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RESEARCH ARTICLE

Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest

Mélina Houle · Daniel Fortin · Christian Dussault · Réhaume Courtois · Jean-Pierre Ouellet

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Abstract Forest harvesting involves the creation of roads and cutblocks, both of which can influence animal habitat use. We evaluated the cumulative effects of forestry on habitat selection by six packs of gray wolf (*Canis lupus*) widely distributed in Quebec's boreal forest. Resource selection functions were used to evaluate cumulative effects at two levels. First, we studied how the response of wolves to roads and cutblocks varied within their home range (HR level) as a function of the local abundance of these habitat features. Second, we assessed whether differences in the response to roads and cutblocks observed among packs (inter-HR level) could be explained by variations in their average abundance among individual home ranges. At the HR level, we found that cumulative effects shaped habitat selection of wolves, and the nature of the effects varied during the year. For example, we detected a decrease in the selection of roads following an increase in local road density during the rendez-vous and the nomadic periods, but not during the denning period. At the inter-HR level, we found a functional response to logging activity only during the denning period. Packs with home ranges characterized by a larger proportion of recent cutblocks selected these cutblocks more strongly. We conclude that cumulative effects of logging activities occur at multiple levels, and these effects can have profound effects on habitat use by wolves, thereby influencing spatial predator–prey dynamics. Wildlife conservation and management in boreal ecosystems should thus account for cumulative impacts of anthropogenic features on animal distribution.

Keywords Cutblocks · Cumulative effects · Habitat selection · Forestry · Mixed effects logistic regression · Predators · Roads · Resource selection functions · Wolves

M. Houle · D. Fortin (✉)
Chaire de recherche industrielle CRSNG-Université Laval en sylviculture et faune, Département de biologie, Université Laval, 1045, Av. de la Médecine, pavillon Alexandre Vachon, Quebec, QC G1V 0A6, Canada
e-mail: Daniel.Fortin@bio.ulaval.ca

C. Dussault
Ministère des Ressources naturelles et de la Faune, Service de la faune terrestre et de l'avifaune, 880, chemin Sainte-Foy, Quebec, QC G1S 4X4, Canada

R. Courtois
Ministère des Ressources naturelles et de la Faune, Service de la biodiversité et des maladies de la faune, 880, chemin Sainte-Foy, Quebec, QC G1S 4X4, Canada

J.-P. Ouellet
Département de biologie, chimie et sciences de la santé, Université du Québec à Rimouski, Centre d'études nordiques, Rimouski, QC G5L 3A1, Canada

Introduction

Understanding the impacts of landscape changes on animal populations constitutes a fundamental challenge for wildlife conservation and management. Over the past century, human activities conducted in the boreal forest have resulted in younger forests and an important reduction in wilderness areas, leading to a substantial loss in suitable habitat for many animal species (Reed et al. 1996a; Apps and McLellan 2006; Nielsen et al. 2006; Hakkarainen et al. 2008). Human activities can alter the composition, structure, and function of forest ecosystems (Reed et al. 1996a; Trombulak and Frissell 2000; Saunders et al. 2002). Among the activities currently conducted in the boreal forest, logging constitutes an important threat to biodiversity.

Forest harvesting involves habitat modifications through the development of a road network and the creation of cutblocks. The presence of roads may result in the fragmentation and loss of habitats (Reed et al. 1996a; Saunders et al. 2002), and even cause animal mortality (Trombulak and Frissell 2000). Animals, such as ungulates, commonly avoid roads (Rowland et al. 2000; James and Stuart-Smith 2000; Fortin et al. 2005). On the other hand, roads can facilitate the movements of predators, thereby increasing their hunting efficiency (James and Stuart-Smith 2000; Whittington et al. 2005). But even for predators, human activities along roads may increase the risk of mortality through increased hunting and trapping efforts and collisions with vehicles (Fuller 1989; Cain et al. 2003; Nielsen et al. 2004; Farmer et al. 2006).

The creation of cutblocks also modifies wildlife habitats (Reed et al. 1996b), with direct consequences on predator–prey relationships (Wittmer et al. 2007). The first and most obvious impact of logging activities is the removal of mature forest stands (Boucher et al. 2009). As vegetation regenerates in cutblocks, species such as moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) may benefit from an increase in browse availability (Newbury and Simon 2005; Potvin et al. 2005a). Moreover, edges of cutblocks often support diverse animal communities because they offer interspersion between food and protective cover (Dussault et al. 2005; Vospernik and Reismoser 2008). Predators often use edges between open areas and forest cover to increase hunting efficiency (Oehler and Litvaitis 1996; Dijak and Thompson 2000; Bergman et al. 2006). High edge density created by logging activities could thus result in increased predation risk for prey and improved success for predators (Yahner and Mahan 1997; King et al. 1998; Farmer et al. 2006).

The recent increase in human activities in forest ecosystems has given rise to cumulative land use effects. Cumulative effects occur when the joint effects of features in close proximity are greater or less than the influence of either of the features alone (Riffell et al. 1996). The impact of a given habitat feature may vary, for example, as a function of its density in the landscape. Responses to cumulative effects of anthropogenic features have been reported for many species (Mace et al. 1996; Bayne et al. 2005; Johnson et al. 2005; Linke et al. 2005). For example, seismic lines affect ovenbirds (*Seiurus aurocapilla*) only once they reach a threshold density of 8.5 km/km^2 (Bayne et al. 2005). Grizzly bears (*Ursus arctos*) avoid landscapes with road density exceeding 6 km/km^2 (Mace et al. 1996). The accuracy of predictions about animal responses to human-altered landscapes depends on our understanding of individual and cumulative effects of human activities.

