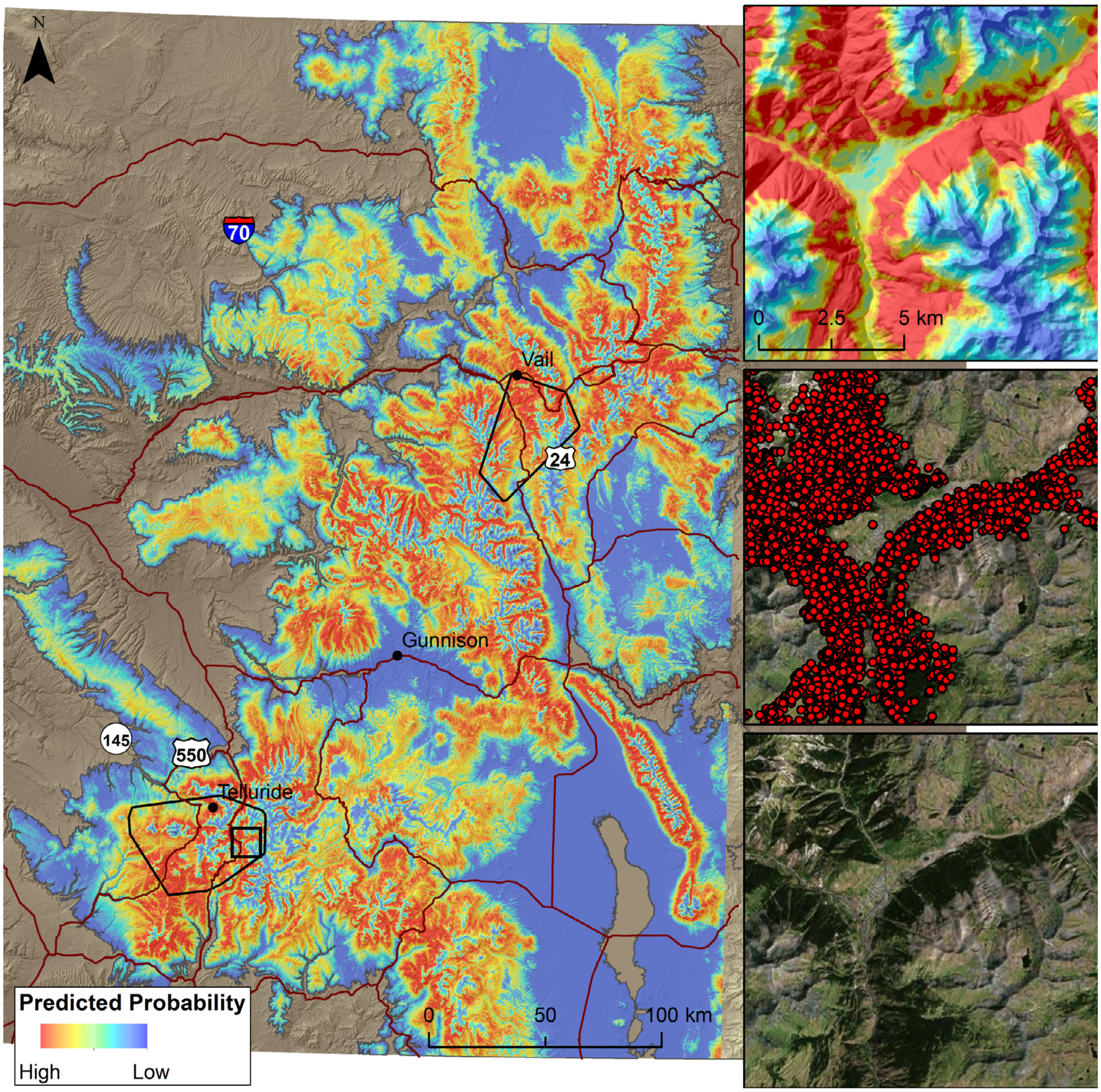

Fig. 2. Predictions of resource selection for Canada lynx (*Lynx canadensis*) across western Colorado, USA, within the elevation zone also suitable for winter recreation based on global positioning system (GPS) telemetry, during winters 2010–2013. Warmer colors indicate higher relative probabilities of selection. Panels at right illustrate the naturally fragmented distribution of forests preferentially selected by Canada lynx in the San Juan Mountain range of southwestern Colorado, USA, located between valley bottoms and alpine mountain peaks (upper panel) as delineated with GPS data points (middle panel) relative to mountainous topography (lower panel).

density, on steeper slopes, but with lower surface roughness that indicates a preference for smoother terrain (Table 2). We also documented 2143 tracks (2,467,060 GPS locations) of winter recreationists that included snowmobilers (n = 686 tracks), backcountry skiers (n = 1111), and hybrid users (n = 346) for a total cumulative distance of 56,000 km of delineated tracks by recreation activity across the two study areas; see Olson et al. (2017) for a complete evaluation of resource selection of winter recreationists. Although Canada lynx and winter recreationists both used high-elevation, mountainous landscapes where high resource overlap would be expected, we found that Canada lynx and winter recreationists selected environmental features in ways that resulted in complex spatial partitioning across these shared landscapes, even in areas of high human activity (Fig. 3).

