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### ARTICLE

Animal Ecology



## Living in fear: How experience shapes caribou responses to predation risk

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## Abstract

Wild prey can reduce predation risk by avoiding areas used by their predators. As they get older, individuals should be able to fine-tune this avoidance based on their increased experience with predation risk. Such learning mechanisms are expected to play a key role in how individuals cope with risk during their life, particularly in altered landscapes where human disturbances have created habitat conditions distinct from those of the past. We studied the role of experience on the avoidance of risky areas by boreal caribou (Rangifer tarandus caribou) in a system where they are under high predation pressure from gray wolves (Canis lupus) and black bears (Ursus americanus). Using telemetry data collected on 28 caribou, 31 wolves, and 12 bears, we investigated whether caribou adjusted their level of predator avoidance with passing monitoring years, a proxy of increasing experience. We observed an increase in the avoidance of areas suitable to wolves (during two study periods) and bears (during all study periods) with passing years. Periods during which caribou did not adjust their behavior toward wolves (winter and calving) were characterized by persistent-potentially innate-avoidance. Our results suggest that, in most circumstances, caribou became more efficient at avoiding areas selected by their predators as they gained experience. Future work should attempt to demonstrate whether such tactics are heritable; if so, our results would suggest that, given time, caribou living in disturbed environments would have the potential to adapt to changing levels of risk. This would give hope for the conservation of caribou, a species at risk in Canada, provided levels of risk do not surpass the limits of their behavioral plasticity.

#### **KEYWORDS**

antipredator behavior, behavioral adjustment, habitat selection, landscape of fear, learning, predation risk, predator-prey interactions

## **INTRODUCTION**

In landscapes where predation risk fluctuates across space and time (e.g., "landscapes of fear" sensu Laundré 

et al., 2010), prey may avoid habitat patches suitable to their predators, thus reducing the risk of a fatal encounter. Such antipredator tactics are largely influenced by predation risk at the landscape scale. Prey can use

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environmental cues (e.g., marks, odors, feces, calls, and carcasses) to evaluate the safety of habitat patches as these cues can inform about the presence or recent passage of predators (Lima, 1998). At a broader scale, landscape features that favor predators or influence the vulnerability of prey should an encounter occur, such as land cover type, canopy closure, or topography, can also act as cues. For example, wild white-footed mice (Peromyscus leucopus) foraged more intensively in closed forests offering shelter from predation than in open forest edges where they were more likely to be attacked by avian predators (Kelleher et al., 2021). While the avoidance of a fatal encounter is certainly beneficial to prey, antipredator behaviors can also deprive prey of good foraging opportunities. The level at which prey display antipredator strategies is thus the result of a trade-off between resource acquisition and safety (Lima & Dill, 1990) and is expected to be more pronounced when safety is of utmost importance, such as when individuals are accompanied by offspring (Mumma et al., 2017).

The level of experience that a prey has with predation should play a key role in shaping the intensity of antipredator behaviors (Laundré et al., 2010). Through experience, prey may develop or fine-tune their perception of risk, that is, learn which animals are dangerous and link them to specific cues in the landscape (Fagan et al., 2013; Gaynor et al., 2019). Experience can be acquired in several ways; surviving an attack or seeing a newborn die from predation are concrete examples of individual experiences that can forge an animal's ability to recognize and avoid risky areas (Berger et al., 2001; Kieffer & Colgan, 1992). Social learning, the mechanism by which animals share information with their conspecifics, can also help prey infer risk (Griffin, 2004). Learning mechanisms are often present to help fine-tune innate but unspecific or insufficient responses to predators (Mezrai et al., 2020).

The role of prey experience on predator avoidance has been revealed in several controlled experiments (e.g., Ferrari et al., 2005; Shier & Owings, 2007), but seldom in nature where it is harder to monitor animals throughout their life, especially in long-lived species. Some studies have shown that older individuals in a population were better at avoiding risk than younger ones (Allen et al., 2022; Mumma et al., 2017), suggesting that experience could play a role in predator avoidance by wild mammals. However, studies documenting this mechanism on wild, aging animals remain scarce (but see Thurfjell et al., 2017 on elk *Cervus elaphus*).