Cumulative effects are generally assessed among individual home ranges (e.g., Hebblewhite and Merrill 2008), whereby the plasticity in habitat selection observed among animals is linked to differences in home range characteristics. Habitat selection is recognized as a multi-scale (Thompson and McGarigal 2002; Johnson et al. 2004; Thogmartin and Knutson 2007; Romero et al. 2009) and multi-level (Bailey et al. 1996; Cushman and McGarigal 2002; Fortin et al. 2003) process. Accordingly, cumulative effects may have repercussions at multiple hierarchical levels. The selection of a given individual may also vary within its home range, depending on the local availability of specific habitat features. The hierarchical nature of cumulative effects remains poorly documented.

Wolves are at the apex of the food chain in boreal ecosystems. The populations of many herbivores are limited, and even regulated by wolves (Messier 1994; Ripple and Beschta 2007). Yet, few studies have evaluated the role of forest harvesting on wolf habitat selection (e.g., Kohira and Rexstad 1997; Kunkel and Pletscher 2000; Kuzyk et al. 2004). The response of wolves to roads is expected to vary as a function of road density (Mladenoff et al. 1995). Roads may be used to facilitate movements at low density, but such benefits may be outweighed by the frequent encounters with humans when roads become abundant

(Mech et al. 1988; Mladenoff et al. 1995; Whittington et al. 2005). Little is known about the effects of logging activities on habitat selection of wolves in the boreal forest, and even less about the cumulative effects of roads and cutblocks on their spatial dynamics. Cumulative effects of roads and cutblocks can be expected to reduce habitat suitability (McGarigal et al. 2001). Human encounters can be more frequent when roads become more abundant (Mladenoff et al. 1995) and areas having a high degree of fragmentation resulting from cutblocks can reduce hunting opportunities, potentially resulting in predators avoiding the area (Potvin et al. 1999). Cumulative effects of roads and cutblocks may therefore have important implications for predator–prey interactions, and the recent acceleration of landscape changes due to forest harvesting provides an incentive to clarify cumulative effects of anthropogenic activities on wolves in the boreal forest.

Our objective was to investigate whether logging activities have cumulative effects on habitat use by gray wolves in the boreal forest within and among home ranges. Specifically, we assessed multi-level cumulative effects by examining functional responses associated with the selection of roads and cutblocks during different periods of the year.

Methods

Study area

The study focused on the habitat selection of six wolf packs. Home ranges were located as far as 500 km apart and over an area covering 10,000 km^2 of boreal forest (i.e., from 47°71′ to 51°41′ N and 68°45′–71°25′W) in the province of Quebec, Canada. They thus covered a broad range of habitat attributes (Table 1). Packs were located in heterogeneous mosaics of mature and regenerating stands resulting from fire and logging activity. Black spruce (*Picea mariana*), balsam fir (*Abies balsamea*) and jackpine (*Pinus banksiana*) were the main tree species. Areas at low altitudes and in river valleys were also covered with mixed and deciduous stands, comprised mostly of paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), yellow birch (*B. alleghaiensis*) and maples (*Acer* spp.). Forest harvesting history also varied broadly among wolf packs (Table 1), which was favorable for the evaluation of cumulative effects. Logging operations created a road network across most of the landscape (Table 1). Major land use activities included logging, non-motorized outdoor recreation (hiking, camping, and fishing), off-road vehicle use (snowmobiles, all-terrain vehicles), recreational hunting, and commercial trapping. The topography was gently rolling with many hills rising from 250 to 1,100 m above the sea level. Snow began to accumulate in early November, reaching a maximum depth of >2 m in mid-March. Snow persisted until early June under forest canopy. Mean daily temperatures ranged from −23°C in January to 19°C in July. Moose, caribou (*Rangifer tarandus*), and black bear (*Ursus americanus*) were the other large mammals found in the study area. White-tailed deer (*Odocoileus virginianus*) were absent from most of the study area.

Table 1 Range of percent composition of land cover types for the six home ranges considered in the analysis of habitat selection by gray wolves in Quebec, Canada, 2005–2007

Variable	Land cover type	Description	Range
Open	Open area	Wet lands, rock outcrops, burned areas, herbs, bryoids and shrubs	5.5–43.3%
Water	Water	Lakes, reservoirs, rivers, streams	1.4–7.2%
Lichab	Conifer with lichen	>20% ground cover or one-third of total vegetation must be lichen	0.2–12.9%
Conif	Conifer	>60% crown closure; coniferous trees are >75% of total basal area	4.6–29.0%
Openconif	Open conifer	10–60% crown closure; coniferous trees represent >75% of total basal area	1.0–44.2%
DecMix	Deciduous-Mixed	Deciduous and coniferous trees represent ≤25% of total basal area	6.4–66.5%
Cut_5	Regenerating cutblock	Cutblock 5–15 years old	0.1–14.2%
Cut_0	Recent cutblock	Cutblock <5 years old	0.7–5.1%
Road	Road	Maintained and logging roads	0.1–7.7 km/km^2

Wolf telemetry program

A total of 11 wolves (six males, five females) that belonged to six packs were monitored with Global Positioning System (GPS) radiocollars (model GPS3300SW, Lotek Engineering Systems, Newmarket, Ontario). One to three wolves were captured in each pack by net-gunning from a helicopter in winter, or using foot-hold traps in summer. Animal locations were taken every 4 h from March 2005 to March 2007. Each pack was radiotracked during an average of 18 months (range: 10–24 months). GPS locations were obtained at the end of the study period by collar retrieval. The success of GPS location acquisition ranged from 77 to 93% per collar, which resulted in a total of 17,906 locations over the 2 years. Using these locations, we calculated the 95% minimum convex polygon (MCP) of each pack from all radio-collared wolves belonging to that pack (McLoughlin et al. 2004; Courbin et al. 2009). Analyses were then restricted to locations falling within the 95% MCPs (i.e., 16,120 GPS locations, with an average of 896 locations per wolf pack per period).

