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Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour?

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The impact of anthropogenic disturbance on the fitness of prey should depend on the relative effect of human activities on different trophic levels. This verification remains rare, however, especially for large animals. We investigated the functional link between habitat selection of female caribou (*Rangifer tarandus*) and the survival of their calves, a fitness correlate. This top-down controlled population of the threatened forest-dwelling caribou inhabits a managed forest occupied by wolves (*Canis lupus*) and black bears (*Ursus americanus*). Sixty-one per cent of calves died from bear predation within two months following their birth. Variation in habitat selection tactics among mothers resulted in different mortality risks for their calves. When calves occupied areas with few deciduous trees, they were more likely to die from predation if the local road density was high. Although caribou are typically associated with pristine forests, females selected recent cutovers without negative impact on calf survival. This selection became detrimental, however, as regeneration took place in harvested stands owing to increased bear predation. We demonstrate that human disturbance has asymmetrical consequences on the trophic levels of a food web involving multiple large mammals, which resulted in habitat selection tactics with a greater short-term fitness payoff and, therefore, with higher evolutionary opportunity.

Keywords: caribou–wolf–bear interactions; fitness; food web; habitat selection tactic; predation; reproductive success

1. INTRODUCTION

Habitat selection is a fundamental mechanism by which animals achieve their distribution, and as such, it is central to a broad range of ecological fields, such as landscape ecology, wildlife conservation and management, and evolutionary ecology [1–4]. Habitat selection decisions can vary broadly among members of a population [5–7], and this behavioural plasticity can yield different fitness payoffs [8]. Nevertheless, most habitat selection studies do not account for the complexity of the selection process (i.e. no multivariate assessment), or when they do, the fitness consequences of selection decisions are generally not assessed [3,8].

The fitness consequences of disturbance events on individuals of a particular species depend on the overall effect of those events on food web properties. Human disturbances can cause substantial changes in the strength of food web interactions [9]. The most adaptive response of prey to human activities and infrastructure may depend on whether top-down or bottom-up forces determine population size, and on the relative impact that humans

have on different trophic levels. For example, selection for human-disturbed sites of a top-down controlled prey species might result in fitness gains if anthropogenic disturbances have stronger consequences on its predators than on its food supply [10]. Given that human infringement on wildlife habitat is increasing rapidly and extensively, some habitat selection tactics may become more adaptive following anthropogenic disturbance, while previously rewarding decisions may become maladaptive [11,12]. To better anticipate the long-term effects of human activities on wildlife, it is valuable to increase our understanding of how humans can alter food webs, and how animals should ultimately adapt to those changes.

Forest-dwelling caribou (*Rangifer tarandus caribou*) provide an opportunity to evaluate fitness-related consequences of habitat selection in human-altered landscapes. This species has declined across most of its range over the last century, largely owing to timber harvest [13]. Logging exacerbates the impact of predation on caribou, which is the proximate limiting factor of caribou populations [14]. Moose (*Alces alces*), grey wolf (*Canis lupus*) and black bear (*Ursus americanus*) are the other key species involved in the caribou's food web, and these species are also strongly influenced by forest harvesting. By increasing the availability of early-seral stands, logging practices are favourable to moose

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[15], an alternate prey species of wolves. The landscape could then sustain more moose and thus higher populations of wolves that can also consume adult caribou [16] and their calves [17]. Black bears are another large mammal species that can benefit from forest regrowth [18] and strongly impact calf survival [19,20].

The survival rate of neonates is an important component of ungulate population growth [21], and can largely determine the inclusive fitness of their parents. Female caribou may modify their behaviour in response to human disturbances, which could in turn influence their own survival and that of their young, especially during calving [22,23]. While the interplay between vital rates and habitat selection tactics has been investigated for adult forest-dwelling caribou [24], the relationship has yet to be clearly established for the mother–calf unit.

We investigated the relationship between female behaviour and calf survival, a fitness proxy, in a threatened forest-dwelling caribou population inhabiting a boreal landscape highly impacted by human activities. We specifically assessed the relationship between habitat selection by adult females and the probability that their calves survived through the period of highest calf vulnerability (first four to six weeks of life [25]).