The addition of recreation, regardless of activity, improved the best-performing RSF model for Canada lynx that considered environmental covariates alone (Appendix S2: Table S1; 527.27 ΔAIC). The best-performing model for Canada

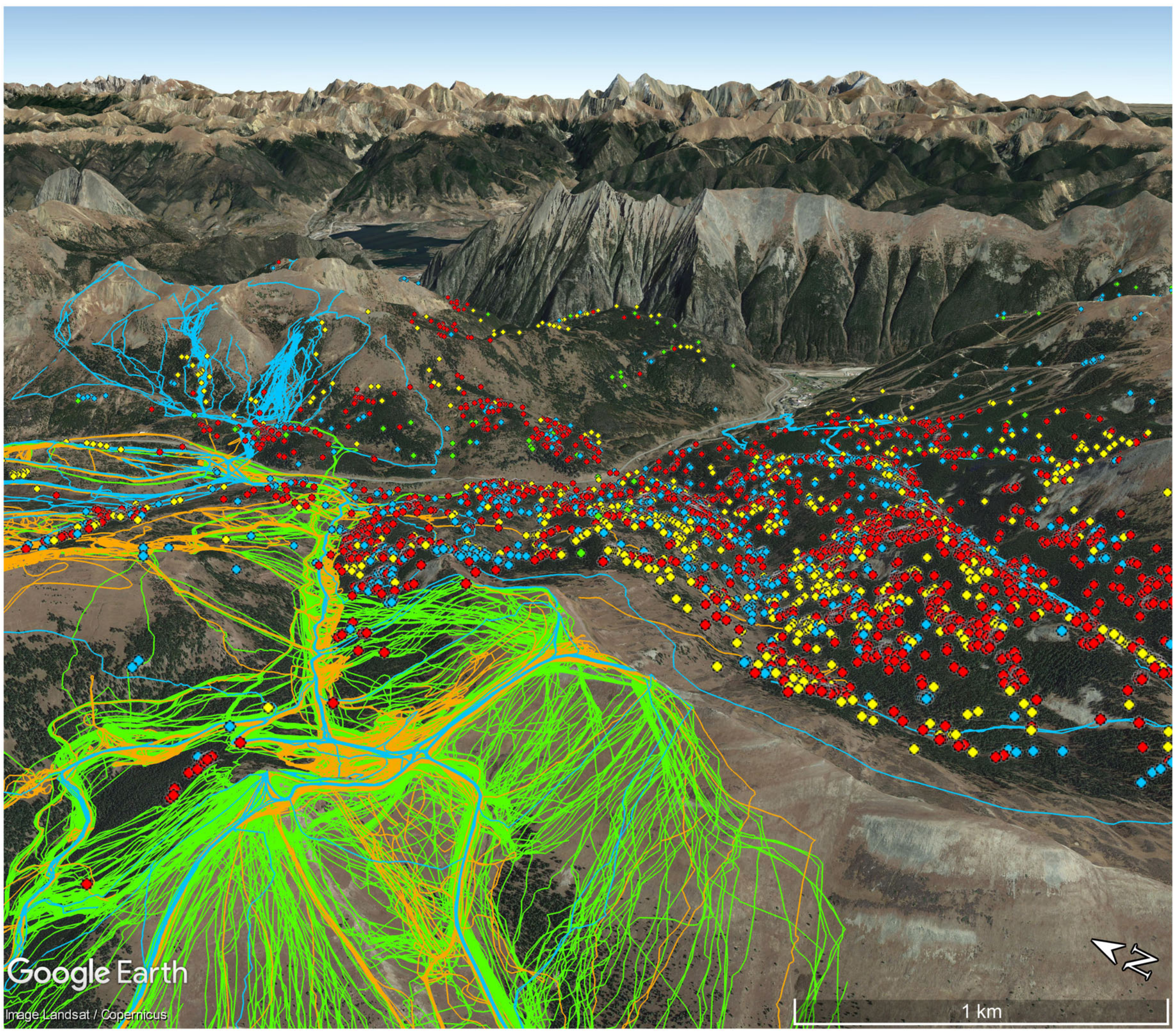

Fig. 3. Dispersed winter recreationists (orange, snowmobiles; green, hybrid—skiers using snowmobiles to access ski terrain; blue, backcountry skiers) and Canada lynx (*Lynx canadensis*, global positioning system locations color-coded by individual) partitioning a mountain landscape, Vail Pass, Colorado, USA. Note the complex spatial partitioning across this mountainous landscape among winter activities and Canada lynx.

lynx was most improved (189.79 ΔAIC) when a probability covariate for all recreation activities combined was included; the second-most supported model included only motorized forms of recreation (snowmobiles on- and off-trail and hybrid snowmobiles). Marginal response plots, which varied over the range of a single covariate while holding all other covariates at their means, provide a means to visualize the relative strength of recreation and environmental covariates (Fig. 4). Based on these plots, Canada lynx tended to use areas that were selected by back-country skiers and avoid areas used by snowmobile recreationists, especially those areas selected by recreationists for off-trail riding (Fig. 4). However, marginal plots also indicated that Canada lynx were most responsive to environmental characteristics in their home ranges when compared to winter recreation despite the improved statistical performance of the lynx-recreation model (Fig. 4). The validation of the top lynx-environmental model when combined with predicted recreation probability was high, with a 0.988 Spearman rank correlation from leave-one-out cross-validation.

Can Canada lynx and recreationists reduce conflict through landscape partitioning?

Based on a GLMM with imposed interactions within the best-performing lynx RSF model across the modes of recreation activities (back-country skiing, hybrid skiing, hybrid snowmobiling, snowmobiling on-road, snowmobiling off-road) and lynx, we found that percent forest

