Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution

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Abstract. Ecological theory predicts that the intensity of antipredator responses is dependent upon the spatiotemporal context of predation risk (the risk allocation hypothesis). However, most studies to date have been conducted over small spatial extents, and did not fully take into account gradual responses to predator proximity. We simultaneously collected spatially explicit data on predator and prey to investigate acute responses of a threatened forest ungulate, the boreal caribou (*Rangifer tarandus*), to the spatiotemporal dynamics of wolf (*Canis lupus*) distribution during spring. Movement analysis of GPS-collared individuals from both species revealed high plasticity in habitat-selection decisions of caribou. Female caribou avoided open areas and deciduous forests and moved relatively fast and toward foraging areas when wolves were closer than 2.5 km. Caribou also avoided food-rich areas only when wolves were within 1 km. Our results bridge the gap between long-term perceived risk and immediate flight responses by revealing dynamic antipredator tactics in response to predator proximity.

Key words: antipredator behavior; boreal woodland caribou; Canis lupus; *Côte-Nord region, Québec, Canada; gray wolf; movement; predation risk; predator–prey relationships; prey cognition;* Rangifer tarandus; *risk effects; step selection functions.*

Introduction

Predation has a profound impact on most ecosystems (Getz 2011), from both the consumptive and nonconsumptive effects on prey populations (Luttbeg and Kerby 2005, Trussell et al. 2006). There is increasing evidence that large mammalian prey display specific antipredator responses to predation risk, as exemplified by the large body of studies involving gray wolves (*Canis lupus*) and their ungulate prey during the past decade (e.g., Fortin et al. 2005, Creel and Christianson 2009, Beschta and Ripple 2011, Kuijper et al. 2013). At the landscape scale, prey generally avoid areas where the risk is perceived as systematically high, reflecting a heterogeneous "landscape of fear" that can vary broadly over space (Searle et al. 2008, Willems and Hill 2009, Laundré 2010). The "risky places hypothesis" (Creel et al. 2008) thus corresponds to chronic responses in space, which do not take into account the immediate presence

of predators. Prey, however, also display acute responses under the threat of predators present in their immediate surroundings, such as increased vigilance (Winnie and Creel 2007, Middleton et al. 2013), as predicted by the "risky times hypothesis" (Creel et al. 2008). Altogether, the presence of highly mobile predators leads to highly dynamic spatial patterns of risk over space and time, because risk further depends on the predators' contemporaneous locations with respect to their prey (Brown et al. 1999, Ripple and Beschta 2004, Courbin et al. 2013). The intensity of antipredator responses is thus expected to be largely dependent upon the spatiotemporal context of predation risk: the risk allocation hypothesis (Lima and Bednekoff 1999, Creel et al. 2008) predicts that the same level of threat, defined as the immediate risk of predation (Weissburg et al. 2014), in areas with different levels of long-term risk, will induce different antipredator responses. Natural selection could therefore favor prey that react to this spatiotemporal heterogeneity in risk through not only chronic but also acute responses (Lima and Bednekoff 1999).

Acute responses, despite their foraging cost (Lima and Dill 1990, Creel et al. 2014), may be adaptive, when prey can gain accurate insights about the location of their

predator that allow them to successfully escape. Prey usually exhibit routine vigilance as a low-cost option to acquire indices of predator presence (Fortin et al. 2004, Pays et al. 2007). As the intensity and number of direct cues of predation risk increase, the behavioral response escalates, with induced vigilance (Blanchard and Fritz 2007, Liley and Creel 2008, Périquet et al. 2012) preceding a flight response (Stankowich and Blumstein 2005). How the increasing perception of risk in turn affects habitat selection and the balance of the food/safety trade-off has rarely been assessed, especially on large mammalian species (Merrill et al. 2010). For example, in a savannah ecosystem where visibility is vital for prey, several African herbivores increase their use of open grassland when lions (*Panthera leo*) are in their vicinity (Valeix et al. 2009). In the Greater Yellowstone Ecosystem (United States), where dense forest cover provides protection against detection by the predators, elk (*Cervus elaphus*) move into heavily wooded areas when gray wolves are present, and, by doing so, reduce their use of preferred grassland foraging areas associated with a higher predation risk (Creel et al. 2005). Recently, another study in the same area highlighted that elk increased their rates of movement, displacement, and vigilance when wolves approached within 1 km (Middleton et al. 2013). Both chronic and acute responses of boreal woodland caribou (*Rangifer tarandus*) and moose (*Alces alces*) were also demonstrated in reaction to wolf presence (Latombe et al. 2014). Once caribou acquired a signal of predator presence, their movement and habitat selection was altered over large distances (several kilometers) and long time scales (several days), according to resource availability.

In this study, we demonstrated the behavioral plasticity in acute antipredator responses exhibited by woodland caribou, with a cursorial predator, gray wolves, in their vicinity. To highlight the most contrasted responses to predation risk vs. available resources, we restricted our study to the period of the year with the greatest level of risk, together with high-demanding needs for foraging. During the spring, caribou (most notably females) increase their movement rate and spread over the landscape in order to limit their spatial predictability to predators for the upcoming calving season (Bergerud et al. 1990). Nonetheless, this behavior results in temporally higher niche overlap with wolves (Basille et al. 2013), and makes the spring dispersal a period of relatively high mortality rates (56% of mortalities in the study area occur during this season; Courtois et al. 2007). High-quality forage is relatively scarce at this time of the year (caribou mostly rely on ground lichen from autumn to spring; Johnson et al. 2001, Courtois et al. 2007, Leblond et al. 2011), but energy demands are high, with virtually all females being pregnant (Courtois et al. 2007).