2. MATERIAL AND METHODS

(a) *Study area*

The core of the study area (5400 km²) was located 100 km north of Québec City, Canada, at the southern limit of the boreal forest. Forest stands in the study area are typical boreal forest; conifer stands were dominated by black spruce (*Picea mariana*), balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), while deciduous stands were mostly composed of white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). Logging is the most important source of forest disturbance with cutovers less than 30 years old covering 28.3 per cent of the study area [26]. Topography was characterized by rolling hills with frequent deep valleys. Elevation ranged from 500 to 1000 m a.s.l., which was relatively high compared with the surrounding areas.

Caribou density was estimated at 3.3 caribou per 100 km⁻² for a total population of about 75 individuals. Other large mammals inhabiting the region were moose (estimated density of 24 individuals per 100 km⁻² [27]), wolf (0.44 individuals per 100 km⁻² [28]) and black bear (22 individuals per 100 km⁻² [29]).

(b) *Capture and monitoring*

Between Spring 2004 and Spring 2006, we captured 23 adult female caribou and fitted them with Global Positioning System (GPS) telemetry collars (model TGW-3680 or TGW-3600, Telonics Inc., Mesa, AZ, USA). Captures followed techniques approved by the Animal Welfare Committee of the Ministère des Ressources naturelles et de la Faune du Québec (certificates no. 04-00-02 and 05-00-04). GPS collars were programmed to record a location every 7 h, except from April to June when the time interval was 3 h. Starting in mid-May, we visually located GPS-collared females by plane or helicopter to determine the onset of the calving period. We flew every 2 or 3 days until we observed the first birth, and generally daily thereafter until most females had given

birth and we had no more evidence of an imminent parturition based on female behaviour and physical traits. We captured as many calves as possible each year ($n = 10$ in 2004, 14 in 2005 and 14 in 2006) and fitted them with radio collars to monitor their survival. We captured caribou calves (more than 12 h old) by hand wearing latex gloves and fitted them with a VHF transmitter (Holohil Al-2C, Carp, Ontario, Canada) or a VHF collar (model M2510B, Advanced Telemetry Systems, Isanti, MN, USA), both equipped with a mortality sensor. We estimated the age (days) of each calf at capture by examining coordination, hooves and umbilicus condition from birth [30,31]. Most calves were captured between 36 and 48 h after birth, and only few ($n = 6$) were caught when approximately 72 h old. We then located young caribou regularly up to 10 July, which corresponded to the last recorded calf mortality event. The total number of flights was 15 in 2004, 19 in 2005 and 18 in 2006, with flights being on average 2.9 ± 0.2 days apart. We recovered collars from dead calves within 72 h, carefully estimating mortality date (see §2d for details). We determined the cause of mortality by an investigation of the carcass and its surroundings. The presence of tooth marks, blood or disarticulated, dispersed or crushed bones was considered evidence of predation [32]. Presence of bear scats, hidden caribou hides, marks on trees indicated bear predation while wolf predation was obvious when the female was also killed [25].

(c) *Habitat composition*

We used digital forest maps supplied by the Ministère des Ressources naturelles et de la Faune du Québec to describe caribou habitat. These maps were based on 1:15 000 aerial photographs taken during 1997–1999. Minimum mapping unit size was 4 ha for forest stands and 2 ha for non-forested areas (water bodies, bogs, etc.). We updated forest maps annually by adding habitat modifications caused by forestry and natural perturbations. Using knowledge of caribou ecology and our hypotheses, we grouped forest stands into 10 land cover types (excluding water bodies) according to their potential to provide food for moose and bears, and the visual obstruction provided by the vegetation (see electronic supplementary material, tables S1 and S2).

(d) *Data analysis*

We limited our investigation to the period when calves were highly vulnerable to predation. We considered female locations from birth until the calf died from predation or until 10 July (i.e. latest date that we observed calf mortality). We determined the time of calf death as precisely as possible by examining the mother's movements around the suspected date of mortality. In most cases, we could easily determine the time of calf death because the female suddenly made an unexpectedly long movement outside the area used during the preceding days. In the few cases for which we did not observe an obvious reaction of the female, we estimated calf mortality time using information collected in the field and removed locations collected when calf status was uncertain to make sure that the dataset only contained locations recorded when the calf was alive, or just before it was killed.

We assessed habitat use by the calves based on the location of their mothers because caribou calves rarely move more than a few metres away from their mother during the first weeks of life. Calves that did not die from

predation ($n = 2$) were excluded from the analyses, because our study focuses on mortality from predation (as observed by McLoughlin [33]) instead of total mortality.