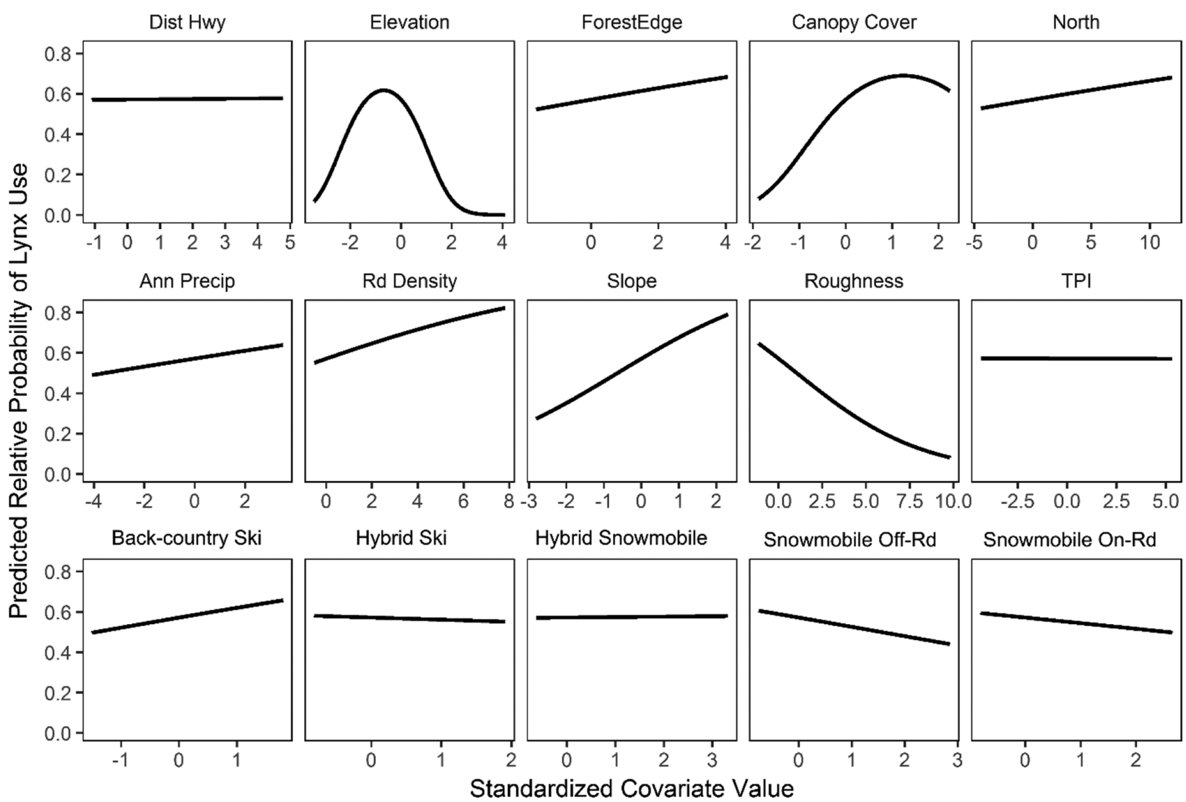

Fig. 4. Marginal response curves of each variable in the top resource-selection model for Canada lynx (*Lynx canadensis*) composed of both environmental and recreation covariates (Appendix S2: Table S1). Plots were created by varying each covariate from the minimum to maximum one at a time, while holding all other covariates at their mean. The change in predicted lynx resource-selection functions values indicates the strength of the individual contribution of each covariate to the model. Plots show standardized covariates with mean values of 0 to allow comparison across covariates with differing ranges.

canopy cover, annual precipitation, forest-road density, and topographic slope were the environmental gradients that most separated winter recreation from Canada lynx (Fig. 5; Appendix S3: Tables S1, S2). Canada lynx selected forests with denser forest canopy cover than did winter recreationists. Motorized recreationists selected more open forest cover compared with nonmotorized recreationists such as hybrid or backcountry skiers who exhibited weak selection for dense forest cover, but not to the same degree as Canada lynx (Figs. 5, 6). Motorized and nonmotorized winter recreationists exhibited strong selection for areas of high annual precipitation compared with Canada lynx that were relatively insensitive to this variable (Fig. 5). High forest-road density was also a strong predictor for motorized and nonmotorized winter recreationists, whereas Canada lynx exhibited a similar positive response to forest roads (seasonally accessible by snow machine only due to deep snow cover), but less pronounced. Lynx preferentially selected areas with steep slopes compared with motorized recreationists who selected terrain with shallow slopes, but to a lesser degree than