Annual periods

We considered three distinct periods characterize wolf ecology: denning (1 April to 30 June), rendez-vous (1 July to 30 September), and nomadic periods (1 October to 31 March). During the denning period, wolves focus on pup rearing (Jedrzejewski et al. 2001; Mech and Boitani 2003), and movements are characterized by frequent returns to the den. As pups become more mobile (i.e., approximately 2 months after birth), wolves move to rendez-vous sites (Mech and Boitani 2003). The rendez-vous period is characterized by the use of transit areas from which forays are made within the territory. During the nomadic period, the pack moves usually as a unit through the whole territory (Mech and Boitani 2003).

Habitat description

A Geographic Information System (GIS) characterized the study area by land cover types, elevation, slope, hard edge density, and snow depth. Six land cover types were derived from a single Landsat Thematic Mapper image (25-m resolution) (Natural Resources Canada, Canadian Forest Service—Laurentian Forestry Centre, 2000) (Table 1). We used data provided every year by the local forestry companies to characterize and update the spatial distribution of roads (maintained and logging roads), regenerating cutblocks (5–15 years post-harvesting) and recent cutblocks (cuts <5 years). Ground surveys revealed high concordance between field observations and land cover map information (86%, $n = 210$). Roads were linear features assumed to have a 30-m width. We distinguished recent cutblocks from regenerating cutblocks, because they offered different amounts of browse for moose, a major prey of wolves. Regenerating cutblocks should have higher browse biomass than recent cutblocks (Courtois et al. 1998). We used a 25-m digital elevation model (DEM) to estimate elevation (range: 150–1,100 m) and slope (range: 0°–77°). We calculated the density of hard edges within 1-km radius buffers. We defined hard edges (range: 0–20.9 km/km^2) as any edge between an open area and forest cover (e.g., edge of cutblocks bordering forest stands). To evaluate the cumulative effects of forestry on habitat selection by wolves, we calculated the density of roads (range: 0–8.8 km/km^2) and the proportion of cutblocks (range: 0–0.8 for proportion of regenerating and recent cutblocks) also within 1-km radius buffers around observed and random locations. Spatial analyses were conducted using Hawth's Tools (Beyer 2006) for ArcGIS 9.2 (ESRI 2007).

In winter 2006, we conducted field surveys to model snow depth across all wolf territories. Every 2 or 3 weeks, we estimated snow depth (with a ruler) in open sites, along 53 transects widely distributed within, or close to the wolf home ranges. Snow was sampled every 10 m along the 70-m transects (i.e., $n = 8$ sampling locations per transect). Snow depth maps were created with a 25-m resolution, based on the snow surveys conducted in open sites and using kriging with elevation as an external drift (Tapsoba et al. 2005). We created snow maps for each survey period conducted in open sites by interpolating values of snow depth according to the best variogram retained by cross validation. Analyses were done with the program ISATIS (2007). Snow depth was sampled twice during the winter at 110–160 stations distributed among the nine land cover types (Table 1) to account for the effect of forest canopy on snow accumulation on the ground. We then calculated the proportion of snow depths measured at each station during the surveys of forest sites with snow depth estimated by kriging for open sites. The forested site/open site proportions associated with the various land cover types were then used to reassign values to individual cells, providing snow maps per home range that were adjusted for the influence of forest canopy. Depending on when they occurred, wolf locations and associated random locations were assigned to the appropriate snow survey conducted in open sites to estimate snow depth relevant to those locations.

We validated the resulting maps of snow depth by cross validation. We first calculated the proportion of snow depth found in each land cover type based on 75% of the land cover stations using the map of snow depth estimated by kriging for open sites. We then built a model adjusted for the influence of canopy cover and contrasted predicted snow depth to the withheld 25% of the data. This process was repeated 10 times. Pearson's correlation (r) showed a strong relationship between observed and predicted estimates ($r > 0.69$, $n = 10$). In winter 2007, we only sampled snow depth in open sites every 3 weeks, and created snow maps using kriging with external drift. The map was then adjusted for the influence of canopy cover based on the proportions measured in 2006.

Habitat selection models

We assessed habitat selection using resource selection functions (RSFs). An RSF is a mathematical function that gives a measure proportional to the probability of resource use by an animal (Manly et al. 2002). We estimated RSFs by comparing habitat characteristics at observed (scored 1) and random (scored 0) locations, with a 1:1 ratio between the number of observed and random locations. The function can then be expressed as:

$$w(x) = \exp\left(\beta_0 + \beta_1 x_{1ij} + \ldots + \beta_n x_{nij} + \gamma_{0j}\right), \qquad (1)$$

where $w(x)$ represents the RSF scores, and β_n is the selection coefficient for habitat variable x_n (i designates the observation and j represents the animal), and γ_{0j} is the random intercept for animal j. Random locations for a given individual were drawn within the 95% minimum convex polygon of all radio-collared members of its pack. The approach thus excluded extraterritorial forays, and defined availability based on a spatial domain in which individuals would be most likely to be found. In other words, most locations should fall within home ranges.

Resource selection function coefficients were estimated using a mixed effects logistic regression, with "individuals within packs" as random effects (Hebblewhite and Merrill 2008). RSFs thus accounted for individual variations among members of a pack, as well as among packs (Gillies et al. 2006; Hebblewhite and Merrill 2008). Observed and random locations were characterized by snow depth, slope, density of hard edges and roads, proportion of recent cutblocks and regenerating cutblocks within a 1-km radius buffer, as well as a set of nine dummy variables representing the land cover types, with open conifer forests as the reference category. We used these independent variables to generate eight candidate models (Table 2) specifically designed to evaluate the potential influence of forestry on wolf habitat selection within home ranges (HR level). We first built simple models that accounted for the effects of natural and anthropogenic habitat features (i.e., models that only included main effects). We then built more complex models that also accounted for cumulative effects by including interaction terms between the use of anthropogenic features (roads and cutblocks) and their local abundance. The level of empirical support received by the different candidate models was evaluated based on the Bayesian information criterion (BIC). BIC is less likely than the Akaike information criterion (AIC) to favor complex models (i.e., cumulative effect models) when sample size is large (Schwarz 1978; Boyce et al. 2002). Analyses were performed using the lme4 package (Bates and Sarkar 2006) with R software (R Development Core Team 2006). The variance inflation factor of any model was <2, indicating the absence of multicollinearity (Hosmer and Lemeshow 2000; Graham 2003).