In situations of risk, the strength of acute antipredator responses will be a function of the quality and intensity of information transferred from predators to prey (Weissburg et al. 2014). There is increasing recognition that predator detection can be a multimodal process relying on the integration of multiple cues (visual, acoustic, mechanical, or chemical) to assess the level of threat and respond accordingly (Ferrari et al. 2009, Weissburg et al. 2014). Movement is the primary behavioral adaptation by which prey deal with hetero-geneity in the distribution of resources and predators at multiple scales (Lima 1998, Nathan et al. 2008, Gorini et al. 2012), allowing them to minimize the fitness costs of predation by balancing resource acquisition and survival or reproductive output (Stephens and Krebs 1986, Sih 1998, Cresswell 2008). Within the predator's sphere of influence, i.e., the distance within which prey react to the predator's presence, distinct responses can be expected as the intensity and number of cues increase, and the prey can better assess not only predator presence, but also their location and threat level (Weissburg et al. 2014).

We thus assessed how caribou responded to increasing levels of threat from a highly mobile predator, by continuously monitoring the distance between caribou and the closest wolves: as proximity to wolves increased, we intended to estimate caribou perceptive range and antipredator responses. Before caribou are able to precisely locate the source of the threat, we expected caribou to avoid foraging areas associated with a higher risk of encountering wolves, while seeking alternative cover types that provide refuge from predation (cover hypothesis; H_c). When the cue information becomes more accurate, caribou may be able to locate the predators, and then favor hasty retreating, characterized by an increased movement rate and a propensity to go in the opposite direction of the risky area (retreat hypothesis; H_r). Due to the multimodal nature of risk information, synergistic or additive responses are expected (Weissburg et al. 2014), so caribou may thus display both types of responses simultaneously and gradually (multimodal hypothesis; H_m), according to wolf proximity. Finally, as the environmental context within which prey are confronted by predator threat (e.g., the presence of refuges; Stankowich and Blumstein 2005) may also alter antipredator responses, we evaluated how spatiotemporal proximity to wolves impacted habitat selection of caribou when they were moving in the most risky areas. Our study revealed the plasticity in the response of caribou to an acute risk of predation, and highlighted how a mobile prey may balance food and safety at a fine spatiotemporal scale.

Material and Methods

Study area and relocation data

The study was carried out from March 2005 to April 2010 in the boreal forest of the Côte-Nord region, Québec, Canada (50–52° N, 68–71° W; see Courbin et al. [2014] for a description of the study area). In the study area (33 900 km²), caribou density was estimated to be 2.3 individuals/100 km², according to an aerial survey

conducted over the study area in March 2007. Nineteen female caribou and nine wolves from the four different packs present in the area were fitted with GPS collars (Lotek Engineering, Newmarket, Ontario, Canada) or ARGOS/GPS collars (Telonics, Mesa, Arizona, USA). Female boreal woodland caribou are spatially segregated from other caribou half of the year, from spring dispersal in April to rut in September, and live in small groups with a dynamic composition the rest of the year. As a consequence, monitored individuals moved over large ranges and rarely stayed together, and accurately described caribou behavior in the overall population. The four wolf packs, each comprised of three to six individuals, were identified during aerial surveys between 2005 and 2007, and covered the entire caribou range in the study area. Particular attention was paid to finely monitor every individual, with one location every hour for caribou, and one location every 2–4 h for wolves.

Based on a clustering analysis, we defined the spring dispersal as the period from 16 April to 21 May (Basille et al. 2013) when female caribou spread out from wintering areas in a spacing tactic aiming at reducing their detectability for the upcoming calving season (Bergerud et al. 1990). This season is characterized by a fast rate of movement, use of relatively low elevations, and the strongest use of deciduous forests, cuts, and roads (Basille et al. 2013). The spring dispersal is temporally distinct from the later calving season (late May–early August), which is characterized by much lower mobility (especially during the first days of calves' life), high elevations, and a sudden drop in the use of human-disturbed areas (Basille et al. 2013). Note that bears, which can have a significant impact on neonatal caribou and moose survival (Ballard 1994, Bastille-Rousseau et al. 2011) were only present at low densities in the area (Courtois et al. 2007, Courbin et al. 2009), and predate ungulate neonates only during a brief period of ~4–6 weeks after calving. The impact of bear on caribou antipredator response during the spring dispersal was thus expected to be minor.

We then selected only caribou locations that could potentially be associated with an immediate response of caribou triggered by wolf proximity. Latombe et al. (2014) identified varying responses of caribou to the passage of gray wolves in winter and summer, with a spatial threshold as large as 4.7 km in summer, and a temporally decaying response decreasing to 5% after 10 d in winter. On this basis, we considered all caribou locations that occurred within 5 km of where a radio-collared wolf was located within the past 15 d. Cohesion within packs is not necessarily assured at all times; this estimate of risk is thus likely to be conservative, as other wolves not monitored may be closer to caribou. As a consequence of using a relatively large spatiotemporal window, we could include every wolf location (i.e., every 2 and every 4 h) to extract the most precise information. We ended up with a total of 2087 caribou locations in

the spatiotemporal vicinity of wolves, i.e., 7.74% of the total number of steps.

