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Predators choose prey over prey habitats: evidence from a lynx–hare system

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Abstract. Resource selection is grounded in the understanding that animals select resources based on fitness requirements. Despite uncertainty in how mechanisms relate to the landscape, resource selection studies often assume, but rarely demonstrate, a relationship between modeled variables and fitness mechanisms. Using Canada lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) as a model system, we assess whether prey habitat is a viable surrogate for encounters between predators and prey. We simultaneously collected winter track data for lynx and hare in two study areas. We used information criteria to determine whether selection by lynx is best characterized by a hare resource selection probability function (RSPF) or by the amount of hare resource use. Results show that lynx selection is better explained by the amount of hare use (SIC = −21.9; Schwarz's Information Criterion) than by hare RSPF (SIC = −16.71), and that hare RSPF cannot be assumed to reveal the amount of resource use, a primary mechanism of predator selection. Our study reveals an obvious but important distinction between selection and use that is applicable to all resource selection studies. We recommend that resource selection studies be coupled with mechanistic data (e.g., metrics of diet, forage, fitness, or abundance) when investigating mechanisms of resource selection.

Key words: Alberta, Canada; boreal; Canada lynx; habitat use; Lepus americanus; Lynx canadensis; *oil development; predator–prey; resource selection; snowshoe hare; statistical modeling.*

Introduction

Resource selection models estimate the probability that a combination of environmental conditions will be selected by an animal (Lele and Keim 2006). Grounded in the understanding that animals select resources based on their need to acquire nutrients, avoid predators, and maintain energy (Werner and Anholt 1993, Dussault et al. 2005), resource selection models are designed to identify interacting factors that influence fitness. However, in many cases the direct relationship between fitness mechanisms and modeled variables is simply assumed but seldom demonstrated.

This assumption is prolific in predator–prey studies, which often presume that prey habitat is representative of prey availability (for predators) or predator habitat is representative of predation risk (for prey). For example, studies on mule deer (*Odocoileus hemionus* [Atwood et al. 2009]), elk (*Cervus elaphus* [Hebblewhite et al. 2005, Atwood et al. 2009]), caribou (*Rangifer tarandus* [Gustine et al. 2006]), Eurasian lynx (*Lynx lynx* [Odden et al. 2008]), Stone's sheep (*Ovis dalli stonei* [Walker et al. 2007]), and bottlenosed dolphin (*Torsiops aduncus* [Heithaus and Dill 2002]) have explicitly assumed a consistent relationship between prey habitat (e.g., resource selection by prey) and resource selection by predators based on food availability, or between predator habitat and resource selection by prey based on avoidance. Other studies, focusing on species such as Atlantic bluefin tuna (*Thunnus thynnus* [Teo et al. 2007]), White-eared and Blood Pheasants (*Crossoptilon crossoptilon* and *Ithaginis cruentus* [Jia et al. 2005]), Spotted Owls (*Strix occidentalis* [Irwin et al. 2007]), macropods (While and McArthur 2005), Pileated Woodpeckers (*Dryocopus pileatus* [Lemaître and Villard 2005]), American marten (*Martes americana* [Slauson et al. 2007]), and dolphins (*Cephalorhynchus hectori* [Bräger et al. 2003]), have relied solely on a "standard of plausibility" (Lima and Zollner 1996), using environ-

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mental variables as surrogates for amount of use by predators or prey.

These assumptions have been substantiated in predator and prey studies. The combination of the marginal value theorem (Charnov 1976) and predation risk predicts that, all things being equal, prey should spend less time in areas that receive greater amounts of habitat use by predators and predators should spend more time in areas that receive greater amounts of habitat use by prey (Brown 1988, Lima and Dill 1990). However, in many cases using surrogates (resource selection or environmental variables) for amount of habitat use may be unjustified and is likely flawed when abundances are low or fluctuate. This is because resource selection may or may not consistently reflect the amount of resource use by animals. The amount of resource use by a species is a function of both their resource selection and population abundance. Low population abundance may lead to low use even in a highly suitable habitat and vice versa, high use in less suitable habitat if the population abundance is high. Consider an example: in a simplified world, we might expect people to select food and water all the time (probability of selection = 1.0). If people are abundant in a region, the amount of use at Lake X or Berry Patch Y would be high. However, in a "last man on earth" scenario, Lake X or Berry Patch Y could reasonably go unused while selection remains high. Thus, we would have a good chance of observing someone at Lake X where humans are abundant but would have a poor chance where humans were rare. This insight is applicable to all resource selection studies and is important because misinterpretation can lead to flawed results, misunderstood mechanisms, incorrect predictions, and misguided management.

