

Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests

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Summary

1. The selection for particular habitat patches can vary as a function of local and regional levels of anthropogenic disturbance. Although such functional responses can better reveal habitat loss for species of precarious status faced with dwindling resources, they remain rarely used in conservation planning. We show that functional responses can occur at multiple levels, even as nested hierarchies, and that they can explain the plasticity in habitat selection observed in threatened forest-dwelling caribou *Rangifer tarandus caribou*, within and among home-ranges.

2. Twenty-seven caribou were followed with global positioning system collars between 2005 and 2010. Generalized linear mixed models served as the basis from which we built multi-level functional responses characterizing how caribou alter their selection for closed-canopy conifer forests, depending upon the availability of these forests and the amount of cutovers and roads.

3. Caribou increased their selection for closed-canopy conifer forests in areas of their home-range that were comprised of a high proportion of recent cutovers during calving and summer and of high closed-canopy conifer forests during winter. Also, caribou that were established in highly disturbed areas displayed an overall stronger selection for conifer forests. These individuals further adjusted their selection for conifer forests in areas of their home-ranges that were largely comprised of recent cutovers. This concurrent response to local and global anthropogenic disturbances provides evidence of nested-hierarchical functional responses.

4. *Synthesis and applications.* Reliable characterization of disturbance effects on animals is necessary for conservation planning. Multi-level functional responses can accurately describe animal distribution, and we provided a framework for modelling these responses. Our multi-level functional responses indicate that fixing habitat requirements based on patterns of habitat selection for the average amount of disturbance can be misleading because it overlooks plasticity in the response of animals to habitat heterogeneity. For example, selection of closed-canopy conifer forests by caribou generally became stronger with increasing disturbance levels. Anthropogenic disturbance thus could not only lead to the functional loss of residual habitat, but it can also increase the 'relative value' of residual patches. Our study provides a tool for more thorough assessments of spatial variation in the attractiveness of resource patches and, presumably, in the fitness benefits.

Key-words: boreal forest, cutovers, generalized linear mixed model, habitat selection, nested-hierarchical functional response, resource selection function

Introduction

The long-term fitness of forest-dependent species in landscapes that have been fragmented by anthropogenic disturbance depends on resource acquisition trade-offs, which are generally

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contingent upon landscape structure and composition (Moody, Houston & McNamara 1996). In human-wildlife relationships, it can be difficult to accommodate cost-benefit trade-off responses in animals when there are gradients of anthropogenic activity across the habitat attributes that they use (Hebblewhite & Merrill 2008). Yet the development of effective strategies to mitigate human impacts on wildlife requires an understanding of the factors that influence spatial distribution, such as predation risk or anthropogenic disturbances (Kramer-Schadt *et al.* 2004; Courtois *et al.* 2007; Courbin *et al.* 2009; Houle *et al.* 2010). Habitat selection studies can provide such information.

Habitat selection is the disproportionate use of different land cover types in relation to their availability in the landscape (Johnson 1980). This selection may be subject to a functional response, whereby the selection for a specific habitat attribute changes as a function of its abundance in the landscape, or as a function of the abundance of other landscape features, such as anthropogenic disturbance (Mysterud & Ims 1998; Hebblewhite & Merrill 2008; Houle *et al.* 2010). Generally, functional response is studied at only one of two levels: within home-range (within-HR level) or among (inter-HR level) home-ranges. Most functional responses that have been described to date have assessed changes in the selection among individuals as a function of variation in home-range characteristics, that is, at an inter-HR level (Mysterud & Ims 1998; Gillies *et al.* 2006; Hebblewhite & Merrill 2008; Herfindal *et al.* 2009; Houle *et al.* 2010). However, individuals can also display within-HR level functional responses by altering their selection based on the local abundance of habitat attributes (Houle *et al.* 2010). The level of investigation, therefore, can be highly relevant to inferring animal spatial dynamics because habitat selection strategies may rely on different criteria at different levels (Senft *et al.* 1987), depending on the scales of variation in limiting factors.

Moreover, there can be strong variation among individuals in terms of their within-HR level functional responses, and part of this variation may be explained by differences in home-range characteristics. For example, individuals may alter their selection for a particular forest cover type following local variations in road density, and thus, the strength of this within-HR functional response may be less important for an individual whose home-range is characterized by high overall road density than for another living in a largely pristine environment. Such nested-hierarchical functional responses have yet to be evaluated but may nevertheless be fundamental to improving our understanding of animal spatial dynamics in rapidly changing environments.

There is an increasing interest in quantifying functional responses in habitat selection for ecosystem management and wildlife conservation (Fortin *et al.* 2008; Hebblewhite & Merrill 2008; Herfindal *et al.* 2009; Houle *et al.* 2010). These models are indeed useful because they can provide more accurate depictions of animal distributions in heterogeneous and dynamic environments (Houle *et al.* 2010). Moreover, functional responses in habitat selection can also serve as

behavioural indicators of changes in the habitat quality – and perhaps even more so for endangered or threatened species. As a population decreases, the reduction in competitive interactions should enable individuals to achieve highest fitness by occupying only the best resource or habitat patches (McLoughlin *et al.* 2010). Habitat selection can provide, therefore, a particularly clear picture of high quality patches for populations occurring at low density, such as those of endangered or threatened species. Moreover, the reason why these species become threatened in the first place is often linked to habitat loss (Kuussaari *et al.* 2009), and a decrease in the availability of certain types of habitat patches can also increase their selection by changing the cost-benefit trade-offs of using those patches (Mysterud & Ims 1998). For example, a decrease in the availability of certain patches may increase predation risk or may reduce food availability, thereby increasing the spatial association of individuals with some habitat components. Functional responses can thus become particularly useful for assessing habitat loss for species of precarious status faced with dwindling resources because of human development. Nonetheless, functional responses have yet to find the place they deserve in the toolkit of wildlife managers and conservationists.

We tested whether forest-dwelling woodland caribou *Rangifer tarandus caribou* Gmelin displayed multi-level functional responses in their selection of closed-canopy mature conifer forests, given variations in the abundance of these forests and of anthropogenic features. This information should delineate more clearly the functional loss of habitat because of human activities. Forest-dwelling caribou are considered to be threatened in Canada (Thomas & Gray 2002), and the decline of their populations seems closely linked to energy development and forest harvesting (Schaefer 2003; Cameron *et al.* 2005; Courtois *et al.* 2007). In the case of timber harvest, caribou compete with the industry for closed-canopy mature conifer forests: caribou use those forests to reduce predation risk and to search for food (e.g. arboreal lichens), while industry harvests conifers for their economic value. Our study demonstrates the conservation relevance of assessing multi-level functional responses to explain the spatial dynamics and to evaluate the functional loss of habitat patches for threatened animal populations confronted with human-induced habitat loss.