We used k-fold cross validation to evaluate the robustness of the top-ranking RSFs by annual period (cf. Boyce et al. 2002). We first estimated an RSF based on 80% of the data, withholding 20% for evaluation (Huberty 1994). RSF scores were then placed in ten bins of equal size representing the percentile range of predicted scores. We then contrasted predicted scores with the frequency of locations in the withheld data (20%) distributed across the bins. To evaluate model performance, we calculated a Spearman rank correlation (r_s) between the frequency of occurrence for the withheld 20% and the ranked

Table 2 Candidate models of habitat selection for gray wolves in managed boreal forests of Quebec, Canada

No.	Model	Model structure
1	Landscape model	Land cover + Slope + Snow depth
2	Road model	Landscape model + Edge density + Road density
3	Cutblock model	Landscape model + Edge density + Proportion of cutblocks
4	Logging activity model	Landscape model + Edge density + Road density + Proportion of cutblocks
5	Road cumulative effect model	Landscape model + Edge density + Road density + Proportion of cutblocks + Road density × Road + Road density × Cut_5 + Road density × Cut_0
6	Regenerating cutblock cumulative effect model	Landscape model + Edge density + Road density + Proportion of cutblocks + Proportion of Cut_5 × Road + Proportion of Cut_5 × Cut_5 + Proportion of Cut_5 × Cut_0
7	Recent cutblock cumulative effect model	Landscape model + Edge density + Road density + Proportion of cutblocks + Proportion of Cut_0 × Road + Proportion of Cut_0 × Cut_5 + Proportion of Cut_0 × Cut_0
8	Logging cumulative effect model	Landscape model + Edge density + Road density + Proportion of cutblocks + Road density × Road + Proportion of Cut_5 × Cut_5 + Proportion of Cut_0 × Cut_0

Landscape variables are described in Table 1

RSF-availability bins (Boyce et al. 2002). The process was repeated ten times and average r_s ($\overline{r_s}$) are reported. We used the top-ranking validated model to create GIS maps of relative probability of occurrence of wolves over the landscapes.

We then used Hebblewhite and Merrill's (2008) two-step approach to determine whether the cumulative effects of forestry created functional responses in habitat selection among wolf packs (inter-HR level). First, we built mixed-effects RSFs taking the form of the logging activity model (Table 2, model no. 4). The RSFs accounted for the non independence of the locations among pack members through random intercepts, and for differences in the response of wolf packs to roads and cutblocks through random coefficients (Gillies et al. 2006; Hebblewhite and Merrill 2008). We then extracted pack-specific random coefficients from the mixed-effects RSFs and related these coefficients to either the mean proportion of cutblocks (log-transformed) or the mean road density (log-transformed) in individual home ranges.

Results

Cumulative effects within home ranges

The cumulative effects of forestry influenced habitat use by wolves throughout the year. Habitat selection at the HR level was best described by models accounting for the effects of roads and cutblocks, as well as their interaction with road density and the proportion of cutblocks within a 1-km radius (Table 3). Other candidate models received virtually no empirical support ($w_i \leq 0.00$), suggesting that models without the cumulative effects of logging activities described habitat selection by wolves relatively poorly (ΔBIC $\geq$ 45 Table 3). Comparison of candidate models indicated that omitting cumulative effects could underestimate the impact of anthropogenic activities on habitat selection (Table 3), providing a potentially misleading description of expected wolf distribution (Fig. 1). Indeed, the consideration of slope, snow depth, and land cover types, in combination with road density (model 2) or with the local proportion of cutblocks (model 3) yielded different predictions about the probability of wolves occurrence compared to models that accounted for cumulative effects (Fig. 1).

Overall, the two best candidate RSFs for each period were either the regenerating cutblock model or the logging cumulative effect model (Table 3). We thus tested whether a complete model combining all variables of both models could be better than either model alone. Using a log-likelihood (L) ratio test (Hilborn and Mangel 1997), we found that adding variables to obtain a complete model increased model fit during the rendez-vous period ($\Delta(-2L) = 27$, $df = 2$, $P < 0.001$), but not during the denning period

Table 3 Model selection for denning, rendez-vous and nomadic periods among the candidate models indicated in Table 2

No.	Candidate model	K_i	LL	BIC	Δ_i	w_i
	Denning period					
6	Regenerating cutblock cumulative effect model	19	−5,196	10,435	0	1.00
8	Logging cumulative effect model	19	−5,203	10,447	12	0.00
5	Road cumulative effect model	19	−5,268	10,578	143	0.00
4	Logging activity model	16	−5,274	10,584	149	0.00
7	Recent cutblock cumulative effect model	19	−5,272	10,585	150	0.00
2	Road model	14	−5,294	10,619	184	0.00
3	Cutblock model	14	−5,325	10,683	248	0.00
1	Landscape model	12	−5,449	10,923	488	0.00
	Rendez-vous period					
6	Regenerating cutblock cumulative effect model	19	−5,445	10,932	0	1.00
8	Logging cumulative effect model	19	−5,453	10,948	16	0.00
5	Road cumulative effect model	19	−5,491	11,024	92	0.00
4	Logging activity model	16	−5,504	11,042	110	0.00
7	Recent cutblock cumulative effect model	19	−5,501	11,046	114	0.00
3	Cutblock model	14	−5,507	11,047	115	0.00
2	Road model	14	−5,535	11,099	167	0.00
1	Landscape model	12	−5,585	11,195	263	0.00
	Nomadic period					
8	Logging cumulative effect model	20	−9,991	20,028	0	1.00
6	Regenerating cutblock cumulative effect model	20	−10,000	20,046	18	0.00
7	Recent cutblock cumulative effect model	20	−10,002	20,050	22	0.00
5	Road cumulative effect model	20	−10,012	20,070	42	0.00
4	Logging activity model	17	−10,017	20,073	45	0.00
3	Cutblock model	15	−10,034	20,104	76	0.00
2	Road model	15	−10,093	20,220	192	0.00
1	Landscape model	13	−10,207	20,443	415	0.00