We assessed habitat selection of the cow–calf pairs using resource selection functions [34], which compared the locations observed for a given pair to an equivalent number of locations randomly distributed within its annual home-range (third order of selection, [35]). We characterized habitat attributes by calculating the proportion of each land cover type (see the electronic supplementary material, table S1) and mean altitude within 220 m radius circles centred on each caribou or random location using ArcGIS 9.2 (ESRI) and a digital elevation model. The buffer radius of 220 m corresponded to the mean median inter-location distance (6 h interval) travelled by females between the day each female gave birth and 10 July. We grouped open lichen woodlands and peatlands with other non-forested areas for analysis because they had similar vegetation characteristics (see the electronic supplementary material, table S2) and very low availabilities within the study area (see the electronic supplementary material, table S1). We used the topographic position index (TPI) v. 1.3a ARCVIEW GIS extension (available from www.jennessent.com/arcview/tpi.htm) to determine the topographical position of each location and whether caribou selected upper slope compared with other slope positions. We finally estimated the density of roads in a 1 km radius around locations with ArcGIS v. 9.2 (ESRI). Preliminary analyses indicated that the influence of roads on habitat selection decreased importantly beyond 1 km (see also [36,37]).

Because calves that did not die were followed longer than those that died, and because habitat selection of the cow–calf pairs might change with time in response to increased calf mobility and environmental changes such as snow melt and vegetation growth, we had to control for calf age when comparing habitat selection of females that did versus did not lose their calves to predation [38]. Not doing so might have confounded the effect of calf age with that of calf fate on habitat selection. We used a bootstrap resampling approach to randomly match individual cow–calf pairs where the calf was killed by predation ($n = 19$) to a cow–calf pair where the calf survived throughout the vulnerability period ($n = 12$). The intent here was to carry out the analysis based on the same number of successive observations between the calves that died and those that survived. For each pair, we thus cut the number of locations associated with the calf that survived to the same number of days as the one that died. After repeating this approach for each calf that died, we used the resulting database ($n = 19$ calves that died and $n = 19$ calves that survived) to compare used versus random locations with mixed-effects logistic regressions with individual and individual \times year as random effects [39]. This method thus controlled for the potential influence of calf age on habitat selection. We used calf status (die or survive) and habitat covariates as independent variables, together with the interaction between calf status and habitat covariates to evaluate whether habitat selection tactics can explain calf fate. We repeated the process 1999 times (each time with random association between a calf that survived and one that died) for each candidate model. In the end, we thus ran 2000 logistic regressions, each time based on 19 pairs of calves that died and did not die from predation. These regressions yielded 2000 coefficients for each covariable of a given candidate model, which were used to calculate the covariable's mean coefficient and associated 90% and 95% CIs.

We performed logistic regression with the GLIMMIX procedure of the SAS statistical software, v. 9.2.

We tested for multi-collinearity with the condition index provided by the REG procedure of the SAS statistical software, v. 9.2. After removing mean altitude from the analysis because of its correlation with TPI, condition index was less than 10. We then used information theory to evaluate the relative empirical support received by four candidate models assessing the relationship between calf survival probability and habitat selection. To limit the number of independent variables included in our models and avoid overfitting, we first conducted a series of univariate analyses testing the influence of each land cover type individually. As suggested by Hosmer & Lemeshow [40], we only considered cover types with $p < 0.25$ in the candidate models. We created our first model using topographical position and all cover types for which univariate analysis yielded $p < 0.25$, except recent cutover and non-regenerated areas (model 1). We tested three additional models by adding either recent cutover and non-regenerated area (model 2) or road density (model 3), or all three variables (model 4) to model 1. We further considered the interaction terms between each independent variable and calf status (died = 1 or lived = 0) in all candidate models. Finally, predators have their highest probability of occurrence in mixed/deciduous stands when they are in the vicinity of anthropogenic features, such as roads (D. Fortin *et al.* 2012, unpublished manuscript). We thus tested these potentially non-independent effects on calf survival using the road density \times mixed/deciduous stands interaction term. We ranked all candidate models according to the Akaike's information criterion adjusted for small sample sizes (AICc, [41]).