The goal of this paper is to test whether prey habitat is a viable surrogate for the amount of resource use by prey. We use Canada lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*; hereafter hare) from northern Alberta, Canada as a model system because lynx are tied to a single prey species, hare, within the northern boreal forest. Lynx are generally known to select for areas used by hare (Squires and Ruggiero 2007, Bayne et al. 2008) and, in northern Alberta, their winter diet is composed almost exclusively of hare (91%; Brand et al. 1976). Here we assess whether lynx selection is better characterized by the amount of hare use (snow tracks per kilometer per day) or hare habitat as estimated using resource selection modeling techniques.

METHODS

Data collection

We recorded lynx and hare tracks in two independent study areas located in northeast Alberta, Canada. Both study areas are characterized by long winters, extensive peatlands, and undulating upland forests. The southern study area (55.9953° N, 111.3080° W) is located south of the Athabasca River where steam assisted oil development has already been established, whereas the northern study area (56.7651° N, 112.0907° W) is located north of the Athabasca River in an area that has experienced oil exploration but has not yet been developed for commercial oil extraction. As a result, the southern study area contains more human development than the northern study area. Snow-tracking surveys were conducted in the winter of 2009 using Finnish triangles (Linden et al. 1996). We positioned triangles using a stratified random design such that all available ecological communities were surveyed. Winter snow-tracking was conducted three to nine days after a fresh snowfall of at least 5 cm. Lynx and hare tracks intercepting the transect line were counted and recorded in 25-m intervals.

Resource selection by hare

We estimated a resource selection model (Lele and Keim 2006) for hare using a use and available study design. We considered two competing model forms: the exponential resource selection function (RSF), which estimates the relative probability of selection, and the logistic resource selection probability function (RSPF), which estimates the probability of selection (Lele and Keim 2006). We defined used locations by individual hare tracks encountered along the surveyed transect. Each used location was measured by a GPS coordinate recorded at the midpoint of the nearest 25-m survey interval. Available locations were defined by a set of systematic points located every 25 m along the surveyed transects, which were replicated by the number of days since a snowfall. Thus, the used and available locations were equally biased by (1) the placement of survey transects, and (2) detection bias due to time since a snowfall. A total of 19 258 hare tracks were observed in the northern study area (79.3 km surveyed) and 6973 hare tracks in the southern study area (72.4 km surveyed). The used and available locations were characterized by environmental covariates (Table 1). Resource selection models were estimated using maximum likelihood methods (Lele and Keim 2006) with the final model form and covariates selected using Schwarz Information Criterion (SIC; Schwarz 1978).

Testing the mechanism of resource selection by lynx

We used SIC to determine whether resource selection by lynx is best characterized by hare RSPF (described in *Results*) or by the amount of hare encounters detected along surveyed intervals. The model forms considered in the lynx analysis were the exponential and logistic, the same as those used to estimate resource selection by hare. Used locations in the lynx resource selection models were defined as the 25-m intervals where we observed lynx tracks, and available locations were defined as the 25-m survey intervals. Both the hare RSPF covariate and the amount of hare use covariate were calibrated by number of days since snowfall to account for detection bias. Acknowledging that lynx were likely to select areas containing contiguous

Table 1. Environmental covariates used to derive the snowshoe hare (*Lepus americanus*) resource selection model.