Species of the Canadian boreal forest have evolved in landscapes shaped by natural disturbance regimes dominated by wildfires. These landscapes are now being modified at an unprecedented rate by anthropogenic

disturbances such as logging, mining, and recreational activities that alter both their structure and composition (Cyr et al., 2009). Landscape changes resulting from human-induced disturbances translate into several impacts for prey, including the advent of new predators (Bytheway & Banks, 2019), the increased predation pressure put forth by native ones (Seip, 1991), or the creation of new environmental cues that may hinder a prey's ability to assess risk (Sih et al., 2011). Human disturbances may thus act on both the real and perceived levels of risk for prey (Gaynor et al., 2019). In most cases, species adaptations lag behind environmental changes (Hoegh-Guldberg, 2012), but behavioral plasticity, such as behavioral adjustments acquired from experience, may allow animals to cope with rapid changes in their habitat and may be key for the maintenance of wild species in disturbed landscapes (Sih et al., 2011).

In this study, we aimed to assess whether individuals from a wild prey population adjusted their behavior to variations in predation risk during their lifetime. We used woodland caribou (Rangifer tarandus caribou)-a species of conservation concern across North America-as a biological model. Boreal populations of woodland caribou (hereafter boreal caribou) are designated as threatened under the Canadian Species at Risk Act (SARA, S.C., 2002, c. 29, schedule 1), owing to the loss, fragmentation, and alteration of their habitat by resource extraction activities. These activities have generated greater proportions of early seral forests, which have led to increases in gray wolf (Canis lupus) densities via an increase in moose (Alces alces americana) populations (Seip, 1991). Younger forests have also favored the growth of black bear (Ursus americanus) populations via an increase in grass, forb, and berry availability (Brodeur et al., 2008). In eastern Canada, black bears are believed to be a relatively new predator of caribou-or at least, a more significant predator than before-as their presence in the boreal forest was scarce prior to the 1970s (Lamontagne et al., 2006). Current habitat conditions, which combine the physical environment and the predation pressure that stems from it (i.e., landscape of fear), are believed to differ considerably from the preindustrial forests to which caribou are adapted (Lafontaine et al., 2019).

We hypothesized that experience allows caribou to fine-tune their perception of risk in the landscape and accordingly adjust their habitat selection. This hypothesis was partly assessed by Mumma et al. (2017), who found that older female caribou displayed a more pronounced avoidance of risky areas in comparison with their younger counterparts. Our associated prediction was that the avoidance of risky areas (and the selection of safe areas) would increase throughout the lifetime of an individual, that is, with passing monitoring years, which we used as

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a proxy of experience. We assessed this hypothesis during periods of the year with high but differential predation pressure by both predators (Gable et al., 2018; Leclerc et al., 2014; Tremblay et al., 2001). Our predictions apply to both wolves and bears, but because these species have distinct evolutionary histories, life cycles, densities, and spatial organizations, we explored differences in the response of caribou toward these two predators using discrete indices of risk.

### **METHODS**

### Study area

The study area covered  $\sim$ 7000 km<sup>2</sup> and overlapped the Charlevoix boreal caribou range in Québec, Canada

(Figure 1). Topography in the area was characterized by high hills and deep valleys, with peaks reaching >1000 m. Mean annual precipitation and temperature were 1300 mm and  $0.6^{\circ}$ C, respectively (Leblond et al., 2016). The forest was representative of the balsam fir (*Abies balsamea*)–white birch (*Betula papyrifera*) bioclimatic domain (St-Laurent & Dussault, 2012); stands were mainly composed of fir and birch at low elevation and black spruce (*Picea mariana*) and fir at high elevation.