Number of parameters (K_i), log-likelihood values (LL), BIC scores, differences in BIC compared to lowest scoring model (Δ_i) and BIC weights (w_i) for the eight candidate models of habitat selection by gray wolves in managed boreal forests of Quebec (Canada), are reported

($\Delta(-2L) = 4$, $df = 2$, $P = 0.14$) or the nomadic period ($\Delta(-2L) = 1$, $df = 2$, $P = 0.61$). Further assessment of wolf-habitat relationships at the HR level was based on the resulting best models (Table 4), which were robust to cross-validation regardless of the annual period (range of $\overline{r_s}$: 0.95–0.96).

Denning period

During the denning period, wolves selected conifer stands with a lichen understory, deciduous-mixed forests, open areas, and areas with a high density of hard edges (Table 4). Conifer forests were used in proportion to their occurrence in the landscape (i.e., 95% CI included 0, Table 4). In addition, the top-ranking model highlighted that the selection for regenerating cutblocks varied as a function of the local intensity of logging activities (Fig. 2). For example, the selection of regenerating cutblocks decreased with an increase in local road density (Fig. 2a). The probability of occurrence of wolves in regenerating cutblocks also decreased as those blocks become more abundant locally (Fig. 2b). When they covered as much as 40–50% of the landscape, regenerating cutblocks were among the most strongly avoided land cover types (Fig. 2b). Regenerating cutblocks were also strongly avoided in areas having recent cutblocks, particularly when these cutblocks covered a large proportion of the area (Fig. 2c).

Rendez-vous period

Similar to the denning period, wolves during the rendez-vous period selected conifer stands with a lichen understory, deciduous-mixed forests, open

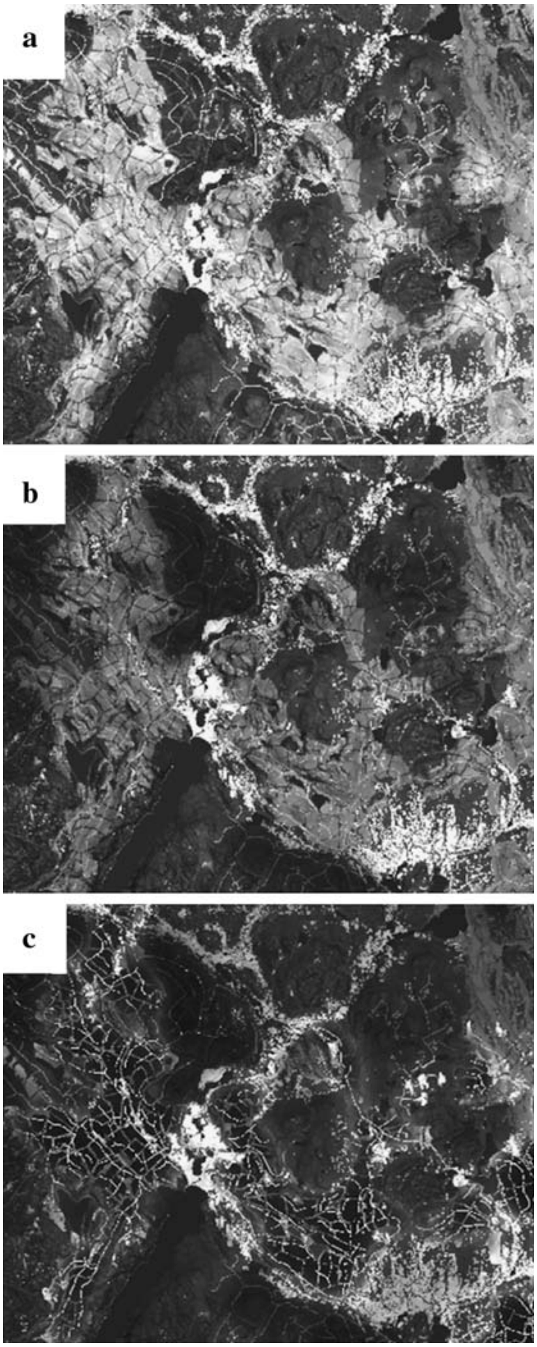

Fig. 1 Relative probability of occurrence of wolves during the denning period in a section of a wolf territory in the boreal forest of Quebec (Canada), based on a set of candidate models explaining wolf distribution based on landscape characteristics. Models included land cover types, together with **a** road density in a 1-km radius buffer (model 2, Table 2), **b** proportion of cutblocks (model 3, Table 2) or **c** both road density and local proportion of cutblocks as explanatory variables (model 6, Table 2). *Light areas* represent high probability of occurrence

areas, and areas comprised of a high proportion of hard edges (Table 4). The cumulative effects of forestry were also characterized by a decrease in the use of regenerating cutblocks with increasing logging activities. The probability of occurrence of wolves in regenerating cutblocks was generally high, but decreased with increasing road density (Fig. 2d), as well as when regenerating cutblocks (Fig. 2e) or recent cutblocks (Fig. 2f) made up an increasing proportion of the local area. We also found that wolves displayed a strong selection for roads in areas where they occurred at low density, but this preference decreased rapidly with increasing local road density (Fig. 2d). Furthermore, wolves generally had a low probability of occurrence in recent cutblocks, especially when they covered a large proportion of the landscape (Fig. 2f).