3. RESULTS

We followed 23 females with GPS telemetry for 1–3 years. Because two females died before their first monitored calving period and five females did not calve every year, our analyses are based on the fate of 38 neonates. Among those, 22 calves died from predation (58%) while 14 survived (37%). The remaining two calves (5%) died from a natural cause (drowning or stillbirth). Black bear was responsible for 95 per cent of the predation events, whereas we could confirm wolf predation only once (5%). Because we could not retrieve data from three collars, we conducted our analyses based on 19 female-years that lost their calves to predation and on 12 female-years that did not.

Information theory underscored the importance of both natural and anthropogenic habitat features in explaining the distribution of female caribou and their calves during the period of high vulnerability. The model receiving the least empirical support did not include anthropogenic features (table 1). Further, the top-ranking model highlighted that differences in habitat selection tactics could explain variations in the probability of calf survival.

We observed four main outcomes of habitat selection tactics, some with and others without detectable impact on calf survival. First, the selection of recent cutovers could not explain variations in the probability of calf mortality (table 2). Second, all females selected upper slope positions, but females that lost their calves to predation displayed stronger selection for these areas. Third, females that did not avoid non-regenerated areas were more likely

Table 1. Relative support of candidate models assessing the relationship between habitat selection of female caribou and the probability that their calf was killed by predation during the first month following birth, in the Charlevoix region, Québec, Canada. Models are listed with their log-likelihood (LL), number of parameters including the intercept (K), difference in Akaike information criterion ($\Delta AICc$) with the best model ($\Delta AICc$), and AICc weight (AICcw).

no.	model	LL	K	$\Delta AICc$	AICcw
1	habitat ^a + topography ^b + habitat \times calf status + topography \times calf status	-1774.2	10	981.4	0
2	model 1 + recent cutover + non-regenerated area + recent cutover \times calf status + non-regenerated area \times calf status	-1609.2	14	686.0	0
3	model 1 + mature mixed/deciduous stands + road density + road density \times calf status + mature mixed/deciduous stands \times road density \times calf status	-1801.1	14	646.7	0
4	model 1 + mature mixed/deciduous stands + recent cutover + non-regenerated area + road density \times calf status + recent cutover \times calf status + non-regenerated area \times calf status + road density \times calf status + mature mixed/deciduous stands \times road density \times calf status	-1470.7	18	0.0	1.00

^aIncludes 50-year-old conifer stand, mature mixed/deciduous stand and regenerating coniferous stand.

^bIncludes the 'upper slope' category of the TPI.

Table 2. Summary statistics of the top-ranking candidate model predicting the probability that caribou calves died or not from predation during the first four to six weeks following birth, given their mother's habitat selection. Each of the model covariables is presented with its coefficient (β), and its 90% and 95% CIs.

variable	β	90% CI		95% CI	
		lower	upper	lower	upper
calf died ^a	0.431	-1.623	0.798	-1.834	1.045
50-year-old conifer stand	0.003	-0.023	0.024	-0.031	0.027
mature mixed/deciduous stand	0.024	-0.008	0.052	-0.016	0.056
regenerating coniferous stand	0.002	-0.034	0.022	-0.042	0.027
TPI: upper slope	1.227	0.619	1.827	0.497	1.933
non-regenerated areas	-0.088	-0.192	-0.028	-0.237	-0.023
recent cutovers	0.038	0.011	0.062	0.005	0.066
road density	-0.523	-1.047	-0.124	-1.150	-0.087
mature mixed/deciduous stand \times road density	0.008	<0.001	0.017	-0.001	0.020
50-year-old conifer stand \times calf died	0.010	-0.011	0.035	-0.015	0.044
mature mixed/deciduous stand \times calf died	0.028	0.001	0.061	-0.003	0.067
regenerating coniferous stand \times calf died	-0.018	-0.042	0.015	-0.046	0.021
TPI: upper slope \times calf died	0.990	0.399	1.581	0.278	1.688
non-regenerated areas \times calf died	0.086	0.026	0.189	0.021	0.228
recent cutovers \times calf died	-0.021	-0.045	0.006	-0.049	0.013
road density \times calf died	0.440	0.043	0.956	0.001	1.064
mature mixed/deciduous stand \times road density \times calf died	-0.020	-0.030	-0.013	-0.032	-0.012

^aBinary variable indicating whether the female lost its calf (coded 1) or not (0) to predation.

to see their calves killed by predators (table 2). Fourth, calf faith depended on the combined local abundance of mature mixed/deciduous stands and roads (table 2). In areas with few roads, calves were more likely to die from predation when those areas were largely comprised of mature mixed/deciduous stands (table 2 and figure 1). In areas with few or no mature mixed/deciduous stands, females were more likely to lose their calf when those areas also had high road density. This negative effect of road density gradually disappeared, however, as the percentage of mature mixed/deciduous stands increased (figure 1).