Note that it was not our intent to set up the 15-d window as a standard approach in studies of predation risk. Rather, we used the best knowledge available together with the data at hand to define an ad hoc temporal window for our study. In order to emphasize the relevance of this window, we contrasted the results with three alternative temporal windows, using all caribou locations that occurred within 5 km of where a radio-collared wolf was located (1) from the beginning of the previous winter (starting November 28; see Basille et al. 2013), (2) within a 15-d period a month after each caribou location, and (3) regardless of time (i.e., the complete wolf data set). For each alternative, we used the same approach as detailed in the next section; none of them returned significant ($P < 0.05$) effects of wolf proximity on caribou movement, supporting the use of the 15-d period preceding each caribou location (see Appendix for the detailed outputs of this comparison).

Movement responses to predation

We analyzed caribou relocations using step selection functions (SSF; Fortin et al. 2005). Series of relocations were first converted into successive steps, which is the straight line segment connecting the current location to the next location. Each observed step was associated to 10 random steps, originating from the same location but with step lengths and turning angles (i.e., the direction of the current step relative to the direction of the previous step; Turchin 1998) drawn from empirical distributions of every step of every individual ($n = 26\,949$), excluding those from the focal individual.

Observed and random steps were then contrasted using a conditional logistic regression for case-control data, in which strata were defined by sets of a single observed step and the 10 corresponding random steps. We estimated robust variances to insure that inferences are valid despite the presence of autocorrelation between successive steps (Fortin et al. 2005). As revealed by an analysis of autocorrelations and partial autocorrelations of the deviance residuals of the full model (Fortin et al. 2005), any two steps from two clusters separated by at least three steps can be considered independent. Sequences longer than 10 steps associated with risk were then cut in shorter series, by dropping segments of three successive steps every other 10 steps, to create 194 independent clusters of successive steps.

Four competing models of movements were fitted to the data. The baseline model (H_b) was used as a basic movement model that does not take predation risk into account; this model included the land-cover type at the end of the step (so as to maximize the contrast from the beginning of the step, as compared to land-cover proportions along the step), the average slope along the step, the movement rate (i.e., distance travelled in 1 h), and directional persistence. Land-cover types were identified using Landsat Thematic Mapper images taken

PLATE 1. A group of boreal caribou (*Rangifer tarandus*) in the Côte-Nord regiou, Québec, Canada. Caribou avoid open areas and move faster when wolves (*Canis lupus*) are closer than 2.5 km. Photo credit: N. Courbin.

in 2000 with a 25-m resolution grid (Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec, Québec, Canada). Satellite images were composed of 48 land-cover classes to which we added recent (≤ 5 yr) and regenerating (5–20 yr) forest cuts, together with the road network, based on information provided annually by local forestry companies. We reclassified the 48 classes into eight broader classes relevant to caribou: open areas and bogs, shrubs, deciduous and mixed forest, open conifer forest, conifer forest with lichen, dense conifer forest, cut blocks and roads, and water bodies. Slope was estimated using a 25-m resolution digital elevation model at the scale of 1:20 000. Finally, we computed the directional persistence as the cosine of the turning angle, which thus ranges from -1 (U-turn) to 1 (straight-ahead movement). Note that, since random steps were drawn from all available steps, irrespective of the proximity to wolves, both speed and directional persistence within the subset of steps at risk may be different than the general speed and directional persistence. Testing both effects is equivalent to testing speed and directional persistence when in proximity to wolves as compared to usual movement regardless of wolves.

All other competing models included a proxy of predation risk, as given by the spatial proximity to wolves, i.e., the inverse of the distance between current caribou location and the closest wolf. Distance to predators has been previously used as an index of risk having an impact on antipredator behavior, such as vigilance, movement, and habitat selection (e.g., Liley and Creel 2008, Middleton et al. 2013, Creel et al. 2014, Latombe et al. 2014), within similar ranges of distance from prey that allow for predator detection (within 1–5 km). Since we were interested in the effect of the level of threat on habitat selection and movement behaviors, the proximity to wolves was used in interaction with the variables of interest of each subsequent model. As observed and random steps of a stratum share the same start point, distance to wolves is the same within a stratum; as a result, there is no main effect of the distance to wolves, and only the interaction term is included in the models to evaluate the impact of distance to wolves on habitat selection of caribou (similar to the assessment of group size effects in Fortin et al. [2009]).

In order to dismiss a response to habitat structure as an alternative mechanism, in the form of a behavioral functional response to the proximity of risky areas instead of wolves per se (Mysterud and Ims 1998, Matthiopoulos et al. 2011), we computed the distance to land-cover types associated to a high predation risk. In the same study area, Courbin et al. (2009) showed that wolves selected open areas and bogs, as well as deciduous and mixed forest during spring. A Pearson correlation between the distance to the closest wolf and

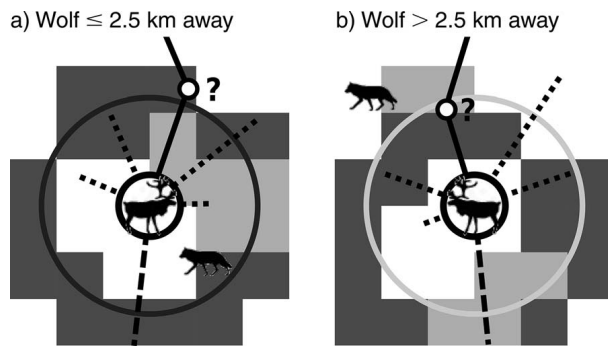a) Wolf ≤ 2.5 km away   b) Wolf > 2.5 km away

Fig. 1. Movement of boreal woodland caribou (*Rangifer tarandus*) in the riskiest areas: the land cover at the end of steps starting in open areas and mixed/deciduous forests (white pixels) when grey wolves (*Canis lupus*) are (a) closer than 2.5 km from the path was compared to when wolves are (b) farther away than 2.5 km, as represented by the 2.5-km circle centered around the current location. Light and dark gray pixels are symbolic of areas with lichen and conifer forests, respectively.

the distance to these four land-cover types indicated no relation between the two ($r = -0.026$).