Materials and methods

STUDY AREA

The study area (50°10'–51°55'N, 68°20'–70°40'W) covers 60 674 km² and is located in the Côte-Nord region, Québec, Canada. This area is dominated by dense coniferous stands of black spruce *Picea mariana* (Mill.) Britton, Sterns & Poggenburg and balsam fir *Abies balsamea* (L.) Mill., interspersed with stands of trembling aspen *Populus tremuloides* Michaux, white or paper birch *Betula papyrifera* Marsh., and jack pine *Pinus banksiana* Lamb. Mean daily temperature ranges from –23 °C in January to 14 °C in July. Mean annual precipitation is 715 mm, with about 36% falling as snow. Caribou density was estimated at 1.9 individuals/100 km² in 2007 (Courbin *et al.* 2009).

CARIBOU TELEMETRY DATA

A total of 27 female caribou were followed between mid-March 2005 and mid-March 2010, with a study duration of 60–1570 days per individual. Caribou were captured by net-gunning triggered from a helicopter and fitted with global positioning system (GPS) collars (3300L; Lotek, Newmarket, ON, Canada) or Argos/GPS collars (TGW3680; Telonics, Mesa, AZ, USA), which took locations every 8 h. On this basis, 100% minimum convex polygons (MCP) were used to define seasonal home-ranges each year. We considered only 2D locations with a horizontal dilution of precision (HDOP) ≤ 10 and 3D locations with a HDOP ≤ 15 , resulting in a precision of ± 25 m (Dussault *et al.* 2001). We obtained a total of 56 447 locations, with an average of 2091 locations per individuals.

PERIODS OF THE YEAR

An algorithm was used to split the year into five distinct periods (Lavielle 2005). Using a minimum penalized contrast, the algorithm detected multiple change-points in our time-series of GPS-location data using means and variances to separate the signals (e.g. displacements of individual caribou by year) into homogeneous sections (see Fig. S1, Supporting information). The breakpoints of the end and beginning of biological seasons were identified from departures in movement rate from the overall mean and variance. We assigned a maximum number of five segments to limit the total number of periods for a year. When the algorithm could not detect changes in means or variances for displacements of a given individual, we defined the related periods based on the mean of all other individuals. For the average individual, the five biological seasons were: spring (24 April–19 May), calving (20 May–4 July), summer (5 July–7 September), rut (8 September–6 December) and winter (7 December–23 April).

HABITAT CHARACTERISTICS

We used Resource Selection Functions (RSF, Manly *et al.* 2002) to characterize habitat selection by comparing habitat characteristics of observed locations with an equal number of locations randomly drawn within the 100% MCP of each caribou for each season. The random locations are used to quantify the availability of the different habitat attributes. Land cover types were characterized at observed and random locations from a single Landsat Thematic Mapper image taken in 2000 with a 25-m resolution grid. The Landsat image was classified into six classes relevant to caribou ecology: closed-canopy mature conifer forest (covering 15% of the study area), open mature conifer forest with lichen (11%), open mature conifer forest without lichen (37%), mixed and deciduous forest (7%), lakes and rivers (11%), and others (11%), which included bush (7%), peatland (<1%), open areas (3%) and unclassified habitat (<1%). Each year, the geographic information system was updated for recent cuts (0–4 years), regenerating cuts (5–15 years) and roads, based on information provided by the local forestry companies. All roads were unpaved forestry roads. We also estimated the local proportions of regenerating and recent cuts, and the local density of roads within a 5-km radius buffers around all locations. Finally, we calculated the overall abundance of anthropogenic disturbance in seasonal home-ranges (100% MCP; Courtois *et al.* 2007; Faillie *et al.* 2010) with ArcGIS 9.3 software (ESRI Inc., Redlands, CA, USA) for each individual, which was specifically used to evaluate inter-home-range functional responses and nested-hierarchical functional responses.

STATISTICAL ANALYSIS

Resource selection function

To model functional responses, we first estimated mixed-effects RSF from the data sets of used and random locations. We considered the same used (coded as 1) and random (coded as 0) locations for all levels of functional responses; the differences among levels come from the use of interaction terms (Functional response at within-home-range level) or of a two-step approach (Functional response at inter-home-range level) or of both (Nested-hierarchical functional response). We thus fit a logistic generalized linear mixed model (GLMM) with a RSF for the i th location of the j th animal in year t of the form:

$$w_{ijt}(\mathbf{x}_{ijt}) = \exp(\boldsymbol{\beta}'\mathbf{x}_{ijt} + \boldsymbol{\gamma}'_{jt}\mathbf{z}_{ijt}), \quad \text{eqn 1}$$

where $\boldsymbol{\beta}$ is the vector of unknown selection coefficients and $\boldsymbol{\gamma}'_{jt}$ depends on the random effects to include in the RSF. For example, if we have covariates x_{1ijt} and x_{2ijt} and wish to have animal-level random intercept and coefficient in front of x_{2ijt} , we set $\boldsymbol{\beta}' = (\beta_0, \beta_1, \beta_2)$, $\mathbf{x}_{ijt}' = (1, x_{1ijt}, x_{2ijt})$, $\boldsymbol{\gamma}'_{jt} = (\gamma_{0jt}, \gamma_{2jt})$ and $\mathbf{z}_{ijt}' = (1, x_{2ijt})$ thus, $w_{ijt}(\mathbf{x}_{ijt}) = \exp\{\beta_0 + \gamma_{0jt} + \beta_1 x_{1ijt} + (\beta_2 + \gamma_{2jt}) x_{2ijt}\}$. In such a model, the selection coefficient β_k represents the mean value of the animal-level random selection coefficients ($\beta_k + \gamma_{kjt}$) in the population. Such mixed-effects models allow RSF inference at animal-specific or at population-averaged levels (Fieberg *et al.* 2010). In this paper, we are mainly interested in subject-specific inferences, because the animal-level random coefficients can reveal heterogeneity among individuals, for example, in their reaction to anthropogenic disturbances. Indeed, the γ_{kjt} random effect represents the difference between animal j 's selection coefficient in year t and β_k , and an estimate of its value, say $\hat{\gamma}_{kjt}$, can be used to assess the functional response. To estimate the selection coefficients and random effects, we used the GLIMMIX procedure of SAS (Version 9.2; SAS Institute, Cary, NC, USA), which can fit GLMM by maximum likelihood using the recommended Gauss-Hermite quadrature. To account for the difference in sample sizes of different individuals and variation in the selection of resources among years because of temporal changes in habitat heterogeneity, such as in human disturbance, we used an 'individual \times year' level random intercept (Gillies *et al.* 2006). To avoid issues of non-independence among observations from different individuals, when >20% of the distances between two individuals of this social species were <200 m, one of these individuals was removed from the analysis. A fourfold cross-validation procedure was used to assess the robustness of the final models (see Boyce *et al.* 2002). More precisely, we randomly kept 75% of the data to fit the model and then used the model to get population-averaged predictions for the remaining 25% of the data. This procedure was repeated 99 times for each RSF, and the mean \bar{r}_s was reported; the higher the \bar{r}_s , the more robust the model.