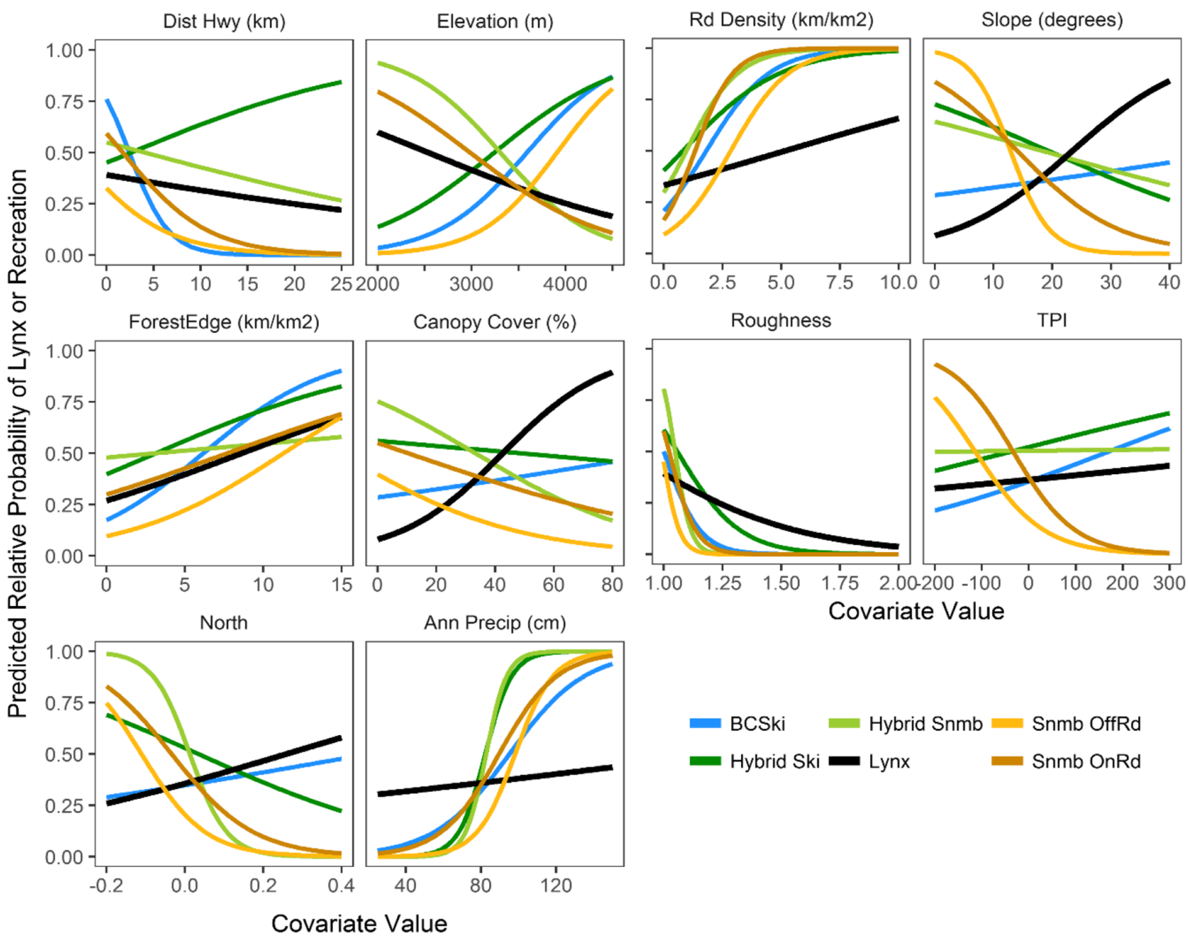

Fig. 5. Predicted relative probabilities of Canada lynx (*Lynx canadensis*) resource selection from the top-performing lynx resource-selection model, Colorado, USA, winters 2010–2013. Winter recreation activity type (backcountry ski, hybrid snowmobile, hybrid ski, snowmobile on-road, and snowmobile off-road) was included as an interaction with each covariate in the model. Each plot represents the modeled slope and intercept for each recreation type and lynx in response to a given covariate, while holding all other covariates in the model at their mean. Predicted lynx values are shown in black, while the various recreation activities are shown in color.

backcountry skiers who selected steeper terrain compared with other recreationists. Canada lynx and all forms of recreation, except hybrid recreationists when skiing, selected areas nearer to highways, but this preference was much stronger for recreationists than for lynx. In addition, Canada lynx, on-trail snowmobiles, and hybrid snowmobiles all selected lower elevations compared with backcountry skiers, hybrid skiers, and off-trail snowmobilers. Canada lynx were similar to winter recreationists (weak for hybrid snowmobiles) in their preferential use of habitats with greater forest edge and neither lynx nor winter recreationists, regardless of activity, preferred areas with high surface roughness. Motorized recreationists across activities and hybrid skiers preferred south-facing slopes, whereas lynx and backcountry skiers showed a weak preference for north-facing slopes. Finally, motorized recreationists (hybrid when on snowmobiles and snowmobiles on- and off-trails) exhibited strong selection for negative TPI values, indicating a preference for drainages, whereas Canada lynx, backcountry skiers, and hybrid skiers selected positive values of TPI (preferences for ridges), although this relationship was weak for lynx.

Canada lynx exhibited functional responses to four of five types of recreation activity (Table 3, Fig. 7). As average suitability for off-trail snowmobile use increased, Canada lynx exhibited a nonlinear, increasing level of avoidance of these areas (Fig. 7). Thus, lynx increasingly avoided areas suitable for off-trail snowmobiles, generally open areas with sparse tree vegetation or cirques, as these areas became more prevalent within a home range (Fig. 7). This same general relationship was true of the other forms of motorized recreation (on-trail snowmobiles and hybrid snowmobiles). In contrast, nonmotorized forms of recreation either exhibited no functional response (use proportional to available, hybrid-ski habitat) or higher use of backcountry ski areas by Canada lynx, especially at mid-levels of backcountry ski-habitat suitability (Fig. 7). Thus, the general patterns of functional responses confirm that lynx generally avoid habitats favored by motorized recreationists, but preferred habitats that were similar to those favored by nonmotorized recreationists (Appendix S2: Table S1; Fig. 7). This pattern of resource use was also supported by the range of predicted recreation habitat (predicted recreation RSF relative probability) that we documented as available in lynx home ranges. For example, the average habitat suitability (predicted RSF relative probability) for on-trail snowmobiles varied between 0.07 and 0.40 (from a possible 0 to 1 range) in lynx home ranges compared with a range between 0.09 and 0.65 for backcountry skiing (Appendix S2: Table S1; Fig. 7). This indicated that lynx home ranges on average included more habitat suitable for skiers and less suitable for motorized winter recreationists.

Although opportunities were limited, we were able to document heliskiing in 2012 (91 downhill tracks with 70 inside lynx home ranges) and 2013 (65 downhill tracks with 53 inside home ranges). Based on these data, heliskiing occurred in alpine areas at higher elevations ($\bar{x}$ = 3634 m, 95% confidence interval [CI]: 3604–3665 m) than the subalpine forests selected by Canada lynx ($\bar{x}$ = 3229 m, 95% CI: 3147–3311 m). Areas selected by heliskiers also had much lower canopy cover ($\bar{x}$ forest canopy—heliski = 13%, 95% CI: 12–15) than forest selected by lynx ($\bar{x}$ = 42%, 95% CI: 37–48). Thus, based on these anecdotal data, Canada lynx were spatially segregated from heliskiing in the Southern Rockies due to elevational and forest canopy environmental gradients.