The Charlevoix caribou population was reintroduced in 1969–1972 after its extirpation from the region in the early 1920s as a result of overharvesting and poaching (St-Laurent & Dussault, 2012). After reaching a peak of 126 individuals in the 1990s, the population declined to ~21 individuals in 2020 (Hins & Rochette, 2020). During the study period, moose were the most



**FIGURE 1** Area where we assessed the ability of boreal caribou to behaviourally adjust to the risk of encountering gray wolves and black bears, in the province of Québec, Canada. The three patterned polygons represent the minimum convex polygons (MCPs) around the locations of 28 GPS-collared boreal caribou (~7000 km<sup>2</sup>), 31 gray wolves (~18,500 km<sup>2</sup>), and 12 black bears (~3000 km<sup>2</sup>). We trained predator models over the wolf and bear MCPs, but we assessed caribou habitat selection over the caribou MCP only.

abundant large herbivore in the region (estimated density of ~22 individuals/100 km<sup>2</sup>; Rochette & Dumont, 2022). Gray wolves and black bears were the main predators of caribou in the study area and reached densities of 0.44 wolves/100 km<sup>2</sup> (Jolicoeur, 1998) and 22 bears/100 km<sup>2</sup> (Jolicoeur, 2004) in the early 2000s; more recent estimates were not available. According to Environment and Climate Change Canada (2020), 80% and 4% of the Charlevoix caribou range were covered by human disturbances (mostly cutovers and forest roads buffered by 500 m) and wildfires, respectively, making it one of the most disturbed boreal caribou ranges in Canada.

# Capture and telemetry of caribou, wolves, and bears

Between 2004 and 2018, 86 adult caribou were captured and fitted with a GPS collar (see Appendix S1: Table S1). Collars recorded a location every 1, 2, or 4 h depending on collar model and year. Monitoring continued for a period of up to 8 years, ending in 2020. For the purposes of this study, we only kept data from adult females that were monitored  $\geq$ 3 years, resulting in 28 adult females monitored between 3 and 8 years (mean  $\pm$  SD: 4.4  $\pm$  2.2), for a total of 146 caribou-years. We focused our analyses on adult females because they could learn from predation attempts on their calf (Berger et al., 2001), contrary to males. Our sample of monitored males was also much smaller (n = 9).

In the same study area, the Québec government monitored gray wolves from 2005 to 2009 and black bears from 2005 to 2006 (Appendix S1: Table S1). Collars collected a location every 3 and 4 h for bears and wolves, respectively. All captures and handling procedures were approved by Animal Welfare Committees (certificates CPA 04-00-02 to 10-00-02, CPA 17-00-06 and CPA 18-00-04 for caribou, CPA-07-00-02 and CPA-27-07-53-R2 for wolves, and CPA 05-00-04 and CPA-06-00-04 for bears) and followed the guidelines of the Canadian Council on Animal Care.

## **Periods of risk**

We identified four annual periods of risk for caribou (Figure 2): (1) winter (22 December–15 March), when palatable vegetation is scarce and wolves actively hunt large herbivores such as caribou (Gable et al., 2018); (2) spring (16 March–24 May), when pregnant caribou females have high nutritional requirements, a low body condition (Cook et al., 2021) and are still being

hunted by wolves; this is also when bears start emerging from their den; (3) calving (25 May–24 June), when newborn caribou are extremely vulnerable to both predators, mainly bears in our system (Leclerc et al., 2014); and (4) summer (25 June–23 August), when caribou calves are more mobile but still vulnerable (Leclerc et al., 2014). We excluded the remainder of the year (24 August–21 December) from our analyses because this period is typically of relatively low risk for caribou in our study system. In fact, bears rarely attack caribou juveniles past the end of summer in our study area (Leclerc et al., 2014), and wolves typically use other food sources at this time (Tremblay et al., 2001).

We determined the start and end dates of each period using movement rates and net squared displacement of monitored individuals (Rudolph & Drapeau, 2012). We calculated the mean start and end dates across all individuals for each period and subtracted one standard deviation from the average starting dates. To help us with period definitions, we had access to birth dates of several calves, and births were confirmed visually via aerial surveys spaced 2–3 days apart during the calving period between 2004 and 2007 (Leclerc et al., 2014; Pinard et al., 2012). We were thus able to confirm that 93 of 102 calving events (91%) were correctly included in the calving period. We applied the same method to all periods for consistency.