We considered 12 different model specifications to assess the functional response in relation to anthropogenic disturbance or closed-canopy mature conifer forest (Table 1; Table S1, Supporting information presents the random effect structure of each model). The habitat attributes included in these models have been recognized as key determinants of caribou distribution (Courtois *et al.* 2007, 2008; Fortin *et al.* 2008; Courbin *et al.* 2009). The level of empirical support received by the different candidate models was evaluated based on the Bayesian information criterion (BIC) for each season. Multicollinearity was low in all candidate models (variance inflation factor < 3.25).

Table 1. Structure of candidate mixed-effects resource selection functions of caribou in managed boreal forests. Random effect structure is provided in Table S1 (Supporting information)

No.	Model	Covariates [†]
1	Landscape*	LD
2	Anthropogenic disturbance	LD + RD + PRGC + PRC
3	Road density	LD + RD + PRGC + PRC
4	Recent cut	LD + RD + PRGC + PRC
5	Regenerating cut	LD + RD + PRGC + PRC
6	F.R. road density	LD + RD + PRGC + PRC + Conifer × RD
7	F.R. recent cut	D + RD + PRGC + PRC + Conifer × PRC
8	F.R. regenerating cut	LD + RD + PRGC + PRC + Conifer × PRGC
9	Conifer	LD + PRDM
10	Conifer and anthropogenic disturbance	LD + RD + PRGC + PRC + PRDM
11	F.R. conifer	LD + PRDM + Conifer × PRDM
12	F.R. conifer and anthropogenic disturbance	LD + RD + PRGC + PRC + PRDM + Conifer × PRDM

*Model landscape included: lake, mixed and deciduous forest, open mature conifer with lichen, closed-canopy mature conifer forest, regenerating cut (5–10-years-old), recent cut (<5-years-old), road and other.

[†]PRGC, PRC, PRDM and RD correspond, respectively, to the local (5-km radius buffer) proportion of regenerating, recent cuts and conifer and local road density; LD corresponds to the landscape model; Conifer corresponds to closed-canopy mature conifer forest.

MODELLING FUNCTIONAL RESPONSE

Functional response at within-home-range level

We modelled functional responses at the within-HR level using:

$$w_{jt}(\mathbf{x}_{ijt}) = \exp\{\beta_0 + \gamma_{0jt} + \beta_{\text{Conifer}}x_{\text{Conifer } ijt} + \beta_{\text{Covar}}x_{\text{Covar } ijt} + \beta_{\text{Interaction}}x_{\text{Conifer } ijt}x_{\text{Covar } ijt} + \dots + \beta_n x_{nijt}\}, \quad \text{eqn 2}$$

where $w_{jt}(\mathbf{x})$ is the relative probability of use as a function of covariates x_n and the β s are the mean selection coefficients for the corresponding variables x . γ_{0jt} is the random intercept for animal j in year t . $x_{\text{Conifer } ijt}$ is an indicator variable that takes a value of 1 if location i of animal j for year t is in the closed-canopy mature conifer forest and takes a value of 0 otherwise. $x_{\text{Covar } ijt}$ represents the covariates used to model the functional responses at the within-HR level, that is, the local proportion (5-km radius buffer) of recent cuts, regenerating cuts or closed-canopy mature conifer forests, or the local road density for location i of animal j during the year t . $x_{\text{Conifer } ijt}x_{\text{Covar } ijt}$ is the interaction between the use of closed-canopy mature conifer forest and the local proportion of anthropogenic disturbances (i.e. proportion of recent or regenerating cuts, or local road density) or closed-canopy mature conifer forests for the location i of animal j in year t . This interaction determines whether or not there is a functional response at the within-HR level.

Inter-home-range level and nested-hierarchical functional responses

We estimated both inter-home-range level and nested-hierarchical functional responses based on a two-step procedure (see Matthiopoulos *et al.* (2011) for an alternate approach to assessing functional responses). First, we used GLMMs to estimate conditional (subject-specific) models from which the selection coefficient for a specific habitat attribute could be extracted for each individual. Specifically, to model functional responses at inter-HR level, we included in each model (Table S1, Supporting information), from eqn 1, a random coefficient for the categorical variable closed-canopy mature conifer forest:

$$w_{jt}(\mathbf{x}_{ijt}) = \exp\{\beta_0 + \gamma_{0jt} + (\beta_{\text{Conifer}} + \gamma_{\text{Conifer } jt})x_{\text{Conifer } ijt} + \beta_{\text{Covar}}x_{\text{Covar } ijt} + \beta_{\text{Interaction}}x_{\text{Conifer } ijt}x_{\text{Covar } ijt} + \dots + \beta_n x_{nijt}\}, \quad \text{eqn 3}$$

where $\gamma_{\text{Conifer } jt}$ is the animal j -level random effect associated with the variable x_{Conifer} in year t . The inter-HR level functional response can then be tested by extracting the random coefficients ($\beta_{\text{Conifer}} + \gamma_{\text{Conifer } jt}$) of all individuals, and then testing for linear and curvilinear relationships between these selection coefficients and habitat features (i.e. road density, proportion of cuts or proportion of closed-canopy conifer forests) available overall in individual home-ranges (100% MCP) (Fig. 1a). To model nested-hierarchical functional responses (combining within- and inter-HR levels), we can add to models 6, 7, 8, 11 and 12 (Table S1, Supporting information), a random coefficient in front of some of the interactions between the use of closed-canopy mature conifer forest and anthropogenic disturbances (i.e. either local proportion of recent or regenerating cuts, or road density) or the proportion of closed-canopy mature conifer forests:

$$w_{jt}(\mathbf{x}_{ijt}) = \exp\{\beta_0 + \gamma_{0jt} + (\beta_{\text{Conifer}} + \gamma_{\text{Conifer } jt})x_{\text{Conifer } ijt} + (\beta_{\text{Covar}} + \gamma_{\text{Covar } jt})x_{\text{Covar } ijt} + (\beta_{\text{Interaction}} + \gamma_{\text{Interaction } jt})x_{\text{Conifer } ijt}x_{\text{Covar } ijt} + \dots + \beta_n x_{nijt}\}, \quad \text{eqn 4}$$

where $\gamma_{\text{Interaction } jt}$ is the animal j -level random effect associated with the variable $x_{\text{Conifer}}x_{\text{Covar}}$ for year t . This approach yields the random coefficient ($\beta_{\text{Interaction}} + \gamma_{\text{Interaction } jt}$) needed to assess whether or not the population displays a nested-hierarchical functional response in habitat selection, that is, whether or not the strength of the functional response to local habitat characteristics within HR depends on some overall characteristic of their HR. This would be the case, for example, if all individuals increased their selection of closed-canopy conifer forests in areas (5-km radius buffer) where these forests are abundant, with some caribou responding strongly and others weakly to the local changes in abundance (Fig. 1b). A nested-hierarchical functional response then emerges if those differences in response could be related to differences in home-range

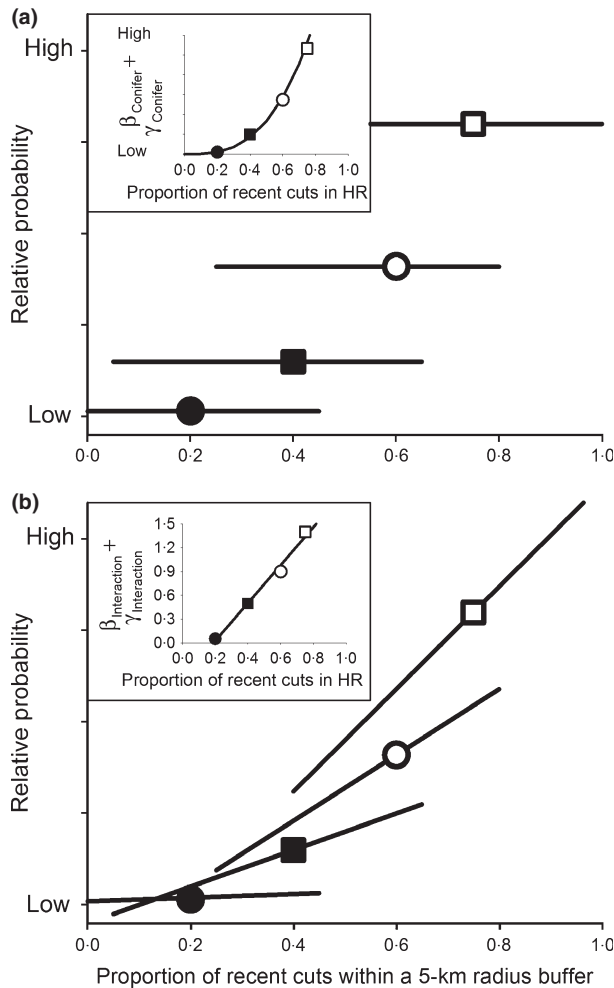


Fig. 1. Example of changes in the relative probability of occurrence in closed-canopy mature conifer forests (x_{Conifer}) as a function of the proportion of recent cut within a 5-km radius buffer for four individuals. (a) The selection coefficient for x_{Conifer} ($\beta_{\text{Conifer}} + \gamma_{\text{Conifer}}$) increase among individuals according to the overall proportion of recent cuts they have in individual home-ranges, which provides evidence of inter-home-range functional response. (b) The selection coefficient for x_{Conifer} increases with the proportion of recent cut within a 5-km radius buffer (within-home-range functional response) for four individuals, and the rate of this increase ($\beta_{\text{Interaction}} + \gamma_{\text{Interaction}}$) is steeper for individuals with home-ranges comprised of a relatively large proportion of recent cuts, which provides evidence of nested-hierarchical functional response.

characteristics among individuals (e.g. global abundance of cuts or closed-canopy mature conifer forests).

Second, we used linear mixed regression (MIXED procedure, Version 9.2; SAS Institute) to test for linear or curvilinear relationships between the random coefficients of each individual [either ($\gamma_{\text{Conifer}}_{ji}$) for inter-HR level assessment or ($\gamma_{\text{Interaction}}_{ji}$) for nested-hierarchical level assessment] and the overall abundance of the focal anthropogenic feature (i.e. road density, or proportion of cuts) or the proportion of closed-canopy mature conifer forests in the home-range of every individual, each year. Whenever appropriate, we used different transformations (e.g. square root) of road density and of the proportion of recent and regeneration cuts to increase model fit. To assess model fit, we calculated the pseudo R -squared statistic defined as the square of the Pearson correlation statistic between marginal predic-

tions and observed values (Vonesh & Chinchilli 1997). We only illustrate relationships with pseudo- $R^2 > 0.10$. Seasonal home-ranges by year with no anthropogenic disturbances were excluded from the linear mixed regression because the response to anthropogenic habitat features (and hence, the random coefficients) could not be estimated.

Results

WITHIN-HOME-RANGE FUNCTIONAL RESPONSE

We found that caribou responded strongly to anthropogenic disturbances. The candidate RSFs receiving the least amount of empirical support at the within-HR level overlooked the response of caribou to cuts and roads (Model 1, Table S2, Supporting information). In contrast, the top-ranking RSFs during calving and summer described a functional response whereby the selection for closed-canopy mature conifer forests varied as a function of local anthropogenic disturbances at the within-HR level (Table S2, Supporting information). Specifically, the functional responses were related to the effect of the local (5-km radius buffer) proportion of recent cuts on the selection for mature forests (Table S2, Supporting information). In winter, the top-ranking model (Model 12, Table S2, Supporting information) accounted for a response of caribou to anthropogenic disturbances, together with changes in their selection for closed-canopy mature conifer forests with changes in the local abundance of those forests. Functional response models performed poorly during the spring and the rut. Instead, the top-ranking RSFs considered that response to closed-canopy mature conifer forests was independent of the proportion of recent cuts (Spring, Model 4, Table S2, Supporting information) and road density (Rut, Model 3, Table S2, Supporting information). Considering that the response to conifer forests was independent of local changes to the relative proportion of recent cuts (Model 4, Table S2, Supporting information), the RSF during calving received nearly as much empirical support as the RSF accounting for the related functional response (Model 7, Table S2, Supporting information).