The cover model (H_c) considered the selection of environmental attributes in response to predation risk. The cover model thus extended the baseline model by including the spatial proximity to wolves in interaction with the four land-cover types associated with a high predation risk, as well as caribou foraging areas (conifer forests with lichens), and two extremes on a cover gradient (open areas and bogs again, and dense conifer forests). The retreat model (H_r) considered caribou responses to predation by adjusting their movement behavior. This model thus extended the baseline model by including change in distance to the closest wolf along the step (as computed by the difference between distances to the closest wolf locations at the start and end points of the step), and the cosine of the direction to the closest wolf (ranging from −1, when caribou move in the opposite direction, to 1 when caribou move straight toward the closest wolf). We also included spatial proximity to wolves in interaction with directional persistence, movement rate, and direction to the closest wolf. Finally, the multimodal model (H_m) included both movement responses and environmental responses at the same time, on top of the baseline model.

SSF models were assessed for multicollinearity using variance inflation factors (VIF). The proximity to the closest wolf was mean-centered to reduce multicollinearity. We then used an information theoretic framework to rank all models based on quasi-likelihood estimation for autocorrelated data using QIC (quasi-likelihood under independence criterion; Pan 2001). The lowest QIC indicates the best model, with QIC weights assessing the weight of evidence for each model being the best (ω_i; Burnham and Anderson 2002). Finally, the robustness of the best model was computed using a k-fold cross validation for conditional logistic regression, which evaluates the performance of the model by

comparing the scores of observed steps to random ones (Fortin et al. 2009).

Movement in potentially high-risk areas

In a second step, we investigated the movement rules specifically in the areas associated with the highest potential risk. In the study area, the probability of encountering a wolf is highest in open areas and deciduous and mixed forests (Courbin et al. 2009). We thus selected every step starting in open areas and deciduous and mixed forests, and split them in two groups, closer and farther away than 2.5 km from the closest wolf, i.e., approximately the threshold distance triggering the avoidance of both cover types, as identified by the best model (see *Results*). For each group of proximities, we computed selection ratios (Manly et al. 2002) to compare the land-cover type at the end of the step between observed and random steps, as computed from the SSFs (Fig. 1).

Finally, an analysis of variance allowed us to further distinguish alternative tactics in the vicinity of wolves for steps ending up in these risky areas (i.e., deciduous forests and open areas) vs. areas providing dense cover (i.e., dense conifer forest). We fitted a linear mixed model on speed, taking temporal autocorrelation into account by adjusting a random effect on clusters of steps, with land-cover category (i.e., risky and cover areas), the two proximity groups (<2.5 km and ≥2.5 km), and their interaction as explanatory variables. Significance of main effects and the interaction was tested by likelihood ratio tests.

All statistical analyses were conducted using R 3.1.2 (R Core Team 2014), and additional R packages dedicated to the study of animal trajectories (adehabitatLT; Calenge 2006) and providing functions dedicated to SSF (hab; Basille 2015).

RESULTS

Movement models

In the subset of caribou locations that occurred within 5 km and 15 d of wolf locations, caribou were located on average at a distance of 3.15 km to the nearest radio-collared wolf, with a minimum of 44 m. The model selection revealed that environmental responses were primarily at play in the system (Table 1). Indeed, the cover model received the vast majority of empirical support, with a QIC weight of 95.52%. In second position, the multimodal model only received limited support ($\omega = 4.13\%$), while both baseline and retreat models received virtually no support ($\omega < 1\%$). The cover model was fairly robust to the k-fold cross validation ($\bar{r}_S = 0.604 \pm 0.176$), and displayed limited multicollinearity: VIF of all variables was ≤2.13, an acceptable level for valid inference analyses (O'Brien 2007).

Caribou avoided steep slopes and lakes compared with open conifer forests, while selectively moving forward (Table 2). As the distance to wolves progres-

TABLE 1. Model selection between the baseline model (Base; H_b), the cover model (Cover; H_c), the retreat model (Retreat; H_r), and the multimodal model (Multi; H_m).