## **Environmental variables**

Based on previously established caribou-habitat relationships assessed in the same study area (Dussault et al., 2012; Leblond et al., 2016; Leclerc et al., 2014), we classified 1:20,000 digital "ecoforest" maps into land cover classes using the dominant vegetation type, disturbance origin, and stand age (Table 1). Ecoforest maps are derived from aerial photos updated annually to include new disturbances (e.g., cutovers, fires). They have a spatial resolution of 4 ha for forest stands and 2 ha for nonproductive areas (e.g., lakes). We used 1:20,000 topography maps and annual road network maps to respectively build a digital elevation model (50 m resolution) from which we derived elevation and slope and to determine distance to the nearest road. We not only separated roads into major (paved and large forestry roads with frequent vehicular traffic) and minor roads (small forestry roads with low human use and high vegetation regeneration) to assess whether wolves and bears used them differentially, but also confounded all roads in some candidate models. All maps were published by the Québec government.



**FIGURE 2** Main events in the annual life cycle of boreal caribou, gray wolf and black bear, during the four periods of risk defined in this study. We delineated the start and end dates of periods based on movement rates and net square displacement of GPS-collared caribou (Animal silhouettes: from Creazilla library; bear silhouette, credit: Natasha Sinegina).

## **Predation risk**

Predation risk can be decomposed into several components, from the abundance or spatial distribution of predators in the landscape to the success rate of predators when pursuing prey in various habitat patches (Lima & Dill, 1990). As telemetry data were the most reliable source of information available to us, we modeled the spatial distribution of predators as a proxy of predation risk for caribou, based on the assumption that risk would be higher where predators are more likely to be found. Only a subset of caribou, wolves and bears wore telemetry collars in their respective populations, meaning that a spatiotemporal analysis of cooccurrence was not feasible. To model this spatial distribution of risk, we built resource selection functions (RSFs; Boyce et al., 2002) describing the habitat selection patterns of wolves and bears in our study area for each period of risk. RSFs compare the habitat characteristics at telemetry locations ("used" locations; coded 1) with those found at an equal number of points ("available" locations; coded 0) drawn randomly within an animal's home range (Boyce et al., 2002). We compared use in "seasonal" home ranges with the availability defined at the annual scale using a logistic regression to improve the contrast between seasonal use by predators and what was available to them across their entire home range. We used 100% minimum convex polygons (MCPs) to delineate home ranges for bears but 95% MCPs for wolves to exclude extraterritorial excursions.

**TABLE 1** Land cover classes considered in models of habitat selection by boreal caribou, gray wolf, and black bear in Charlevoix, Québec, Canada.

Land cover classes			Availability	
Caribou and wolf	Bear	Description	(% cover) <sup>a</sup>	
Wetlands	>90-year-old conifer stands and wetlands	Bogs, fens, flooded areas, and alder stands	2.8	
>90-year-old conifer stands		Open woodlands often rich in lichens, >90-year-old conifer stands, bare areas	10.2	
50–90-year-old conifer stands	≥50-year-old mixed or deciduous	50–90-year-old conifer stands	27.2	
≥50-year-old mixed or deciduous stands	stands, and 50–90-year-old conifer stands	≥50-year-old mixed and deciduous stands	11.2	
Regenerating stands	Regenerating stands	21–50-year-old regenerating stands originating from natural or anthropogenic disturbances	11.3	
6–20-year-old disturbances	≤20-year-old disturbances	6–20-year-old natural disturbances (mostly fires) and cutblocks	28.1	
≤5-year-old disturbances		≤5-year-old natural disturbances and cutblocks	3.6	
Other	Other	Human infrastructures, water bodies, non-regenerated areas and rare habitat features	5.7	

Note: Land cover classes are grouped in bear models to prevent overparameterization.

<sup>a</sup>Percentage of the caribou range covered by each land cover class. Values reported here correspond to the availability in 2004.