The top-ranking RSFs revealed that, in all seasons, caribou avoided water bodies, mixed and deciduous forests, regenerating and recent cuts, and roads relative to open mature conifer forests without lichen (Table 2). Open areas with lichen were selected during spring, rut and winter. During calving, caribou also avoided high-road density areas of their home-range (Table 2). The functional responses detected during calving and summer indicated that caribou more strongly selected closed-canopy mature conifer forests in areas with a high local proportion of recent cuts (Fig. 2). For example, the probability of occurrence of caribou during calving was similar or even lower in closed-canopy mature conifer stands than in mixed/deciduous stands or in open mature conifer forest with or without lichen when they were in unlogged landscapes (5-km radius buffer). However, closed-canopy mature conifer stands became selected over all other cover types in landscapes comprised of more than 2% of recent cuts (Fig. 2). During winter, the top-ranking model (Model 12, Table S2, Supporting information) revealed that caribou selected more strongly

Table 2. Selection coefficients and associated standard errors ($\beta \pm \text{SE}$) of the top-ranking resource selection functions for caribou during five biological seasons

Fixed effect	Spring $\beta \pm \text{SE}$	Calving $\beta \pm \text{SE}$	Summer $\beta \pm \text{SE}$	Rut $\beta \pm \text{SE}$	Winter $\beta \pm \text{SE}$
Basic land cover type (dichotomic variable)					
Lake	-1.59 \pm 0.25	-2.48 \pm 0.28	-2.43 \pm 0.17	-2.64 \pm 0.12	-0.84 \pm 0.22
Open with lichen	0.54 \pm 0.13	0.08 \pm 0.15	0.08 \pm 0.09	0.48 \pm 0.08	0.98 \pm 0.10
Mixed or deciduous	-0.27 \pm 0.15	-0.39 \pm 0.12	-0.39 \pm 0.1	-0.50 \pm 0.10	-0.45 \pm 0.14
Conifer*	-0.85 \pm 0.09	-0.34 \pm 0.11	0.01 \pm 0.08	-0.77 \pm 0.07	0.87 \pm 0.35
Regenerating cut	-0.34 \pm 0.33	-3.76 \pm 0.89	-4.54 \pm 0.87	-2.04 \pm 0.50	-2.90 \pm 0.77
Recent cut	-0.01 \pm 0.33	-2.38 \pm 0.20	-3.98 \pm 0.76	-3.39 \pm 0.50	-0.89 \pm 0.43
Road	-0.45 \pm 0.32	-1.81 \pm 0.73	-1.11 \pm 0.42	-1.92 \pm 0.59	-1.43 \pm 0.57
Other	0.43 \pm 0.22	-0.17 \pm 0.21	-0.17 \pm 0.13	0.25 \pm 0.13	0.50 \pm 0.17
Open conifer forest without lichen†	0	0	0	0	0
Proportion or density of land cover types within a 5-km radius buffer					
PRGC ^{0.5}	-0.22 \pm 1.19	3.53 \pm 1.62	-0.76 \pm 1.28	-1.73 \pm 1.05	3.99 \pm 2.30
PRC ^{0.5}	0.21 \pm 0.62	4.15 \pm 2.77	0.83 \pm 1.92	-0.94 \pm 1.48	-2.33 \pm 2.88
PRMD ^{0.5}	—	—	—	—	4.29 \pm 2.89
RD ^{0.5}	-0.62 \pm 2.15	-2.68 \pm 1.10	0.6 \pm 0.65	0.08 \pm 0.64	-0.87 \pm 1.09
Interaction terms for within-home-range functional response					
Conifer \times PRC ^{0.5}	—	1.58 \pm 0.84	1.25 \pm 0.75	—	—
Conifer \times PRMD ^{0.5}	—	—	—	—	-3.42 \pm 0.90
Random effects					
	Variance \pm SE	Variance \pm SE	Variance \pm SE	Variance \pm SE	Variance \pm SE
γ_{0it}	0.66 \pm 0.32	0.72 \pm 0.33	0.16 \pm 0.06	0.36 \pm 0.13	108.59 \pm 196.79
$\gamma_{\text{Conifer } j \times \text{Conifer } ijt}$	0.18 \pm 0.08	0.39 \pm 0.09	0.24 \pm 0.05	0.13 \pm 0.04	2.66E-18 \pm 0.00
$\gamma_{\text{RD } j \times \text{RD } ijt}$	—	—	—	5.08 \pm 1.67	—
$\gamma_{\text{PRC } j \times \text{PRC } ijt}$	134.40 \pm 65.54	89.22 \pm 39.58	55.08 \pm 21.06	—	—
$\gamma_{\text{PRMD } j \times \text{PRMD } ijt}$	—	—	—	—	284.49 \pm 123.21
Random effects for nested-hierarchical functional response					
$\gamma_{\text{Conifer_PRC } j \times \text{Conifer_PRC } ijt}$	—	4.92 \pm 2.46	8.08 \pm 3.62	—	—
$\gamma_{\text{Conifer_PRMD } j \times \text{Conifer_PRMD } ijt}$	—	—	—	—	2.53 \pm 0.59
4-fold: \bar{F}_s (range)	0.67 (0.47–0.95)	0.54 (0.20–0.98)	0.39 (0.18–0.54)	0.87 (0.73–0.93)	0.90 (0.85–0.96)

*Conifer stands for closed-canopy mature conifer forest. PRGC^{0.5}, PRC^{0.5}, PRMD^{0.5} and RD^{0.5} correspond, respectively, to the square root of the local (5-km radius buffer) proportion of regenerating, recent cuts and conifer and local road density.

†Reference category.