Discussion

Our research documented how Canada lynx and winter recreationists partitioned landscapes based on GPS technology that similarly characterized human and carnivore resource selection. Canada lynx in the southern Rocky Mountains generally selected areas within winter home ranges at mid-elevations on relatively steep slopes with low topographic roughness within forests with mid- to high levels of canopy cover (Table 2). These areas were naturally highly fragmented and spatially distributed between valley bottoms and alpine ecosystems given the steep mountainous topography (Fig. 2). We demonstrated that Canada lynx and winter recreationists partitioned environmental gradients in ways that reduced the potential for recreation-related disturbance (Figs. 2, 4, 5). For example, Canada lynx selected different environmental gradients of forest canopy closure, road density, annual

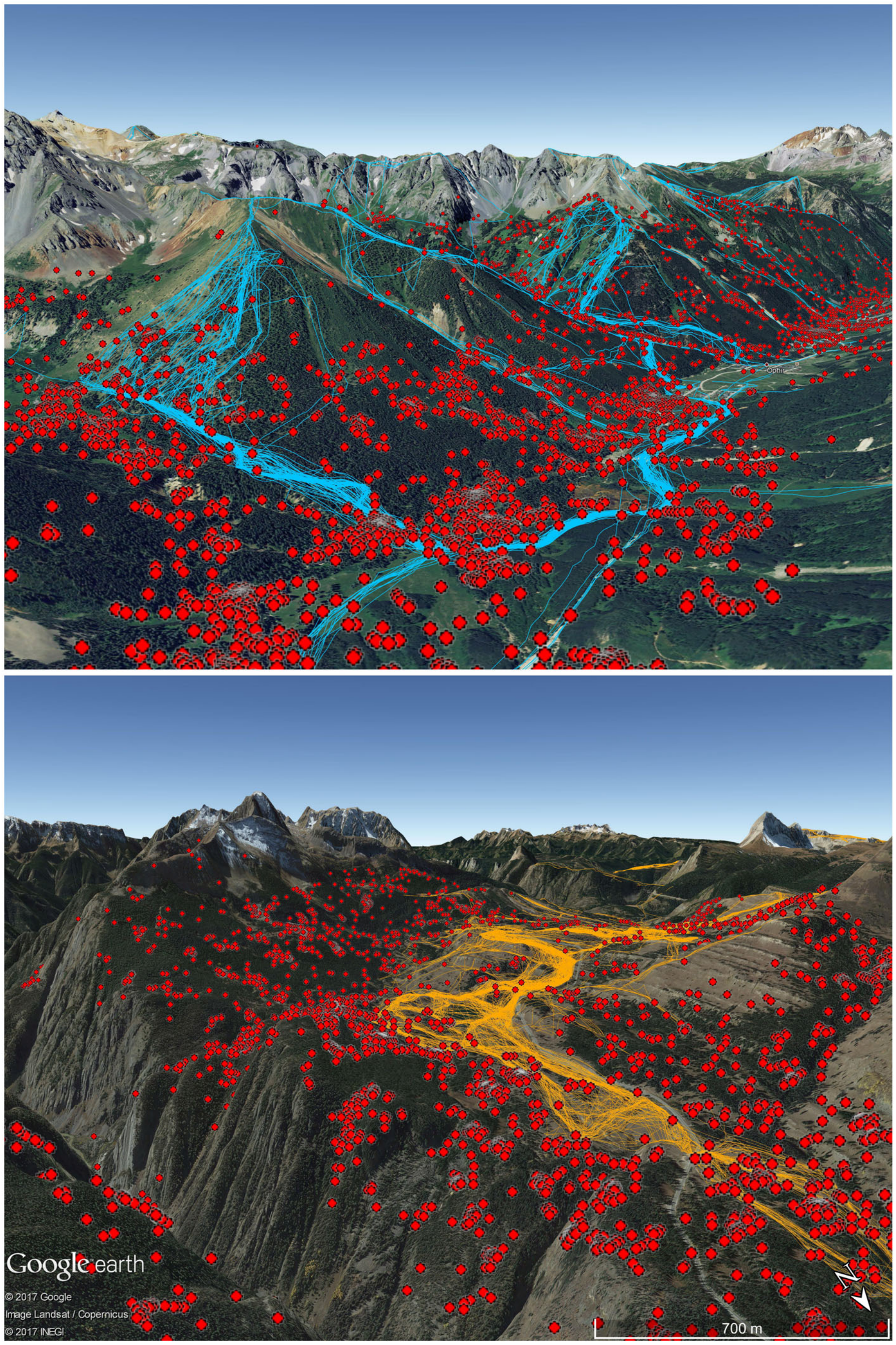

Fig. 6. Backcountry skiers in the southern Rocky Mountains, near Ophir, Colorado (blue, top panel), and snowmobilers near Molas Pass, Colorado (orange, bottom panel), recreating in a landscape used by Canada lynx (*Lynx canadensis;* lynx global positioning system data points), 2012–2013. Note that backcountry skiers and lynx tend to show more habitat overlap, since both select areas with greater forest canopy cover, compared with snowmobile recreationists that selected more open forest cover.

Table 3. Parameters estimated from models assessing the presence of a functional response between Canada lynx (*Lynx canadensis*) use and available recreation-suitable habitat, as predicted from resource-selection models for each recreation type.