4. DISCUSSION

Our study highlights fitness consequences of individual variation in habitat selection tactics observed among females in a population of the threatened forest-dwelling caribou. Different tactics were indeed associated with different mortality risks for calves and, therefore, different

fitness rewards for their parents. Elements of successful tactics pertained to the response of caribou to human activities. Anthropogenic disturbances had asymmetrical consequences on predators and plants (see the electronic supplementary material, table S2 [2,6,42]), and some caribou were able to capitalize on these uneven effects on trophic levels.

Recruitment of caribou in Eastern North America is limited by wolf and bear predation [25,43,44]. Given that only 5 per cent of all deaths of caribou calves in the Charlevoix region could be attributed to wolf predation, the habitat selection tactics appear effective at avoiding this predator. Wolves can make extensive use of the road network and tend to move across the landscape along habitat features generally occurring at low elevations, such as river valleys and roads [45,46]. Caribou thus could reduce predation risk by dispersing at relatively high elevations, avoiding high road densities, and then concentrate on rich foraging sites available at

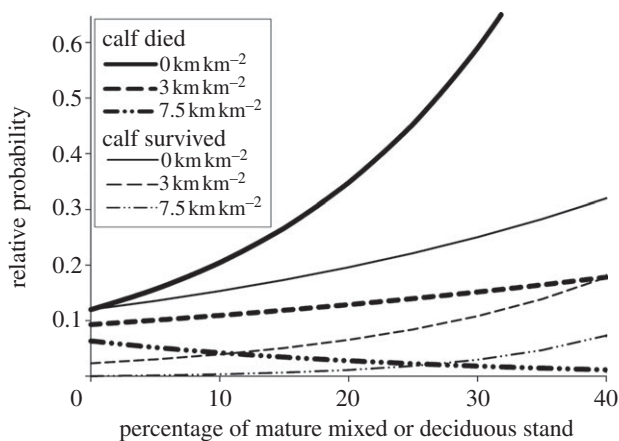


Figure 1. Relative probability of occurrence of female caribou that did or did not lose their calves to predation, as a function of the percentage of mature mixed or deciduous forest in a 1 km radius, for three road densities (0 km km^{-2} , 3 km km^{-2} and 7.5 km km^{-2} , corresponding to the 15, 50 and 85th percentiles of availability, respectively).

those elevations [47]. The selection of high elevations that we observed has been qualified as a wolf avoidance strategy for caribou [31], moose [48], elk (*Cervus elaphus*) [49] and pronghorn (*Antilocarpa americana*) [50]. Although this tactic was successful in avoiding wolves, it did not enable caribou to escape black bears, which ended up being responsible for 95 per cent of predation events. Similarities in the response of black bears and caribou to topography seem to occur mostly during spring when both species are found at relatively high elevations [18]. The selection for upper slope positions was a costly tactic for the mothers, as it increased the risk of bear predation on their calf.

The reaction of caribou to forest management had fitness consequences by affecting the probability that an adult contributes to population growth in any given year. The avoidance of non-regenerated areas and high road densities was an efficient tactic for reducing the risk of calf mortality. Non-regenerated areas and roadsides offer relatively high biomass of vegetation consumed by black bears (cf. [6]). Gustine *et al.* [31] also reported an increase in predation risk for caribou calves in areas of high vegetation biomass. Wolves can also make extensive use of the road network when moving across their territory [2,49]. We found, however, that the negative effect of road density on calf survival tended to disappear as the local percentage of mature mixed/deciduous stands increased. This interaction might reflect the fact that both landscape features provide predators with food-rich areas to search for food, thereby spreading the risk for caribou by lessening the danger imposed by each land cover type individually. Of course, this explanation is based on the assumption that predator density is not higher in these areas of high abundance of roads and mixed/deciduous stands than elsewhere in the landscape, an assumption that future studies should verify.