Covariate	Description
Con	Density of coniferous tree (*Picea*, *Pinus*) cover. A density of 1.0 is ~100% coniferous tree cover and a density of 0 contains no or few coniferous trees.
Decid	Density of deciduous tree (*Betula*, *Populus*) cover. A density of 1.0 is ~100% deciduous tree cover and a density of 0 contains no or few deciduous trees.
Terr	A measure of the variance in elevation within a 200 m radius of a site. Variance was standardized across the study area to scale values between −1 (low terrain complexity) and >1 (high terrain complexity).
Shb	Areas dominated by woody vegetation 2–6 m in height.
NV	Areas where dominant vegetation height is <1 m. During the winter study period this represented areas of non-vegetated areas given snow cover.
Con × Terr	Interaction of conifer density and terrain complexity.

Note: Covariates were adapted from vegetation and digital terrain data in northeast Alberta, Canada.

concentrations of hare or hare habitat, we calculated the mean amount of hare track encounters (hare tracks per 25 m per day) and mean probability of hare selection within 250-m intervals of the surveyed transects. We chose a 250-m interval because it accounted for the long daily movements of lynx (Mowat et al. 1999), and it allowed us to measure contiguous concentrations of hare and hare habitat. Although we had a small sample size of lynx tracks ($n = 69$ lynx tracks), because only two variables were considered in each lynx selection model, the sample size was adequate to evaluate the hypothesis that lynx selected for the amount of prey use over prey habitat.

Last we used linear regression to determine how the amount of hare track encounters (hare tracks per 25 m per day) was related to the hare RSPF (mean probability in 250-m intervals) and to study area. This allowed us to assess whether the hare RSPF is a consistent surrogate for predicting amount of use by hare in both study areas and whether difference in the count of hare tracks encountered in each study area could be explained by hare RSPF along the sampled transects.

Results

Resource selection by hare

Our results indicate that the logistic RSPF provides a better estimate of hare selection than the exponential RSF model form. The parameter estimates and standard errors for the final RSPF model are provided in the Appendix. Selection is foremost related to conifer density, a forest resource that provides hare with cover (Orr and Dodds 1982, St-Georges et al. 1995) and forage (Buehler and Keith 1982). Once conifer density is accounted for, selection is best explained by a quadratic relationship with deciduous tree density. This relationship reflects the fact that deciduous trees are selected more if in combination with coniferous tree cover but that pure deciduous stands are less important (Litvaitis et al. 1985). We then found that hare selected locations with moderate amounts of terrain complexity, which in northeast Alberta corresponds to peatland–upland ecotones. The selection of ecotones is consistent with literature that suggests hare use ecotones (Ferron and Ouellet 1992) for cover and access to nearby forage (St-Georges et al. 1995). Once conifer trees, deciduous trees, and terrain complexity were accounted for, hare select for shrub-dominated habitats but avoid non-forested areas. This corresponds well with the understanding that dense shrub cover provides hare with forage (Keith et al. 1984) and shelter from predators (Buehler and Keith 1982). Finally, a positive interaction between conifer density and terrain complexity identifies that hare select for ecotones containing high conifer cover more than other ecotones. When the final model covariates are considered in combination, it is evident that hare select resources based on cover and forage.

Resource selection by lynx

Our results indicate that lynx selection, even after controlling for differences in study area, is much better

Table 2. Schwartz's Information Criterion (SIC) values for candidate models explaining lynx (*Lynx canadensis*) resource selection in boreal Alberta.

Model	Covariates	SIC Logistic RSPF	 Exponential RSF
1	intensity of hare use	−19.47	0.27
2	snowshoe hare RSPF	−16.71	1.08
3	study area	−4.83	−4.83
4	hare RSPF + study area	−8.03	−7.14
5	intensity of hare use + study area	−21.15†	−5.12

Notes: A model with a smaller SIC value is considered to provide a better fit. Covariates for each model are presented in order of relative importance (highest to lowest). The final model selected is indicated by a dagger (†). RSPF is the resource selection probability function; RSF is the resource selection function.