Nomadic period

During the nomadic period, wolves selected deciduous-mixed forests, conifer stands with a lichen understory, open areas, areas comprised of a high proportion of hard edges, and areas with low snow accumulation (Table 4). Also, wolves avoided forests dominated by conifers as well as areas with deep snow (Table 4). The cumulative effects of forestry resulted in a decrease in the probability of wolf occurrence on roads and in regenerating and recent cutblocks as the local abundance of these habitat attributes increased (Fig. 2). Despite this decrease, the probability of wolf occurrence on roads remained relatively high over their entire range of road density (Fig. 2g), whereas wolves only had a relatively high probability of being found in recent cutblocks in areas where these blocks covered a small portion of the landscape (Fig. 2i).

Cumulative effects among wolf packs

At the inter-HR level, we found that the wolf packs for which recent cutblocks cover $<3\%$ of their home range avoided these cutblocks during the denning period, whereas packs with home range characterized by a larger percentage of recent cutblocks made selective use of these habitat attributes (Fig. 3). This relationship thus reflected a functional response during the denning periods (R^2-adjusted $= 0.52$, $P = 0.06$). We did not, however, detect such a

Table 4 Coefficients (β), standard error (SE) and 95% confidence intervals (CI) for cumulative effects top ranking models of habitat selection by gray wolves in managed boreal forests of Quebec, Canada for each period of the year

Variable	Denning period (Regenerating cutblock cumulative effect model)			Rendez-vous period (Regenerating cutblock and logging cumulative effect model)			Nomadic period (Logging cumulative effect model)		
	β	SE	95% CI	β	SE	95% CI	β	SE	95% CI
Open	0.530	0.086	(0.36:0.70)[a]	0.549	0.089	(0.37: 0.72)[a]	0.208	0.063	(0.08:0.332)[a]
Water	−0.800	0.147	(−1.09:−0.51)[a]	−0.476	0.130	(−0.73:−0.22)[a]	−0.336	0.092	(−0.52:−0.16)[a]
Lichab	1.170	0.103	(0.97:1.37)[a]	0.662	0.105	(0.45:0.86)[a]	0.201	0.078	(0.04:0.35)[a]
Conif	−0.122	0.094	(−0.31:0.06)	0.087	0.092	(−0.09:0.27)	−0.193	0.068	(−0.33:−0.06)[a]
DecMix	0.333	0.090	(0.16:0.51)[a]	0.492	0.090	(0.31:0.67)[a]	0.327	0.063	(0.20:0.45)[a]
Cut_5	3.017	0.287	(2.45:3.58)[a]	2.829	0.290	(2.26:3.40)[a]	0.522	0.149	(0.23:0.81)[a]
Cut_0	−0.053	0.198	(−0.44:0.34)	−0.045	0.38	(−0.80:0.71)	0.538	0.270	(0.01:1.07)[a]
Road	0.862	0.114	(0.64:1.09)[a]	2.110	0.211	(1.68:2.53)[a]	0.833	0.185	(0.44:1.17)[a]
Road density	0.280	0.029	(0.22:0.34)[a]	0.136	0.027	(0.08:0.19)[a]	0.132	0.022	(0.09:0.17)[a]
Proportion of Cut_5	0.623	0.243	(0.15:1.10)[a]	1.641	0.224	(1.19:2.08)[a]	1.908	0.159	(1.61:2.22)[a]
Proportion of Cut_0	−1.737	0.370	(−2.46:−1.01)[a]	−1.877	0.393	(−2.64:−1.10)[a]	−0.650	0.259	(−1.17:−0.15)[a]
Road density × Road	–	–	–	−0.341	−0.067	(−0.47:−0.21)[a]	−0.179	0.062	(−0.29:−0.05)[a]
Road density × Cut_5	−0.294	0.084	(−0.46:−0.13)[a]	−0.484	0.080	(−0.64:−0.32)[a]	–	–	–
Proportion of Cut_5 × Cut_5	−5.781	0.548	(−6.86:−4.71)[a]	−4.530	0.544	(−5.59:−3.46)[a]	−1.954	0.350	(−2.65:−1.28)[a]
Proportion of Cut_0 × Cut_0	–	–	–	−1.068	1.21	(−3.44:1.31)	−2.394	0.740	(−3.83:−0.93)[a]
Proportion of Cut_0 × Cut_5	−4.063	1.727	(−7.45:−.68)[a]	−4.026	1.821	(−7.60:−0.45)[a]	–	–	–
Slope	−0.039	0.004	(−0.05:−0.03)[a]	−0.094	0.004	(−0.10:−0.09)[a]	−0.027	0.003	(−0.03:−0.02)[a]
Edge density	0.080	0.008	(0.06:0.09)[a]	0.058	0.007	(0.05:0.07)[a]	0.050	0.005	(0.04:0.06)[a]
Snow depth	–	–	–	–	–	–	−0.086	0.040	(−0.17:−0.01)[a]

Open conifer stands were used as the reference category. Land cover types variables are described in Table 1