Surprisingly, female caribou selected recent cutovers without any detectable impact on the fate of their calves. This land cover type generally provides grasses and forbs (see the electronic supplementary material, table S2), which are central to the diet of caribou

during the snow-free period [51], especially in early spring before leaves of deciduous trees emerge. In our study area, the tree regeneration in recent cutovers had not reached the height (1.8–2.0 m), density, and composition needed to attract moose [52,53] and subsequently wolves [2]. Further, recent cutovers support relatively little food for bears and, instead, these omnivores focus their activities in land cover types offering greater amounts of vegetation during spring [6,54]. This negative response of black bears to sites recently disturbed by logging activities [6,42] offered a suitable trade-off between the predation risk for calves and the nutritional requirements of the mothers. Recent cutovers offered good concealment cover near the ground (see the electronic supplementary material, table S2), while also providing good visibility for early predator detection [31,55,56], which has been found to be an important habitat feature for female ungulates with their calves [57]. Our results support previous claims [58] to the effect that recently burnt areas could provide suitable foraging habitat for caribou, at least for a few years following disturbance.

We did not detect fitness consequences related to the selection of cutovers over the short term, but the interpretation of this result deserves caution. First, although we had a relatively large sample of mother–calf units given the difficulties of collecting such information, the statistical power of our analysis might still have been limited. We reduced the risk of type II error by drawing our conclusions while also considering the 90% CI of our predictive model's coefficients. Second, we assessed fitness consequences over 3 years whereas caribou have the potential to reproduce for more than 10 years. The selection for recent cutovers became detrimental to caribou as regeneration took place. When female caribou selected non-regenerated areas (mostly mid-age cutovers, 5–20 years old), their calves experienced higher risk of mortality. This outcome raises conservation concerns for this threatened species because female caribou often exhibit high fidelity to their calving sites [26,59], with the consequence that they may continue to use harvested areas despite the increase in local predation risk. At least, site fidelity tends to decrease as the proportion of disturbed areas increases in the landscape [26].

We identified black bears as the main threat for caribou calves, a situation likely to occur in other forests managed for timber across caribou range. In fact, socio-economic pressures to maintain short timber harvest rotations should lead to forest-dwelling caribou inhabiting younger forests than they currently do in many parts of their range, with changes in the relative strength of food web links and with black bears having a stronger effects on caribou recruitment and population dynamics. Because bears hunt calves on an opportunistic, even accidental, basis [6], predation often occurs in land cover types that bears use transiently. This increases the challenge of managing the landscape in a way that can maintain low predation pressure on caribou calves. A suitable habitat management plan should aim at creating spatial segregation between roads and regenerating stands, heavily used by bears, and areas where caribou focus their foraging activities during the spring. Alternative management options include temporary predator control until habitat conditions become of relatively poor quality to black bears [24,60].

Given that less than 50 per cent of the calves survived more than two months [25], there can be strong fitness advantages for their mothers to adopt a habitat selection tactic successful in avoiding black bear predation during spring. The asymmetrical effects of human disturbance on different trophic levels can be such that the selection for human-disturbed sites might bear no fitness costs, at least over the short-term, even for a prey species typical of old-growth forests, such as forest-dwelling caribou. For example, recent cutovers appear to provide as much food (forbs and graminoids) to caribou as many other land cover types during spring (see the electronic supplementary material, table S2), but would be among the cover types providing the least amount of vegetation that black bears consume [6]. The short-term impact of logging would therefore be stronger on the food supply of bears than that of caribou. Moreover, wolves [2] and moose [6], their main prey, do not select recent cuts during this period. As a result, the selection of recent cutovers by female caribou does not increase the risk of mortality for their calves. The impact of human disturbance on the habitat of this threatened caribou population is relatively recent, but extensive. Over time, calving in land cover types suitable for black bear should therefore have notable population consequences and become strongly selected against [4], thereby increasing the fitness value of habitat selection tactics efficient at avoiding bear predation.

More generally, our study provides empirical evidence that asymmetrical effects of anthropogenic activities on trophic levels can alter food web properties such that prey species typical of 'pristine' environments may start selecting human-disturbed areas without experiencing short-term fitness costs. Conservation plans for threatened and endangered species faced with habitat loss should be developed by considering the global consequences of human activities on spatially structured food webs.

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