Model	Quasi-LL	K	Trace	QIC	ΔQIC	ω
Base	−3957.458	10	12.302	7939.520	11.444	0.003
Cover	−3949.173	14	14.865	7928.076	0	0.955
Retreat	−3955.621	15	16.239	7943.720	15.643	0.000
Multi	−3947.932	19	19.247	7934.358	6.282	0.041

Notes: The quasi-likelihood under independence criterion (QIC) penalizes the quasi-likelihood (Quasi-LL) by the matrix trace function estimated using robust variances (Trace), which is close, but not exactly equal to K, the number of parameters in the model (for all models, $n = 18\,358$). The best model (Cover) presents the lowest QIC (with the difference of each model to the best shown in ΔQIC), and is supported by a very high weight of evidence that it is the best (ω_i). See Pan (2001) for details about the computation of QIC.

sively diminished, caribou successively shifted to an avoidance of deciduous forests, open areas, and conifer forests with lichen. Indeed, the model predicts a strong avoidance of deciduous and mixed forests, open areas, and conifer forests with lichen when wolves are closer than 2.87 km, 1.67 km, and 0.37 km, respectively (Fig. 2a, b, d). When wolves were closer than 0.74 km, caribou shifted markedly from an avoidance to a selection of dense conifer forests (Fig. 2c), although the model did not report the positive interaction between the selection for dense conifer forests and the proximity to wolves as significant. Finally, caribou also increased their rate of movement and directional persistence in proximity to wolves (Table 2).

Movement in open areas and mixed/deciduous forest

Caribou moving in risky areas (open areas and deciduous/mixed forests) targeted open conifer with lichen, although less so when they were closer to wolves (Fig. 3). While moving at a short distance from wolves (<2.5 km), caribou also avoided deciduous forests and open areas (Fig. 3).

Caribou moved faster in deciduous forests and open areas than in dense conifer forests ($\chi^2 = 9087.1$, df = 1, $P \leq 0.001$), which is consistent with the difficulty of moving in dense cover. However, there was no difference when closer to wolves, neither as a fixed effect of distance to wolves ($\chi^2 = 0.003$, df = 1, $P = 0.959$), nor in interaction with the cover type ($\chi^2 = 0.320$, df = 1, $P = 0.572$).

DISCUSSION

This study provides one of the few examples of fine-scale behavioral plasticity in antipredator tactics of large mammalian prey in the vicinity of its predator. Our results bridge the gap between behavioral studies addressing the risky times hypothesis (often without explicitly accounting for predator proximity in favor of a binary presence/absence of predators on site) and ecological studies addressing the risky places hypothesis (that do not incorporate immediate threats) by detailing acute antipredator responses in space and time. Using simultaneous telemetry monitoring of both predators and prey, movement analyses (based on SSF; Fortin et

TABLE 2. Coefficients and 95% confidence intervals (CI) for the final step selection function (SSF) model for 19 caribou (*Rangifer tarandus*) in situation of predation risk during dispersal in Côte-Nord, Québec, Canada, 2005–2010.

Variable	β	Lower CI	Upper CI
Open	0.51	0.13	0.90
Conifer with lichen	0.51	0.35	0.66
Shrub	0.28	−0.02	0.57
Cuts	−0.14	−0.48	0.20
Deciduous	−0.13	−0.35	0.10
Conifer	−0.23	−0.46	−0.01
Water	−0.83	−1.32	−0.35
Speed	0.49	0.32	0.66
DirP	0.09	0.02	0.17
Slope	−0.02	−0.04	0.00
Conifer × Wprox	0.28	−0.21	0.77
C.Lichen × Wprox	−0.21	−0.31	−0.11
Deciduous × Wprox	−1.97	−3.52	−0.42
Open × Wprox	−2.66	−4.87	−0.45