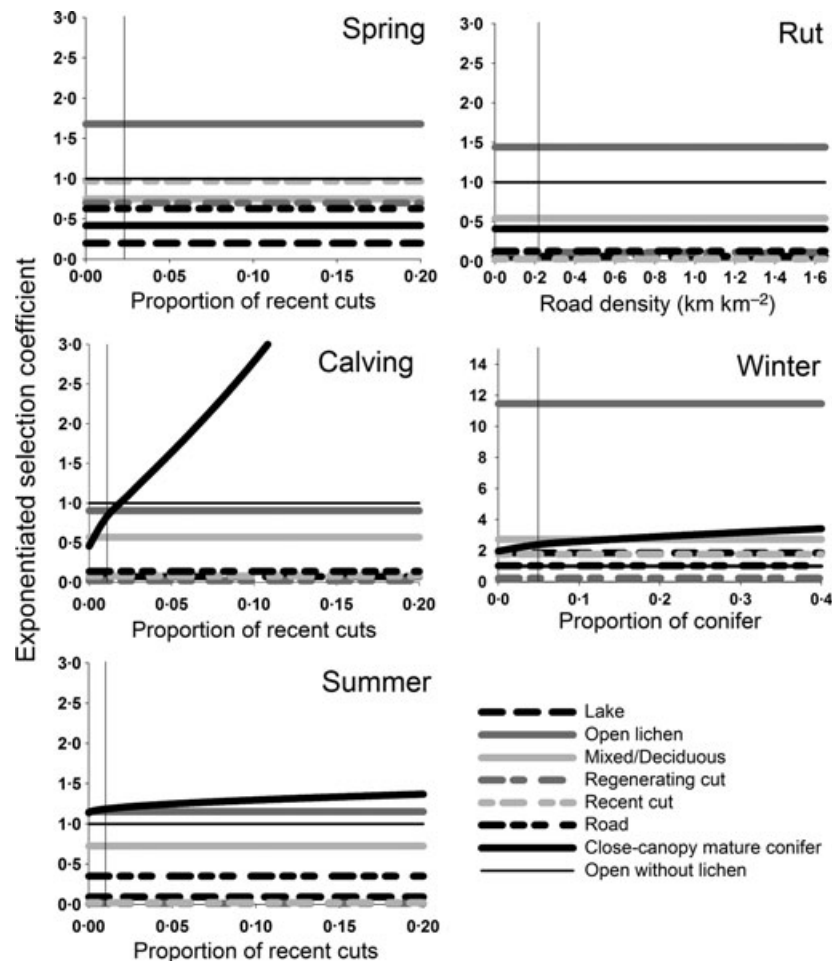


Fig. 2. Within-home-range functional responses in the selection of closed-canopy mature conifer forests as a function of the abundance of recent cuts or close-canopy conifer forests, as estimated from Table 2. The black vertical line corresponds to the mean proportion of recent cuts or the mean road density estimated within 5-km radius buffers.

for closed-canopy mature conifer forests in areas with a high local abundance of these forests (Table 2, Fig. 2).

INTER-HOME-RANGE FUNCTIONAL RESPONSE

We observed strong variation in the selection for closed-canopy mature conifer forests among caribou (Fig. 3). During calving, summer and winter, some of this variation could be explained by differences in the overall abundance of roads and recent cuts among home-ranges. During calving and summer, the selection for closed-canopy mature conifer forests tended to be stronger in home-ranges comprised of a relatively large proportion of recent cuts (Calving: $\text{Pseudo-}R^2 = 0.14$, $P = 0.07$; Summer: $\text{Pseudo-}R^2 = 0.15$, $P = 0.05$, Fig. 3). We did not detect inter-HR functional responses during spring, rut or winter.

NESTED-HIERARCHICAL FUNCTIONAL RESPONSE

We observed strong inter-individual variation in how caribou altered their selection for closed-canopy mature conifer forests, as a function of the spatial distribution of roads and cuts within

their home-range (see Random effects for nested-hierarchical functional response in Table 2). Part of the inter-individual variation in the within-HR level functional response was related to differences in overall availability of anthropogenic disturbances among home-ranges. Nested-hierarchical functional responses were indeed observed during calving and summer. Whereas caribou increased their selection for closed-canopy mature conifer forests in areas of their home-range that were largely comprised of recent cuts during calving (Fig. 2), this response was weaker (i.e. nested-hierarchical functional response) for individuals with home-ranges that were comprised overall of a large proportion of recent cuts than for those living in more pristine environments ($\text{Pseudo-}R^2 = 0.19$, $P = 0.01$, Fig. 3). Thus, the magnitude of the response appeared to depend on the fraction of the home-range disturbed by anthropogenic activity. During summer, the selection for caribou was stronger for closed-canopy mature conifer forests in areas of their home-range that contained a large proportion of recent cuts (Fig. 2), and this response was even stronger (i.e. nested-hierarchical functional response) for individuals that were established in a home-range largely comprised of recent cuts ($\text{Pseudo-}R^2 = 0.18$, $P = 0.02$, Fig. 3).

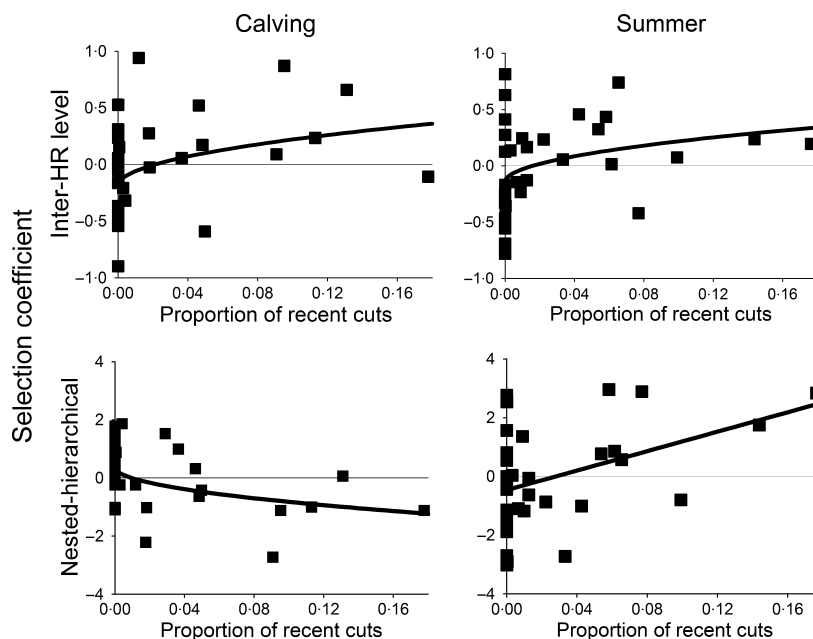


Fig. 3. Inter-home-range level and nested-hierarchical functional responses in the selection of closed-canopy mature conifer forest by caribou, as a function of the overall abundance of recent cuts in individual home-ranges during calving and summer.