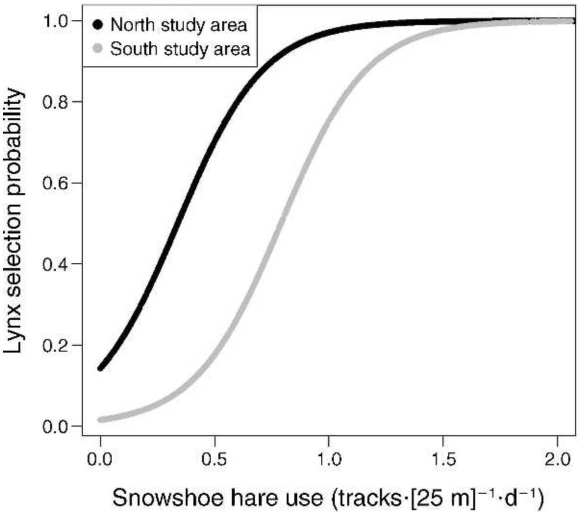

FIG. 1. Estimated relationship between the probability of lynx (*Lynx canadensis*) selection and the average intensity of snowshoe hare (*Lepus americanus*) tracks encountered along 250-m transect intervals in two study areas in northeast Alberta, Canada. The northern study area is associated with lower levels of human development related to oil extraction.

explained by the amount of hare use (SIC = −21.15) than the RSPF of hares (SIC = −16.71) (Table 2). Lynx were found to exhibit strong selection for contiguous areas having $>$1.0 hare tracks·25 m^{-1}·d^{-1}, a result consistent with Squires and Ruggiero (2007) who detected an average of 4.7 hare tracks per 100 m of lynx path in Montana, USA. A strong study area effect remains in the lynx resource selection model (Fig. 1) wherein lynx are more probable to select the northern and less developed study area. The study area effect was considered because the two study areas have varying levels of industrial development and hare resource use.

The amount of hare use (tracks per kilometer per day) is positively related with hare RSPF, but is significantly higher in the northern study area once hare RSPF is accounted for in the sampled transects (Appendix). As is evident by an insignificant interaction term ($P = 0.53$), the relationship between amount of hare use and hare RSPF in the two study areas has similar positive slopes but has different intercept values (Fig. 2). On average there are $\sim$30% more hare tracks in the northern study area than in the southern study area with sampling conducted in otherwise the same types of hare RSPF. This result suggests that the difference in hare use in the two study areas is not explained by the hare RSPF alone but is also affected by hare abundance.

DISCUSSION

Why do lynx select for areas with greater amounts of use by hares more so than hare habitat? Optimal foraging theory predicts that animals should distribute themselves according to energetic gains (Charnov 1976). Because predator fitness is largely driven by the ability to obtain prey, predators should select locations that increase the chance of encountering prey. This leaves predators with two options: select prey habitat (locations that are selected by prey) or locations used by prey. We contend that lynx select for areas that receive higher amounts of use by hares because selecting prey habitat can result in lost opportunity costs when prey is rare or exhibit population cycles. Our results demonstrate that lynx from the northern study area would spend much of their time in low-hare areas if they were to select hare habitat rather than hare use in the southern study area.

Lost opportunity costs arise from the disparity between resource use and resource selection (i.e., amount of use is sensitive to both abundance and selection probability). The disparity between use and selection arising from low or variable abundances has implications for many resource selection studies. If a resource is abundant and noncyclic, species do not need to discriminate between the resource and the habitats selected by the resource. However, if a resource is variable in its abundance or distribution, species must respond to the resource itself. Resource selection studies that approximate resources such as prey availability (Odden et al. 2008), predator availability (Gustine et al. 2006), and competitors (Johnson et al. 2000) using habitat-based covariates will therefore include error associated with any disparity between the amount of resource use and resource selection.

The amount of hare use was lower in the study area containing commercial oil development, while resource selection by hares remained constant in both areas. This suggests that human development may influence abundance but not resource selection for some species, a finding relevant to monitoring studies that employ