Parameters	B_0	B_1	R^2
Snmb Off-Tr†	0.01 (−0.04 to 0.06)	0.72 (0.51–0.93)	0.64
Snmb On-Tr†	0.07 (0.00–0.13)	0.71 (0.46–0.97)	0.54
BC-Ski†	Third-degree polynomial (P = 0.40)		0.92
Hybrid Snmb†	0.03 (−0.02 to 0.08)	0.54 (0.29–0.80)	0.40
Hybrid Ski	0.01 (−0.04 to 0.07)	0.92 (0.73–1.11)	0.78

Notes: For each recreation type, B_0 is the estimated intercept (90% confidence intervals given in parentheses) and B_1 the estimated value for the slope of a linear model; R^2 gives the coefficient of determination.
† Recreation types with a statistically significant functional response.

precipitation, and slope than winter recreationists regardless of recreation activity (backcountry skiing, hybrid skiing, hybrid snowmobiling, snowmobiling on-road, snowmobiling off-road; Fig. 5). Further, we documented a dichotomy in the responses of Canada lynx to motorized vs. nonmotorized winter recreation. Canada lynx exhibited a functional response of increasing avoidance as areas preferred by motorized recreationists (e.g., snowmobile off-trail and hybrid snowmobile) were more available in home ranges (Fig. 7). In comparison, Canada lynx exhibited either no functional response to nonmotorized recreationists (use proportional to available—hybrid ski) or they used similar areas in home ranges also selected by nonmotorized recreationists (e.g., backcountry skiers; Fig. 7). This pattern of use was consistent with Canada lynx selecting environmental gradients that were most similar to nonmotorized recreationists, especially relative to slope, TPI, and north aspects (Fig. 5). Therefore, understanding the spatial relationships between Canada lynx and winter recreationists required an integrated approach that coupled analyses specific to individual recreation activity to measures of environmental heterogeneity that most influenced resource selection.

We recognize the difficulty in distinguishing between real impacts of winter recreation in terms of the direct response of Canada lynx to human disturbance (i.e., landscape of fear; Gill et al. 1996, Laundré et al. 2001) from apparent segregation between this carnivore and recreationists due to differences in habitat choice. Ideally, from an inferential viewpoint, we would have experimentally manipulated the activity, proximity, and duration of winter recreation to Canada lynx. For example, moose (*Alces alces*) movement rates were 33-fold faster one hour post-disturbance from backcountry skiers (Neumann et al. 2010), and black grouse (*Tetrao tetrix*) exhibited elevated corticosterone metabolites (a stress hormone) when experimentally flushed by skiers (Arlettaz et al. 2015). However, we were unable to use experimental approaches given the extreme mountainous topography of the southern Rocky Mountains and the extensive home ranges of Canada lynx at the southern range periphery (Aubry et al. 2000). We were also unable to sample and develop RSFs for lynx in more isolated areas. Such individuals (and associated RSF models) might have provided better controls against which to compare overlap of lynx and recreation RSFs if the lynx we sampled adjacent to recreation areas had already responded to recreation when selecting their home range. Instead, we investigated recreation relationships through integrated resource-selection modeling (Boyce et al. 2002, Johnson et al. 2006) coupled with evaluations of functional responses (Mysterud and Ims 1998, Hebblewhite and Merrill 2008, Holbrook et al. 2019) based on spatial depictions of human and carnivore movements. One strength of this study was the ability to delineate human movements through landscapes with one of the largest spatial datasets of winter recreationists documented using GPS telemetry (Miller et al. 2017, Olson et al. 2017, Squires et al. 2018), so we could define recreation habitat specific to the various dispersed snow sports present in occupied lynx home ranges.

One potential explanation for improved RSF model performance with added recreation is that