Discussion

Our study illustrates the conservation relevance of functional responses for species living in habitats being degraded by human activities. We showed that threatened forest-dwelling caribou altered their selection for closed-canopy mature conifer forests depending on the landscape context, such as the local proportion of closed-canopy mature conifer forests or recent cutovers. Such functional responses provide a more faithful description of the animal-habitat spatial relationship (lower BIC), and they should become basic tools for wildlife managers and conservationists, especially for those dealing with threatened and endangered species. First, functional responses are generally detected whenever tested on various species (e.g. Mysterud & Ims 1998; Hebblewhite & Merrill 2008; Godvik *et al.* 2009; Hansen *et al.* 2009; Herfindal *et al.* 2009; Gillies & St Clair 2010), including threatened ones (e.g. Mauritzen *et al.* 2003; current study). Secondly, threatened and endangered species generally occur at low density, which is when habitat selection should be strongest because of low intraspecific competition (as illustrated in Fig. 1 of McLoughlin *et al.* 2010). Therefore, functional responses can reveal how the value of different land cover types varies for species of conservation concern, given spatio-temporal variations in landscape characteristics. In fact, a promising avenue for those species would be to evaluate how the selection of certain habitat features changes as a function of population size or group size. In this case, the population indices can be directly imbedded into RSFs, and density-dependent changes in the selection could be revealed through interaction terms (McLoughlin *et al.* 2010).

Our study also demonstrates that functional responses can exist at multiple levels, including as nested hierarchies. Many studies have characterized functional responses in habitat

selection at the inter-HR level (e.g. Mysterud & Ims 1998; Fortin *et al.* 2008; Godvik *et al.* 2009; Hansen *et al.* 2009; Herfindal *et al.* 2009; Gillies & St Clair 2010; Houle *et al.* 2010). We also observed such functional responses in caribou during calving and summer. For example, closed-canopy mature conifer forests were selected during calving and summer by caribou with home-ranges that contained > 2.5% of recent cuts. Below this threshold, however, caribou tended to use these conifer stands less than would be expected randomly. Roads and cuts are generally associated with greater risk for caribou. Indeed, wolves *Canis lupus* tend to increase their selection for recent cutovers in landscapes where these cuts are most abundant (Houle *et al.* 2010). Consistently, the probability of caribou mortality generally co-varies with the level of anthropogenic disturbance in their home-range (Courtois *et al.* 2007). The functional responses indicate that closed-canopy forests become more prized as the level of anthropogenic disturbance increases, perhaps because of the protective cover they can provide.

Only a few studies have characterized functional responses to spatial heterogeneity within home-ranges (e.g. Houle *et al.* 2010 on wolves). During calving and summer, caribou selected closed-canopy mature conifer forests more strongly in areas of their home-range largely comprised of recent cuts. As with functional responses at the inter-HR level, caribou responded to local increases in anthropogenic disturbances within their home-range by making stronger use of closed-canopy forest stands. These functional responses demonstrate the value of considering multi-level heterogeneity in habitat attributes to characterize animal distributions more faithfully in complex landscapes.

Our study further demonstrates that functional responses in habitat selection occurred simultaneously at two nested levels. Although the value of hierarchy in habitat selection has been

well-established (Johnson 1980; Senft *et al.* 1987), hierarchical processes have remained essentially ignored in the context of functional responses. Nested-hierarchical functional responses occur when the strength of within-home-range functional responses varies among individuals, depending on the overall characteristics of their home-ranges. In summer, for example, the increase in the selection for closed-canopy mature conifer forests in areas that were largely comprised of recent cuts was stronger for individuals with home-ranges that, overall, had been highly disturbed by forest harvesting. The strength of within-home-range functional response thus may vary among individuals, according to the overall level characteristics of their home-ranges. Further, we found that the nature of the nested-hierarchy functional response differed strongly during the course of the year. During the calving season, caribou tended to avoid closed-canopy mature conifer forests in locally disturbed areas, an avoidance that was even stronger for individuals occupying highly disturbed home-ranges. Caribou generally abandon logged areas (Chubbs *et al.* 1993; Smith *et al.* 2000; Courtois *et al.* 2008; Faille *et al.* 2010). Individuals that decide to maintain their home-range location despite anthropogenic activities appeared to be less sensitive to anthropogenic disturbance (cutovers) during calving. The fitness consequences of this behaviour are unclear and, perhaps, maladaptive.

MANAGEMENT IMPLICATIONS

The persistence of forest-dwelling caribou populations is precarious across North America (Courtois *et al.* 2008), and management strategies could benefit from a reliable description of habitat selection patterns. Current habitat selection models, however, often present conflicting observations (Osco *et al.* 2004). For example, many studies have reported a stronger selection of closed-canopy mature conifer forest (Chubbs *et al.* 1993; Courtois *et al.* 2004; Ferguson & Elkie 2004; Fortin *et al.* 2008), as it provides protective cover against predators (Gustine *et al.* 2006). In contrast, Courbin *et al.* (2009) reported an avoidance of closed-canopy conifer forests, relative to more open conifer forest, during most of the year. None of these studies have examined the impact of anthropogenic disturbances or the availability of conifer forests on the selection of caribou for forest cover through functional response analysis. Multi-level functional responses could reconcile conflicting observations among field studies: the response of caribou to conifer forests depends on the spatial context, and these forests tend to be more strongly selected in highly disturbed landscapes but are used less than would be expected randomly in more pristine environments. We showed that selection for forest cover within and among home-ranges can be explained by the level of anthropogenic disturbance in home-ranges. Functional responses in habitat selection can serve as behavioural indicators of changes in the habitat quality for endangered or threatened species. Functional responses can thus become particularly useful for assessing habitat

loss for species of precarious status faced with dwindling resources because of human development.

Multi-level functional responses can offer insights into the role of residual habitat patches in landscapes that have been fragmented by anthropogenic activities. These statistical models underscore subtle, yet important, spatial differences in the selection of resource patches that are linked to spatial heterogeneity at multiple levels. Our study thus warns about fixing habitat requirements based on patterns of habitat selection for the average level of disturbance. Our study indicates that, while closed-canopy conifer forests might not be critically important in largely pristine landscapes, the ecological importance of these forests for forest-dwelling caribou seems to increase with the level of disturbance. Consideration of such differences may reflect spatial changes in the trade-off between food acquisition and risk avoidance, and as such, they should be considered in management plans, especially when the conservation of threatened or endangered species is at stake.