Notes: Confidence intervals were computed using robust standard errors. Variables included in the SSF model are the land-cover type at the end of the step (open for open areas, conifer with lichen [C.Lichen] for open conifer forests with lichen, shrubs, cuts for cut blocks (<20 years), deciduous for deciduous or mixed forests, conifer for dense conifer forests, and water for water bodies), the speed, the directional persistence (computed as the cosine of the turning angle, DirP), the average slope along the step (slope), and the proximity to wolves (*Canis lupus*) (computed as the inverse of the distance to the closest wolf, Wprox) as an interaction term.
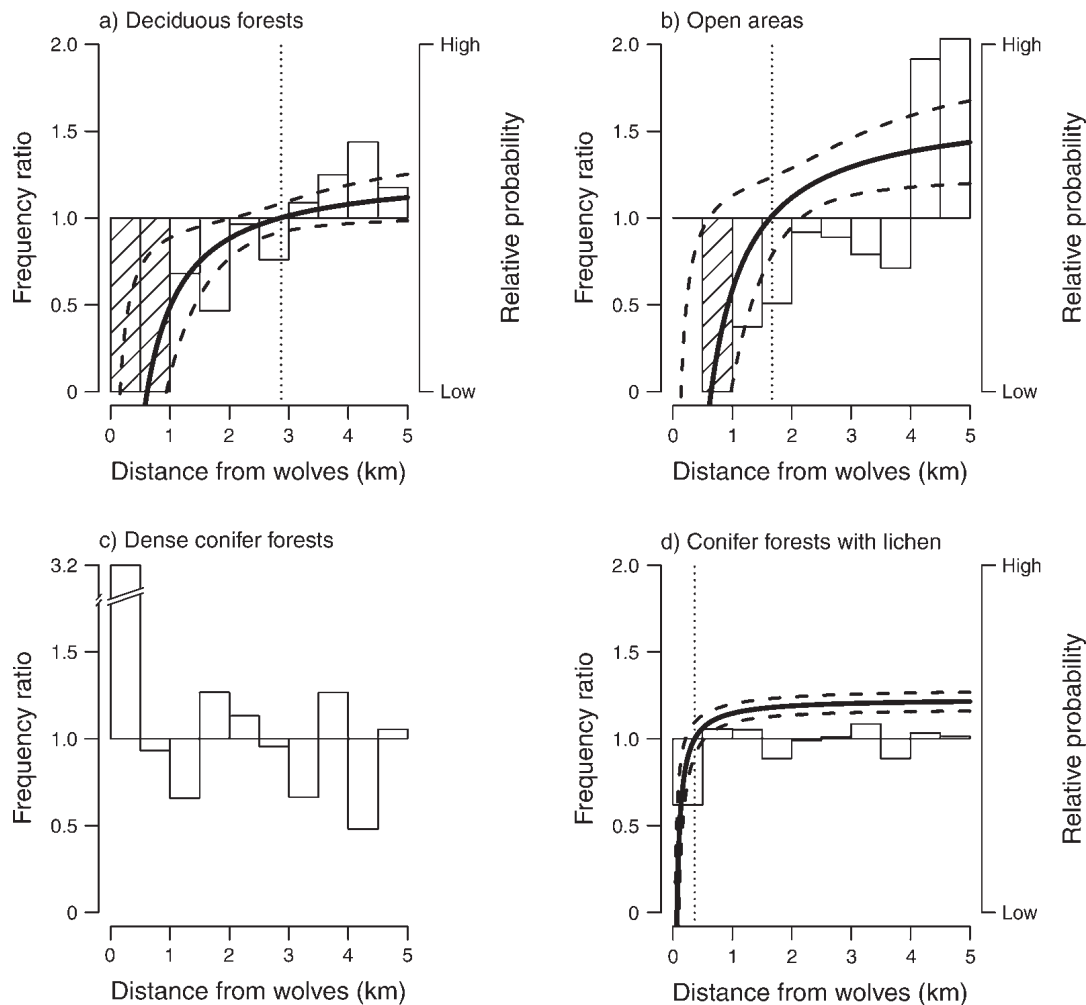
Fig. 2. Caribou selection for (a) deciduous and mixed forests, (b) open areas, (c) dense conifer forests, and (d) conifer forests with lichen, as a function of the distance to the closest wolf. The distance was divided into 10 bins between 0 and 5 km. For each bin, a selection ratio was computed as the proportion of observed steps in this bin divided by the proportion of random steps. A horizontal line at $y = 1.0$ indicates null selection. Negative and positive bars imply that the proportion of observed steps was less and more, respectively, than random expectation. Hatched bars indicate no observed steps in a bin and were set to 0. All graphs are on the same scale to allow for visual comparison, but note that the y-axis in (c) is broken on its upper limit because of the high selection of dense conifer forests in close proximity to wolves. The predictions of the final step selection function (SSF) model were added as black lines, with dashed lines indicating 95% confidence intervals. Caribou avoided deciduous and mixed forests, open areas, and conifer forests with lichen when closer to wolves than 2.87 km, 1.67 km, and 0.37 km, respectively.

al. 2005) revealed that, when in proximity to their predator, caribou avoided the most potentially risky areas, i.e., areas associated with a relatively high probability of wolf encounter. When risk became more acute by wolves being closer to their prey, however, caribou switched to a strong avoidance of preferred foraging areas in favor of areas providing a denser cover. In addition, we highlighted that caribou crossed the most risky areas at relatively high speed, and used these areas simply as stepping stones to reach limiting food patches. Altogether, these results illustrate the fine-scale trade-off between food and safety for a mobile prey facing a threat from a cursorial predator, and indicate a gradation of context-dependent responses refining the risk allocation hypothesis.

Our study clarifies decision-making of caribou in situations of risk, and illustrates that balancing food and safety can result in frequent and rapid changes in movement decisions. Except in very close proximity to wolves, caribou selected lichen woodlands, which provide the most abundant source of forage from autumn to spring (Johnson et al. 2001, Courtois et al. 2007, Leblond et al. 2011). They also sought more for open areas and stayed on flat terrain, which facilitates movement between foraging areas; a characteristic most important at the time of the year when their movement rate is at its highest (Basille et al. 2013; see Plate 1). On the one hand, caribou moved faster in open areas and deciduous forests than in mature conifer forests, where the dense cover impedes their movements (see, e.g., Avgar et al. [2013] and references therein). On the other

hand, snow also starts melting earlier in open areas, at times where there is still plenty of snow in densely forested areas (Koskinen et al. 1997), and snow-free open areas will further improve caribou movements in the landscape (Avgar et al. 2013).

In a second step, when the predators were in closer proximity (<2.5 km), caribou moved faster, and avoided open areas and deciduous forests. These areas are the most risky areas, where wolves are more likely to be encountered (Courbin et al. 2009). This avoidance of areas used more heavily by predators is a behavior generally found in ungulates (e.g., Creel et al. 2005). Finally, in situations of most acute risk (wolves closer than 1 km), caribou strongly avoided their preferred foraging areas, i.e., conifer forests with lichens, illustrating the foraging cost of predation for caribou (Brown and Kotler 2004), and favored instead dense forest to seek protective cover from their predator (Mysterud and Østbye 1999, Fortin et al. 2005). This behavior may reflect a leapfrog effect (Sih 1998, Laundré 2010), whereby prey avoid food-rich areas while predators inspect those areas. It should also be noted that the distance to the closest wolf can be seen as a conservative estimate of predation risk (Creel et al. 2013): large mammals can travel long distances in a fairly short time, e.g., between two successive locations, and wolves could actually be closer to caribou than measured on a discrete time lag; in addition, not every wolf within each pack was monitored, and other wolves (from the same pack or another) may have been closer to caribou, while remaining undetected. As a consequence, our results on the influence of wolf proximity are also likely to be conservative (see, for instance, Creel et al. [2013] for a demonstration of the impact of data collection biases in the underestimation of antipredator responses).