[a] Coefficients for which the 95% confidence intervals excluded zero

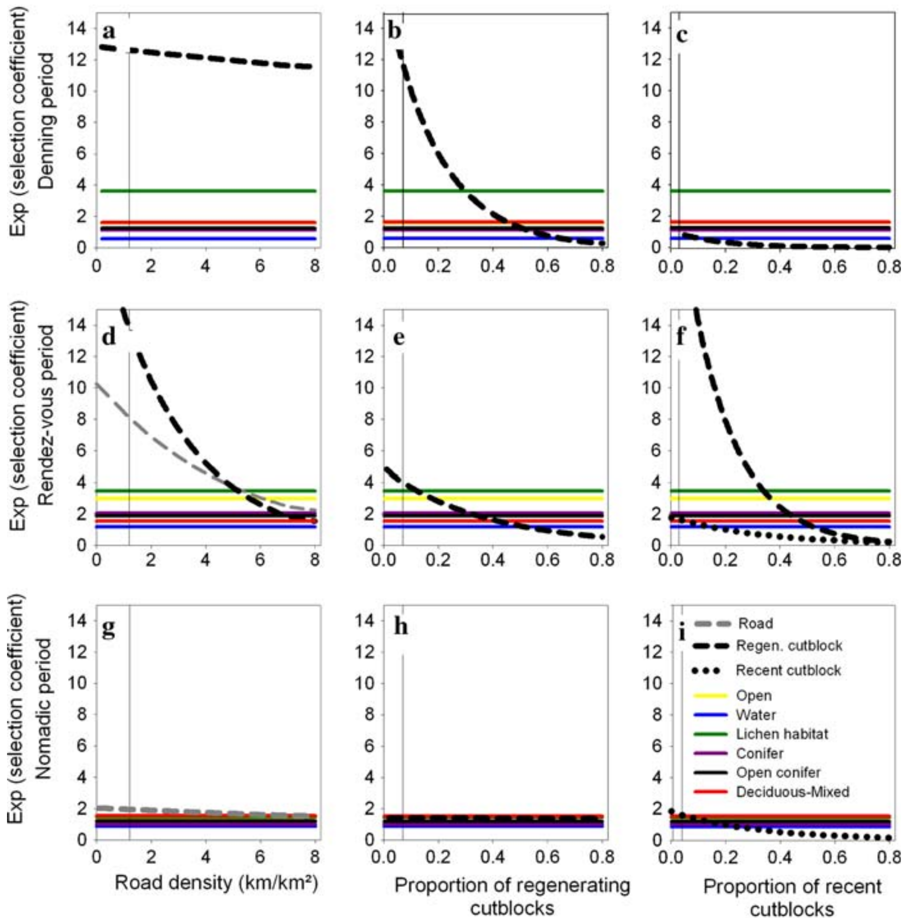

Fig. 2 Functional response in the use of regenerating cutblocks by wolves as a function of the proportion of roads and regenerating (Regen.) and recent cutblocks according to the top ranking model for each period of the year in 2005–2007 in the boreal forest of Quebec (Canada). Proportions of each logging attribute were estimated within 1-km radius buffers. Open conifer stands were used as the reference category. Values are displayed only over the range of densities observed within wolf territories. *Vertical lines* correspond to the observed mean density

functional response at the inter-HR level during other periods of the year or for other anthropogenic habitat features (Fig. 3).

Discussion

Our study indicates that cumulative effects of forestry have a strong influence on patterns of habitat selection by wolves in boreal ecosystems. Very few studies of wolf-habitat interactions have been based on field sampling as intensive over time and extensive over space as the one presented here (but see Gustine et al. 2006; Hebblewhite and Merrill 2008). We assessed the cumulative effects of forestry at two levels. First, we evaluated whether wolves responded to spatial variations in the abundance of anthropogenic habitat attributes within their home range (HR level). Second, we used Hebblewhite and Merrill's (2008) approach to evaluate whether differences in home range characteristics could explain inter-pack differences in the overall selection for anthropogenic features (inter-HR level). We detected cumulative effects at both levels.

Cumulative effects within home ranges

At the HR level, we found that the selection for roads and cutblocks by wolves varied with the local abundance of these features within their home range, suggesting that decisions related to habitat selection are context-specific. An accurate characterization of

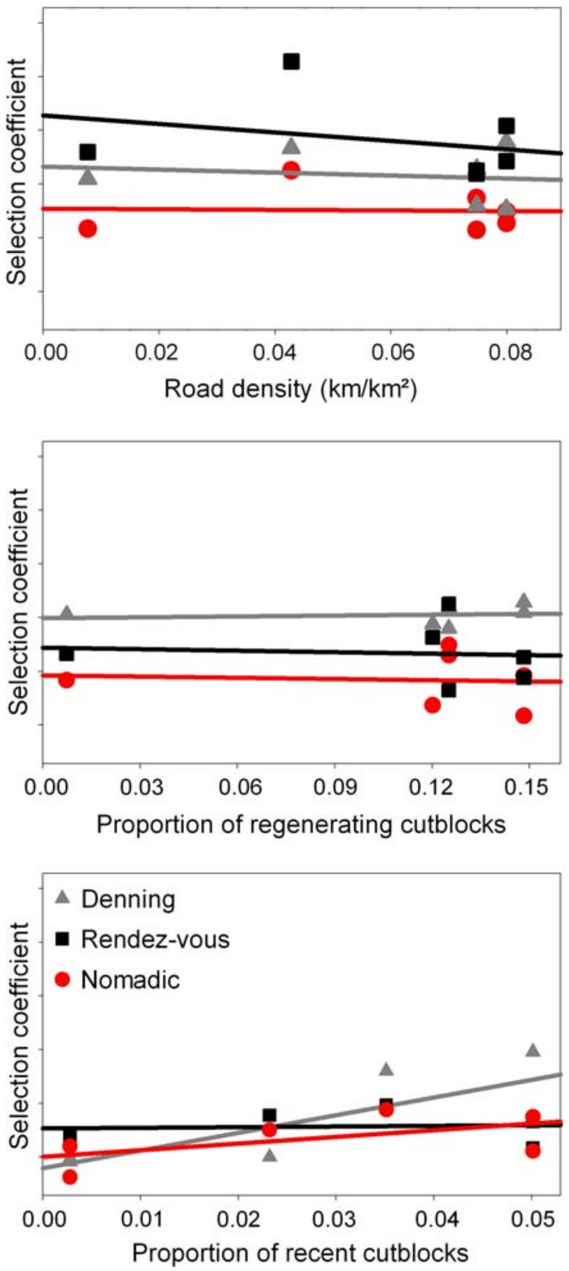

Fig. 3 Functional response in the selection of roads, regenerating and recent cutblocks by wolves as a function of their abundance in individual home ranges, for each period of the year in 2005–2007 in the boreal forest of Quebec (Canada). Road densities and proportion of regenerating and recent cutblocks were estimated within multi-annual home ranges. Selection coefficients of resource selection functions were estimated for each wolf pack from mixed effects generalized linear mixed model

wolf distribution in a harvested landscape should thus consider not only roads and cutblocks, but also their local representation in the landscape and temporal changes in the level of disturbance during the course of the year.