Acknowledgements

Financial support was provided by the NSERC-Sylviculture and Wildlife Research Chair, and the Ministère des Ressources naturelles et de la Faune of Quebec. We thank the editor, Carolyn Nerserian and William Parsons for comments on the paper. We also thank Laurier Breton, Bruno Rochette, Denis Gay, Bruno Baillargeon, Dominic Grenier, Daniel Dorais and Jean-Yves Lacasse for their help in the field.

References

- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.
- Cameron, R.D., Smith, W.T., White, R.G. & Griffith, B. (2005) Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. *Arctic*, **58**, 1–9.
- Chubbs, T.E., Keith, L.B., Mahoney, S.P. & McGrath, M.J. (1993) Responses of woodland caribou (*Rangifer tarandus caribou*) to clear-cutting in east-central Newfoundland. *Canadian Journal of Zoology*, **71**, 487–493.
- Courbin, N., Fortin, D., Dussault, C. & Courtois, R. (2009) Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landscape Ecology*, **24**, 1375–1388.
- Courtois, R., Ouellet, J.P., Dussault, C. & Gingras, A. (2004) Forest management guidelines for forest-dwelling caribou in Quebec. *The Forestry Chronicle*, **80**, 598–607.
- Courtois, R., Ouellet, J.P., Breton, L., Gingras, A. & Dussault, C. (2007) Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*, **14**, 491–498.
- Courtois, R., Gingras, A., Fortin, D., Sebbane, A., Rochette, B. & Breton, L. (2008) Demographic and behavioural response of woodland caribou to forest harvesting. *Canadian Journal of Forest Research*, **38**, 2837–2849.
- Dussault, C., Courtois, R., Ouellet, J.P. & Huot, J. (2001) Influence of satellite geometry and differential correction on GPS location accuracy. *Wildlife Society Bulletin*, **29**, 171–179.
- Faille, G., Dussault, C., Ouellet, J.-P., Fortin, D., Courtois, R., St-Laurent, M.-H. & Dussault, C. (2010) Range fidelity: the missing link between caribou decline and habitat alteration? *Biological Conservation*, **143**, 2840–2850.
- Ferguson, S.H. & Elkie, P.C. (2004) Habitat requirements of boreal forest caribou during the travel seasons. *Basic and Applied Ecology*, **5**, 465–474.
- Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S. & Frair, J.L. (2010) Correlation and studies of habitat selection: problem, red herring, or opportunity? *Philosophical Transactions of the Royal Society B*, **365**, 2233–2244.
- Fortin, D., Courtois, R., Etcheverry, P., Dussault, C. & Gingras, A. (2008) Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. *Journal of Applied Ecology*, **45**, 1392–1400.

- Gillies, C.S. & St Clair, C.C. (2010) Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology*, **47**, 182–190.
- Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E. & Jerde, C.L. (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887–898.
- Godvik, I.M.R., Loe, L.E., Vik, J.O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, **90**, 699–710.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006) Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, **165**, 1–32.
- Hansen, B.B., Herfindal, I., Aanes, R., Saether, B.E. & Henriksen, S. (2009) Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. *Oikos*, **118**, 859–872.
- Hebblewhite, M. & Merrill, E. (2008) Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, **45**, 834–844.
- Herfindal, I., Tremblay, J.P., Hansen, B.B., Solberg, E.J., Heim, M. & Saether, B.E. (2009) Scale dependency and functional response in moose habitat selection. *Ecography*, **32**, 849–859.
- Houle, M., Fortin, D., Dussault, C., Courtois, R. & Ouellet, J.P. (2010) Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. *Landscape Ecology*, **25**, 419–433.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.
- Kramer-Schadt, S., Revilla, E., Wiegand, T. & Breitenmoser, U. (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, **41**, 711–723.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Ockinger, E., Partel, M., Pino, J., Roda, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution*, **24**, 564–571.
- Lavielle, M. (2005) Using penalized contrasts for the change-point problem. *Signal Processing*, **85**, 1501–1510.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd edn. Kluwer, Dordrecht, the Netherlands.
- Matthiopoulos, J., Hebblewhite, M., Aarts, G. & Fieberg, J. (2011) Generalized functional responses for species distributions. *Ecology*, **92**, 583–589.
- Mauritzen, M., Belikov, S.E., Boltunov, A.N., Derocher, A.E., Hansen, E., Ims, R.A., Wiig, O. & Yoccoz, N. (2003) Functional responses in polar bear habitat selection. *Oikos*, **100**, 112–124.
- McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010) Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, **79**, 4–12.
- Moody, A.L., Houston, A.I. & McNamara, J.M. (1996) Ideal free distributions under predation risk. *Behavioral Ecology and Sociobiology*, **38**, 131–143.
- Mysterud, A. & Ims, R.A. (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology*, **79**, 1435–1441.
- Osco, T.J., Hiltz, M.N., Hudson, R.J. & Wasel, S.M. (2004) Moose habitat preferences in response to changing availability. *The Journal of Wildlife Management*, **68**, 576–584.
- Schaefer, J.A. (2003) Long-term range recession and the persistence of caribou in the taiga. *Conservation Biology*, **17**, 1435–1439.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987) Large herbivore foraging and ecological hierarchies. *BioScience*, **37**, 798–799.
- Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C. & Hervieux, D. (2000) Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. *Canadian Journal of Zoology*, **78**, 1433–1440.
- Thomas, D.C. & Gray, D.R. (2002) COSEWIC assessment and update status report on the woodland caribou, *Rangifer tarandus caribou*, in Canada. *COSEWIC Committee on the Status of Endangered Wildlife in Canada*, pp. 1–98. Environment Canada, Ottawa, ON, Canada.
- Vonesh, E.F. & Chinchilli, V.M. (1997) *Linear and Nonlinear Models for the Analysis of Repeated Measurements*, pp. 419–424. Marcel Dekker, New York.

Received 22 August 2011; accepted 22 March 2012

Handling Editor: Mark Hebblewhite

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Example of temporal representation of the year for an individual, divided into five distinct periods, using an algorithm detecting homogenous periods that is based on variation in movement means and variances.

Table S1. Random effect structure of candidate mixed-effects resource selection functions of woodland caribou in managed boreal forests of the Côte-Nord region, Québec (Canada).

Table S2. Relative support of candidate resource selection functions (see Table 1 for description) for woodland caribou in Québec (Canada), during each of the five biological seasons.

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