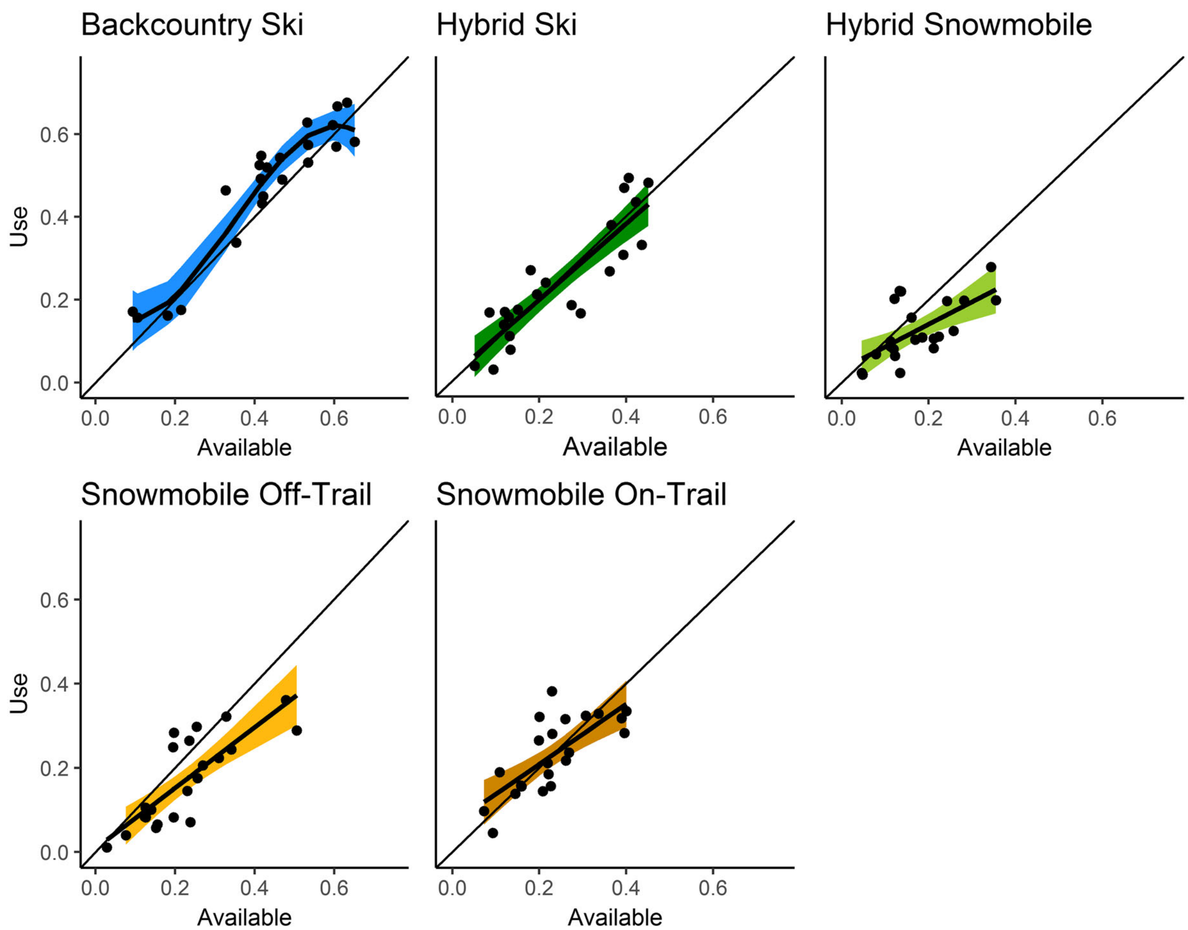

Fig. 7. Predicted relationships visualized by functional responses of resource selection by Canada lynx (*Lynx canadensis*, $N = 22$ home ranges) in western Colorado, USA, to winter recreation activities. Diagonal lines illustrate random (i.e., proportional) habitat use. Global positioning system location data from Canada lynx were used to calculate use-availability response and 95% confidence intervals. For example, a slope less than 1, below the 1:1 line, recreationists such as hybrid snowmobile and snowmobile off-trail, and to a lesser extent snowmobile on-trail, indicated increased avoidance of a habitat most suitable for motorized recreation as it becomes increasingly available in home ranges.

human activity created a landscape of fear (Gill et al. 1996, Laundré et al. 2001) sufficient to modify a species' access to resources like was documented for elk (*Cervus Canadensis*; Ciuti et al. 2012), red deer (*Cervus elaphus*; Coppes et al. 2017*a*), moose (Harris et al. 2014), mountain caribou (*Rangifer tarandus caribou;* Seip et al. 2007), and wolverines (*Gulo gulo*, Heinemeyer et al. 2019). We believe the patterns of spatial separation we documented between Canada lynx and winter recreationists, such as in areas of low tree canopy cover selected by snowmobilers, were mostly a function of resource-use decisions rather than a landscape of fear that precluded access. That is, adding recreational activities to our models may have, in some sense, been a proxy for adding stem density and horizontal cover, which is a primary factor affecting lynx resource use across the species' southern periphery (Squires et al. 2010, McCann and Moen 2011, Ivan and Shenk 2016, Holbrook et al. 2017). Therefore, lynx were negatively related to motorized use in part because motorized users are naturally restricted to open areas that lynx tend to avoid. Conversely, lynx were positively associated with backcountry ski habitat because skiers often skin-up to climb snow slopes through heavily treed areas, and many prefer to ski the trees on their return as well. Thus, we suggest that the model improvement we observed after adding recreation most likely indicates that Canada lynx respond to the same environmental gradient that most dictates the spatial-use patterns of winter recreationists.

Despite our belief that lynx and recreationists may partition areas due to differing patterns of selection, we recognize that there are disturbance thresholds from winter recreation that modify the movements and behaviors of Canada lynx like other species (Sato et al. 2013, Larson et al. 2016). For example, Olson et al. (2018) documented that lynx from this same population tended to avoid high levels of human activity present on developed ski areas, similar to other mammalian (Nellemann et al. 2010, Richard and Côté 2016, Slauson et al. 2017) and avian (Patthey et al. 2008, Braunisch et al. 2011) species. Canada lynx on our study areas also exhibited behavioral responses in terms of decreased movement speeds and increased time spent stationary in areas of highest intensity of backcountry skiing and snowmobiling, suggesting that lynx are responsive to human activity with some increased vigilance (Olson et al. 2018).

A strength of our approach was the integration of functional responses, resource-selection analyses, and GLMMs with imposed interactions to disentangle how Canada lynx and winter recreationists responded to environmental heterogeneity. An added strength was the consideration of lynx response to recreation across motorized and nonmotorized winter sports because habitat-selection response not only is a function of total people present, but also varies by specific human activities (Gill et al. 1996, Ciuti et al. 2012, Bonnot et al. 2013). We demonstrated through functional responses based on use-availability comparisons (Mysterud and Ims 1998, Holbrook et al. 2019) that Canada lynx responded differently to areas selected by motorized vs. nonmotorized recreationists. Canada lynx increasingly avoided areas suitable to motorized recreation as it became more available within home ranges (Fig. 7). Other studies have documented a similar response to motorized winter recreation. For example, moose preferentially selected habitats away from areas of high snowmobile-trail density (Colescott and Gillingham 1998, Harris et al. 2014) and intensive snowmobile activity displaced woodland caribou (*R. tarandus caribou*) from suitable habitat (Seip et al. 2007). Female wolverines tend to avoid motorized winter recreation resulting in significant habitat loss (Heinemeyer et al. 2019). Results from our study demonstrated that lynx were most responsive to environmental heterogeneity related to habitat characteristics as hypothesized (Table 2, Fig. 4), but the addition of winter recreation significantly improved our understanding of lynx resource use (Appendix S3: Tables S1, S2; Fig. 5).

We documented some evidence that Canada lynx used islands of suitable habitat on the areas (Fig. 3) that were surrounded by some of the highest levels of motorized and nonmotorized winter recreation in the western United States on the Vail Pass Recreation Area (Miller et al. 2017, Olson et al. 2017). Although this information is anecdotal due to small samples, the size of forested islands surrounded by very high levels of motorized and nonmotorized recreation that were used by Canada lynx averaged 211 ha (range = 106–316 ha) on the Vail Pass Recreation Area (N = 5 forest-patch islands) in central Colorado and 7 ha (range = 0.4–22 ha) on Molas Pass (N = 9) in southern Colorado. Thus, Canada lynx used small patches of habitat surrounded by high-recreation activity when avoidance or buffering of use around these areas would be expected if direct human disturbance prevented access. Possibly, Canada lynx had the cognitive ability to distinguish between threatening and nonthreatening human behavior that resulted in habituation to human activity (Tablado and Jenni 2017) similar to some avian species (Carrete and Tella 2011, Lendvai et al. 2013) and other carnivores, such as cougars (*Puma concolor*) in rural regions that exhibit less sensitivity to anthropogenic features than their counterparts in wilderness environments (Knopff et al. 2014).