Logging activities are reduced in the study area from December to June, leading to temporal changes in the level of human disturbance. During the denning period (1 April to 30 June), wolves selected regenerating cutblocks in areas where the abundance of roads and cutblocks was low, but tended to avoid them in highly altered parts of their home range. Logging activities are generally concentrated in space, and once the forest has been harvested, human disturbance largely decreases in the area. Disturbance should therefore be relatively infrequent in regenerating cutblocks compared to recent cutblocks. But the area also needs to provide good hunting opportunities. The abundance of moose depends on a suitable interspersion of food and protective cover (Dussault et al. 2006). While the high availability of browse found in regenerating cutblocks (Newbury and Simon 2005; Potvin et al. 2005a) could attract moose, protective cover may become limited in landscapes fragmented by a high abundance of cutblocks and roads. In other words, moose may not use habitat with high edge density despite high food availability because of the lack of cover from predators. Wolves would then have little incentive to use these areas if moose abundance is low.

During the rendez-vous period (1 July to 30 September), we observed cumulative effects of forestry on the use of roads and cutblocks by wolves. Logging activities were extensive during that period. Heavy traffic on roads leads to frequent disturbance, which can have profound effects on the functional relationship between habitat selection and wolf distribution (Thurber et al. 1994; Theuerkauf et al. 2003). Road density is considered one of the most important predictors of wolf spatial dynamics in landscapes with limited logging activities (Mladenoff et al. 1995; Potvin et al. 2005b; Whittington et al. 2005). We found that roads were selected more strongly where their local density was low. An increase in the density of roads not only decreased their selection, but also led to a decrease in the selection of regenerating cutblocks. The selection of regenerating cutblocks also decreased where cutblocks made up a larger proportion of the area. This response was especially strong in areas having a high proportion of recent cutblocks, which is when human disturbance was most important. Browse availability for moose is generally lower in areas having a high proportion of recent cutblocks compared to areas having a high proportion of regenerating cutblocks (Courtois et al. 1998). Moreover, an increase in the proportion of recent cutblocks would reduce the size of the remaining forest patches, which might become too small to provide an important prey base for wolves (Potvin et al. 1999). Wolves might then have little to gain from intensive use of this part of their home range.

During the nomadic period (1 October to 31 March), we detected cumulative effects related to both the abundance of roads and cutblocks. Logging activities were low during this period, which resulted in infrequent use of roads by humans, but a generally strong selection by wolves. In fact, roads remained the land cover types with the highest probability of wolf occurrence, despite a decrease in their selection following an increase in road density. Cumulative effects were also observed for the use of regenerating and recent cutblocks. Wolves decreased their selection for recent cutblocks as they made up a larger proportion of the local area. These cutblocks even became the most strongly avoided land cover types where they made up more than 20% of the area.

These functional responses were detected in multivariate RSFs that also accounted for the response of wolves to multiple other habitat attributes within their home range. For example, we found that wolves avoided conifer forest during the nomadic period, a response consistent with previous reports (Kunkel and Pletscher 2001; Fortin et al. 2005). Also, wolves preferred open areas, conifer stands with a lichen understory, and deciduous-mixed forests during all periods. These land cover types may be used preferentially because they provide the forage and protective cover needed by ungulates (Courtois et al. 2002; Mosnier et al. 2003; Dussault et al. 2005). By using these land cover types, wolves could increase their chance of encountering prey. Likewise, we found that wolves preferred areas with a relatively high density of hard edges, a trend previously reported (Bergman et al. 2006). Hard edges create a structural change (e.g., boundary between a cutblock and a forest stand) that could impede the movements of prey towards forest cover. The switch in landscape structure could slow down prey, thereby providing an advantage to predators (Bergman et al. 2006).

Cumulative effects among wolf packs

Including random coefficients in RSF models allowed us to test for the presence of functional responses in resource selection at the inter-HR level. Hebblewhite and Merrill (2008) previously used this approach to understand wolf-human relationships and they found that as human activity increased, wolves were constrained to select areas closer to human activity. We did not detect any functional response to the abundance of roads and regenerating cutblocks among wolf packs at the inter-HR level. A functional response in the selection of recent cutblocks was detected, however, during the denning period. Packs with home ranges made up of <3% of recent cutblocks avoided these habitat attributes, whereas those with home ranges comprised of >3% of cutblocks selected them. In our study, recent cutblocks made up only a small proportion of the landscape (range among home ranges: 0.1–5.0%). Changes in the selection of recent cutblocks as their local abundance increases should reflect a trade-off between acquiring essential resources efficiently and minimizing the risk of being disturbed (Kunkel and Pletscher 2000). Changes in trade-offs may be such that the relationship that we observed might not remain linear beyond the range of abundance observed in our study. It would be valuable to assess the response of wolves to recent cutblocks in landscapes characterized by greater levels of anthropogenic disturbance.

Conclusion

Understanding the relationships between animals and their environment in systems undergoing rapid changes has significant conservation value (Pickens and Root 2009). We showed that habitat selection by wolves in boreal ecosystems is a complex response to both natural and anthropogenic habitat features and that this response operates at multiple hierarchical levels. The influence of roads and cutblocks on wolf distribution varies spatially, depending on the local abundance of these habitat features across the home range (HR level). The average road density and cutblock abundance could not generally explain inter-pack differences in the overall selection of these features (inter-HR level), except during the denning period when only wolf packs with home ranges comprised of at least 3% of recent cutblocks selected these blocks. Our study thus highlights the hierarchical nature of cumulative effects of forestry on wolf habitat selection. By neglecting the consideration of cumulative impacts of human activities on landscape use by wolves, erroneous conclusions about the influence of anthropogenic disturbance on wolf distribution could be drawn. Effective management of wolf habitat in human-altered landscapes thus requires the consideration of cumulative effects.

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