Prey can assess the presence of predators using visual, acoustic, mechanical, or chemical cues (Weissburg et al. 2014). Vision (e.g., vigilance) is often the most effective sense for immediate detection of predators or prey (Cronin 2005). Flight behavior, also often triggered by visual signals, is typically displayed when a predator is within a very short range from prey, e.g., flight initiation distance <150 m in Columbian black-tailed deer (*Odocoileus hemionus columbianus*) (Stankowich and Coss 2007), or 80 m in Svalbard reindeer (*Rangifer tarandus*) (Tyler 1991). Visual cues, however, have somewhat limited value in forested environments, and prey might react more often to acoustic and chemical cues, which can reach long distances and last longer than visual cues (Kats and Dill 1998, Kuijper et al. 2014). Many large ungulates have been shown to react to predator odors, such as Columbian black-tailed deer, Alpine goat (*Capra hircus*), wapiti (*Cervus elephus canadiensis*), or sheep (*Ovis ares*) (see Apfelbach et al. [2005] for a review). Even if predators have already left the area, chemical cues provide evidence of their recent presence, and, thus, some indication of the likelihood of
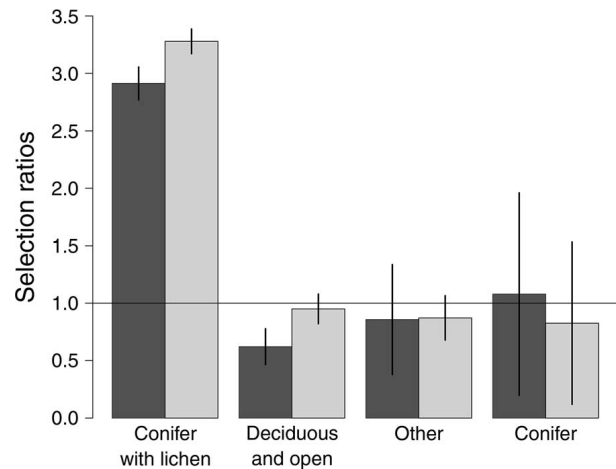

Fig. 3. The selection ratios for land-cover types at the end of steps starting in the potentially riskiest areas when the closest wolf is closer than 2.5 km (dark gray) and farther away than 2.5 km (light gray) from caribou. The bars are ordered by decreasing selection when the closest wolf was farther away than 2.5 km from caribou. A horizontal line at $y = 1$ indicates null selection.

their presence in the area in the near future (Latombe et al. 2014), which has been termed the "ghost of predation future" (Kats and Dill 1998). In particular, Kuijper et al. (2014) highlighted increased vigilance of red deer (*Cervus elephus*) within one week of a fresh wolf scat deposition, while visibility in the forest did not have an effect on prey behavior. We were able to detect strong antipredator signals in the range 0.4–2.9 km from the closest predator, which is consistent with the range of distance thresholds (0.2–4.7 km) reported by Latombe et al. (2014). Similarly, Liley and Creel (2008) reported elevated vigilance in elk induced by the presence of wolves at distances up to 3 km. Although caribou can travel long distances during the 1-h relocation interval, and may thus be able to use direct visual cues to assess predation risk, their displacement during the relocation interval, as measured by the Euclidean distance between successive locations, was extremely low (mean = 163 m; median = 57 m). While this measurement does not account for potential exploration during the relocation interval, our results thus seem to support an assessment of predation in a highly dynamic environment based on multimodal cues, allowing them to identify a predation threat at distances potentially larger than the visual extent in the forest, and gradually producing combined responses when the risk increases (Weissburg et al. 2014).

In conclusion, we demonstrated strong behavioral plasticity in the response of a large ungulate to the spatiotemporal dynamics of predator distribution. We provided a link between immediate responses in the situation of encounter with the predator (e.g., flight) and responses to the perceived risk at the landscape scale (e.g., distribution; Courbin et al. 2009). Altogether, our results provided a mechanistic explanation of changes in

habitat selection as an antipredator response in the proximity of the predator (Fortin et al. 2005), and underline the importance of intensive monitoring data to reveal fine-scale behaviors.

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Supplemental Material

Ecological Archives

Plastic response of fearful prey to the spatio-temporal dynamics of predator distribution
—Appendix 1: Choice of the temporal window—

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Guillaume Bastille-Rousseau,   Jean-Pierre Ouellet
& Réhaume Courtois

April 15, 2015

Abstract

In this document, we compare of four temporal windows for the evaluation of anti-predator responses: 1) 15 days prior to each caribou location, as presented in the main text; 2) 15 days a month after each caribou location; 3) every wolf locations from the beginning of winter; 4) every wolf locations regardless of time. We show that only the selected 15-day temporal window provided anti-predator responses.

The definition of the temporal window to investigate anti-predator responses of caribou to the proximity of wolves was based on the best of our knowledge of the data on hand and previous studies addressing the issue in this study system. However, a lack of a strong biological framework for this decision calls for a better justification to decide the temporal window.