Understanding how species respond to linear features (i.e., roads, trails, and seismic lines) is particularly important when managing human activity in critical habitats required by endangered species (Lesmerises et al. 2017). Roads can influence a species' feeding rate (e.g., elk; Ciuti et al. 2012), spatial use (e.g., kit fox *Vulpes macrotis*, Jones et al. 2017; grizzly bears *Ursus arctos*, Northrup et al. 2012), movement speed (e.g., wolves, Dickie et al. 2017; wolverine, Scrafford et al. 2018), distribution (e.g., woodland caribou, James and Stuart-Smith 2000), and predation risk (e.g., roe deer *Capreolus capreolus*, Bonnot et al. 2013). The ecological consequence of roads to wildlife is highly variable given the many different life histories of species and their response to an array of road infrastructures, traffic volumes, and speeds (Trombulak and Frissell 2007). For example, Canada lynx in the southern Rocky Mountains cross two-lane highways approximately every other day with little evidence of spatial avoidance immediately adjacent to highways (Baigas et al. 2017). The forest roads included in this study were snow-covered during winter that precluded travel by wheeled vehicles. Forest roads were strongly selected by winter recreationists on our study areas for both motorized and nonmotorized activities (Olson et al. 2017). We documented that Canada lynx selected areas adjacent to forest roads, but to a lesser degree than recreationists (Fig. 5). Thus, Canada lynx were neutral or exhibited a slight proclivity to use roaded areas similar to lynx populations in the northern Rockies (Squires et al. 2010). In contrast to bighorn sheep (*Ovis canadensis nelson*) that adjusted space-use near high-use recreation trails (Longshore and Thompson 2013), Canada lynx also exhibited little behavioral response to backcountry ski trails as evidenced by their increased probability of use near (<250 m) trails and no diel pattern in their association with trails despite varying levels of human disturbance during day (high disturbance) vs. night (no disturbance, Olson et al. 2018). Thus, we believe the proclivity of Canada lynx to associate with roads and trails was due to their patterns of resource selection in forested landscapes with associated road and trail infrastructures rather than responding to human activity present along these linear structures.

One caveat to our study is that we could only quantify the spatial-use patterns associated with the dominant recreation activities present on our study areas (Miller et al. 2017, Olson et al. 2017). Snow cycles represented a new technology at the time of our study and were used by too few recreationists for us to quantify their spatial movements or disturbance impact. Snow cycles are standard off-road motorcycles that are modified with a narrow rotating backtrack and a front tire replaced by a ski. Snow cycles are designed to navigate denser forested slopes compared with the high-performance snowmobiles that were included in this study. Therefore, based on the patterns of resource selection and functional responses that we documented, snow cycles may cause habitat displacement given they provide motorized access through the same high-canopy forests selected by Canada lynx. However, we were unable to evaluate their actual biological impacts.

Conservation implications

Our study areas in the southern Rocky Mountains included some of the highest levels of dispersed winter recreation found in North America (Miller et al. 2017, Olson et al. 2017). Despite these high levels of recreation activity, we believe that in most cases, Canada lynx selected environmental gradients within home ranges that facilitated low overlap with snowmobile recreation and moderate overlap with backcountry skiing. The functional response of Canada lynx to increasingly avoid areas selected by motorized recreationists and share landscapes at fine scales with nonmotorized users (Fig. 7) provides land managers a useful framework to consider recreation impacts. The environmental gradients that are most important for managers to consider when evaluating potential disturbance between lynx and recreationists are forest canopy closure, road density, annual precipitation, and slope (Fig. 5). Management actions that relate to or alter these gradients (canopy, roads) are those that will most likely alter spatial relationships between Canada lynx and winter recreationists. For example, given the sensitivity of Canada lynx and winter recreationists to changes in forest canopy cover (Table 2; Figs. 4, 5), management actions that modify forest canopy cover through tree removal in recreation areas, whether for silviculture or fire/fuels management, could increase the spatial footprint of motorized winter recreation and decrease critical habitat for Canada lynx, especially in mid-elevation forests located on north-facing slopes (Fig. 4). The fact that motorized and nonmotorized winter recreationists exhibited strong selection for forest roads when accessing mountain terrain (Fig. 5; also see Olson et al. 2017) suggests that management actions such as road improvement, snow packing, or decommissioning may significantly alter the spatial relationship between Canada lynx and winter recreationists. Thus, forest-road management that alters winter access or road density could be a tool that either encourages or segregates recreation activity from the spatial-use areas selected by Canada lynx. Given that backcountry skiers, hybrid skiers, and off-trail snowmobilers generally selected higher elevations than lynx, efforts to encourage or direct dispersed winter recreation to high elevations (at or above tree line) through relaxed road and parking access, packed trail systems, and public outreach could be implemented with a low probability of impacting spatial-use patterns of Canada lynx. Results from this study, coupled with understandings of behavioral responses of lynx to winter recreation reported by Olson et al. (2018), provide a basis for assessing impacts of dispersed winter recreation to this federally listed carnivore. In general, with the caveats previously stated, Canada lynx were able to partition landscapes and maintain spatial use of home ranges with current levels of dispersed winter recreation, but recreation intensity thresholds likely exist (e.g., developed ski areas) beyond which lynx become increasingly intolerant of human activity.

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