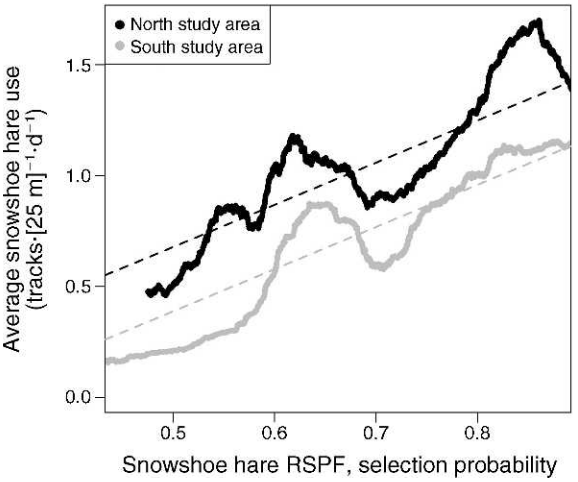

FIG. 2. Relationship between intensity of snowshoe hare tracks and snowshoe hare RSPF (resource selection probability function) encountered along 250-m transect intervals in two study areas. The dashed lines show a significant linear relationship that is provided in the Appendix ($P < 0.001$). The solid lines depict the winter track data smoothed as a moving average function.

resource selection alone. However, because we did not consider covariates related to human development in the RSPF analyses, our data provide only indirect support for this conclusion. Our data also reveal an indirect link that lynx selection is related to the human development levels associated with the two study areas. We contend that additional data on hare and lynx abundances with mechanistic relationships linking both abundance metrics (e.g., population demographics, recruitment, survival, mortality rates) and resource selection to human development factors are required to test these inferences.

Our study indicates that prey habitat cannot be assumed to represent the amount of habitat use by prey (prey availability). Although this assumption may lead to spurious conclusions and poor management, it is important to recognize the value of surrogate measures. At present we cannot reliably extrapolate prey availability or predation risk across a landscape. However, the ability to extrapolate resource selection models across a landscape allows ecologists to prioritize conservation areas, plan development activities, and stratify monitoring effort. We therefore recommend that ecologists obtain prey availability data (e.g., amount of prey use) for predator studies (and predation risk data for prey studies) and either estimate selection based on prey availability or, in cases where spatial extrapolation is desired, estimate selection based on prey habitat only after characterizing the relationship between prey habitats and amount of use.

Predators likely select areas where prey are not only more abundant, but also easier to capture (Andruskiw et al. 2008). Our study focuses on how two measures of hare availability influence resource selection by lynx. A logical next step specific to our study is to consider the effects of hare use and vulnerability to capture as it relates to lynx selection. Understanding how predator use and selection is related to both prey use and vulnerability may have valuable consequences for management. For example, managers may be able to conserve prey populations by altering resource conditions to reduce prey vulnerability. However, if the amount of use by the predator is low (which we demonstrate cannot be presumed from selection, alone), managers will become aware that this strategy may have no effect on conserving prey populations and consider alternate strategies.

In a broader context, resource selection studies should be coupled with mechanistic data (e.g., metrics of diet, forage, fitness, or abundance [Buskirk and Millspaugh 2006]). Lima and Zollner (1996) argue that our ability to develop meaningful models is restricted by a limited understanding of behavioral mechanisms. Nevertheless, most resource selection studies continue to base ecological interpretation solely on a standard of plausibility (Lima and Zollner 1996). Recent studies have demonstrated that combining resource selection studies with information on life requisites and fitness metrics can inform wildlife conservation and management by providing additional insight into the mechanisms and consequences of resource selection (Aldridge and Boyce 2007, McLoughlin et al. 2008, Mosser et al. 2009; S. K. Wasser, J. L. Keim, M. L. Taper, and S. R. Lele, *unpublished manuscript*). The value in incorporating information on life requisites and fitness metrics cannot be overstated. When considered in isolation, a resource selection model from northeast Alberta suggests that woodland caribou (*Rangifer tarandus caribou*) avoid human activity. However, when combined with hormone data, the same model reveals a cause–effect relationship between human activity, habitat selection strategy, and two fitness metrics (S. K. Wasser, J. L. Keim, M. L. Taper, and S. R. Lele, *unpublished manuscript*). In light of these studies and our own results, we recommend that resource selection studies include or be corroborated by independent mechanistic data. We recognize that wildlife studies are often limited by logistics and finances and that independent data are not always available. In the absence of data, we suggest that researchers support the results of resource selection analyses with mechanistic explanations and a description of assumptions to provide direction for future study.

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APPENDIX

Parameter values and results for snowshoe hare resource selection probability function (RSPF) and a linear model relating the intensity of snowshoe hare tracks with snowshoe hare RSPF (*Ecological Archives* A021-047-A1).