In order to better understand the impact of the temporal window, we thus implemented the approach detailed in the manuscript using four different temporal windows to select wolf locations:

1. The preceding 15 days, which is the approach selected in the manuscript [W_{15}];

2. A 15-day period in the future, a month after each caribou location (this is to prevent the 15 days immediately after each caribou location to be too similar to the 15 days immediately before) [W_{future}];

3. All wolf locations from the beginning of winter, which was defined as November 28 for wolves (see Basille et al., 2013, for more details on the delineation of seasons) [W_{season}];

4. All wolf locations, regardless of time [W_{total}].

For all four temporal windows, we use the same analytic protocol as detailed in the manuscript:

- Extracting only caribou steps with wolves closer than 5 km within the temporal window;

- Drawing 10 random steps for each observed step, using the complete data set of caribou locations;

- Fitting a conditional logistic regression for case-control data (i.e. Step Selection Functions, Fortin et al., 2005) to contrast observed and random steps: only the full model (corresponding to H_{multi}) was fit, to allow comparison of effects for each temporal window. The full model included the land cover type at the end of the step, the average slope along the step, speed and directional persistence, as well as the spatial proximity to wolves in interaction with the 4 risky land cover types, with speed, with directional persistence, and with the direction to the closest wolf. Every model took into account the stratified structure of the data (observed vs. random), and estimated robust variances using clusters of independent steps (see *Material and Methods* for more details).

The results of the full model for the four different temporal windows are shown in Table 1 of this document. Since we were primarily interested in the effect of predation risk, as given by the proximity to wolves, we focused on the significance of the interaction of this variable with other variables of interest. While the results are qualitatively consistent between all four models regarding main effects, we can see that none of the interactions with wolf proximity (indicated by "*var* × Wprox" in Table 1) are significant for other temporal windows than the original 15-day: 95 % confidence intervals for all interaction terms overlap with 0. The only exception is the effect of wolf proximity on speed using all wolf locations regardless of the time. In other words, none of the alternative temporal windows provided results that highlighted an effect of wolf spatial proximity on caribou movement, which clearly supports the relevance of the original 15-day window.

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Table 1: Coefficient and 95 % confidence intervals for the full Step Selection Function (SSF) model, using four different temporal windows.

	W$_{15}$			W$_{future}$		
Variable	β	CI 2.5	CI 97.5	β	CI 2.5	CI 97.5
Open	0.51	0.12	0.89	-4.92	-12.98	3.15
Conifer w. lichen	0.51	0.35	0.66	0.28	0.04	0.53
Shrub	0.28	-0.01	0.58	0.35	-0.25	0.94
Deciduous	-0.13	-0.35	0.10	0.33	0.00	0.67
Cuts	-0.14	-0.48	0.19	0.01	-0.42	0.44
Conifer	-0.23	-0.46	-0.01	-0.16	-0.52	0.20
Water	-0.83	-1.32	-0.34	-1.16	-2.01	-0.31
Slope	-0.02	-0.04	0.00	-0.04	-0.08	0.00
Speed	0.49	0.31	0.67	0.64	0.40	0.88
DirP	0.10	0.02	0.14	0.14	0.02	0.26
Conifer × Wprox	0.30	-0.24	0.84	-0.06	-0.25	0.13
C.Lichen × Wprox	-0.22	-0.39	-0.05	0.04	-0.26	0.33
Deciduous × Wprox	-1.98	-3.55	-0.42	0.14	-0.05	0.34
Open × Wprox	-2.66	-4.87	-0.45	-10.72	-26.82	5.39
DiffProx	0.01	-0.17	0.20	0.74	0.41	1.07
Speed × Wprox	0.11	-0.24	0.46	0.11	-0.09	0.30
DirP × Wprox	0.08	0.00	0.15	-0.03	-0.15	0.09
Wangle	0.00	-0.07	0.06	-0.10	-0.23	0.03
Wangle × Wprox	0.08	-0.04	0.20	0.03	-0.13	0.19

	W$_{season}$			W$_{total}$		
Variable	β	CI 2.5	CI 97.5	β	CI 2.5	CI 97.5
Open	0.09	-0.28	0.46	0.36	0.16	0.57
Conifer w. lichen	0.24	0.14	0.34	0.32	0.25	0.40
Shrub	0.20	0.05	0.36	0.13	0.02	0.25
Deciduous	-0.06	-0.18	0.06	-0.15	-0.23	-0.06
Cuts	-0.10	-0.38	0.19	0.16	-0.11	0.43
Conifer	-0.45	-0.55	-0.34	-0.34	-0.42	-0.26
Water	-0.79	-1.26	-0.32	-0.84	-1.21	-0.46
Slope	-0.02	-0.03	0.00	-0.02	-0.03	-0.01
Speed	0.43	0.30	0.56	0.42	0.28	0.56
DirP	0.07	0.03	0.12	0.09	0.06	0.13
Conifer × Wprox	0.01	-0.05	0.07	0.00	-0.01	0.01
C.Lichen × Wprox	-0.04	-0.12	0.03	-0.02	-0.04	0.00
Deciduous × Wprox	0.02	-0.07	0.11	0.00	-0.04	0.05
Open × Wprox	-0.08	-0.18	0.01	-0.06	-0.13	0.00
DiffProx	0.86	0.72	1.00	2.02	1.82	2.22
Speed × Wprox	0.04	-0.05	0.14	0.07	0.04	0.11
DirP × Wprox	-0.01	-0.04	0.01	0.00	0.00	0.01
Wangle	-0.16	-0.20	-0.11	-0.19	-0.22	-0.16
Wangle × Wprox	-0.01	-0.03	0.01	0.00	0.00	0.01