At each used and available location, we extracted land cover class, elevation (in meters), and slope. We also measured the minimum Euclidean distance (in meters) to the nearest major and minor roads. Following Carpenter et al. (2010), we converted Euclidean distances into decay distances to account for the nonlinear, decreasing impact of roads on animal behavior with distance. Decay distances varied from 0 to 1, with high values representing distances further away from roads, and we standardized elevation and slope using the scale function in R. These two operations improved model convergence and helped limit bias in the estimation of selection coefficients. We had to combine some land cover classes to avoid overparameterization for bear models (Table 1). We fit RSFs using generalized linear mixed models (GLMMs) with individual-year as a random effect on the intercept to control for pseudoreplication (Gillies et al., 2006). The resulting RSF scores informed about the intensity of selection or avoidance of environmental variables at each period by each predator separately. For each period-year, we mapped the relative probability of occurrence of wolves or bears (between 0 and 1) and extracted probability values as proxies for the risks of encountering wolves or bears (Leblond et al., 2016) under all used and available caribou locations.

## Habitat selection and use of risky areas by caribou

We also built RSFs to contrast caribou habitat use for each period of risk. We defined availability at the scale of the entire length of the monitoring period for any given individual, as determined using 100% MCPs over all years of GPS monitoring. Caribou were captured as adults or subadults (>1.5 years old). Age was estimated at capture for most individuals using tooth wear patterns, but given the significant biases (from -5 to +6 years) in the application of this method (according to Hewison et al., 1999), and because many technicians and biologists of varying levels of experience collected these data over a period of 14 years, we decided against using age estimates. This method was also found to be imprecise due to the uneven influence of different food items on tooth wear (Schaefer et al., 2016). Because we did not know the exact age of caribou, we used the beginning of the monitoring as the time of entry of individuals in our analyses. As such, the time elapsed since the beginning of the monitoring represented every passing year during which animals were subjected to experience. The effect of age was therefore included in the effect of passing years, but for reference, we note that the age distribution from tooth wear indices ranged from 1.5+ years at the beginning of the monitoring period to 9.5+ years at the end. We refer to the complete monitoring period, from the collaring of the individual to the end of its monitoring, as the "adult life" of an individual, which spanned between 3 and 8 years in our study. Not all individuals died at the end of the monitoring period; in fact, most monitoring periods ended following a programmed collar drop-off, but because we lost sight of the individual at this time, we considered the monitoring period to be the best information available to study the adult life of an individual. We built caribou RSF models using combinations of land cover classes (dummy variables), predation risk variables (continuous from 0 to 1), and interactions between predation risk and time elapsed since the beginning of monitoring. We included these interactions to test if caribou adjust their behavior to predation risk with increasing experience. In all models, we used the individual as a random effect on the intercept.

Prior to all RSFs (caribou, wolves and bears), we evaluated multicollinearity using the variance inflation factor (VIF). Maximum VIF values never surpassed 2.2 (wolves), 2.4 (bears), and 8.3 (caribou), all under the threshold suggesting collinearity problems (Graham, 2003). We evaluated multiple candidate models with different combinations of explanatory variables (including different decay distances to roads for predators) and identified the most parsimonious model using Akaike information criterion corrected for small sample sizes (AIC<sub>c</sub>). To avoid overparameterization, we ensured, for all candidate models, that the number of parameters k was smaller than the sample size n, and we validated that our approach complied with the best conditions for obtaining unbiased estimates, as found in Street et al. (2021). We considered that a covariate was "selected" when its coefficient was positive ( $\beta > 0$ ) and its 95% CI excluded zero (i.e., statistically significant); covariates were "avoided" when the same conditions were met for negative coefficients ( $\beta < 0$ ). We defined selection and avoidance of land cover classes relative to a reference category (that varied across species and periods), which corresponded to the land cover class with the use/availability ratio closest to 1. To visualize interactions, we built interaction graphs where RSF coefficients were converted into relative probabilities of occurrence ranging from 0 to 1 (equation 2 in Boyce et al., 2002). Relative probabilities of occurrence >0.5 represented selection and <0.5, avoidance. We evaluated the robustness of the most parsimonious models using k-fold cross-validation with 10 iterations (Boyce et al., 2002), and we report the mean  $r_s$  values. We conducted spatial analyses in ArcGIS 10 (ESRI, 2019) and statistical analyses in R v. 4.1.2 (R Core Team, 2021; lme4 package for RSFs).

### RESULTS

We converted the habitat selection behavior of wolves and bears into maps of relative probability of occurrence to estimate spatiotemporal variations in predation risk for caribou, but we were more interested in understanding how experience can shape caribou responses to predation risk. Thus, we focus on the caribou's response to risk but direct the reader to Appendix S1 for the habitat selection patterns of predators (candidate models: Appendix S1: Tables S2 and S3; RSF results: Appendix S1: Table S4; examples of predation risk maps: Appendix S1: Figure S1).

The most parsimonious models describing habitat selection by caribou included all land cover classes as well as the interactions between predation risk by both predators and the time elapsed since the beginning of the monitoring (Table 2). These models (one for each period of risk) were robust to cross-validation with mean  $r_s$  values ranging from 0.89 to 0.99. Across all periods, adult female caribou selected wetlands, >90-year-old conifer stands and  $\leq$ 5-year-old disturbances, and avoided 50–90-year-old conifer and  $\geq$ 50-year-old mixed or deciduous stands (Table 3). Caribou also avoided regenerating stands during all periods except spring, when they selected them. Finally, caribou selected 6–20-year-old disturbances during spring and summer but avoided them during winter.

The interaction between wolf risk and monitoring years was statistically significant during most periods, indicating that the behavior of caribou toward the risk of encountering wolves changed with time elapsed since the beginning of monitoring. However, the way in which caribou adjusted their behavior differed between periods of risk, providing only partial support to our hypothesis. During spring and summer, the relative probability of occurrence of caribou in areas with a high risk of encountering wolves decreased with passing monitoring years, and increased in areas of low wolf risk, supporting our main hypothesis (Figure 3a,c). In contrast, during the calving period, the occurrence of caribou in areas of high wolf risk increased with monitoring years. Selection remained lower than 0.50 during this period, however, indicating that caribou avoided areas suitable to wolves throughout their adult life, with the intensity of this avoidance decreasing with passing years (Figure 3b). During winter, we found no significant effect of the interaction between wolf risk and monitoring years, suggesting that, during this period, caribou avoided areas with a high risk of encountering wolves consistently throughout their adult life (Table 3). The interaction between bear risk and monitoring years was negative and statistically significant during all periods of risk,

		. 1 0	0	
Period of risk	Model	k	LL	$\Delta AIC_{c}$
Winter	Land cover + wolf risk × monitoring year	13	-80,818.12	0.00
	Land cover + wolf risk	11	-80,822.68	5.11
	Land cover	10	-81,027.72	413.20
	Wolf risk	4	-87,295.54	12,936.82
Spring	Land cover + wolf risk × monitoring year + bear risk × monitoring year	15	-84,851.65	0.00
	Land cover + wolf risk $\times$ monitoring year + bear risk	14	-84,887.69	70.08
	Land cover + wolf risk + bear risk $\times$ monitoring year	14	-84,935.04	164.78
	Land cover + wolf risk + bear risk	12	-84,956.02	202.74
	Land cover + wolf risk	11	-85,158.96	606.63
	Land cover + bear risk	11	-88,571.07	7430.84
	Land cover	10	-89,738.69	9764.07
	Wolf risk + bear risk	5	-90,539.93	11,356.56
Calving	Land cover + wolf risk × monitoring year + bear risk × monitoring year	15	-37,763.18	0.00
	Land cover + wolf risk + bear risk $\times$ monitoring year	14	-37,765.45	2.55
	Land cover + wolf risk $\times$ monitoring year + bear risk	14	-37,830.91	133.45
	Land cover + wolf risk + bear risk	12	-37,842.03	151.69
	Land cover + wolf risk	11	-37,879.52	224.67
	Land cover + bear risk	11	-38,242.87	951.39
	Land cover	10	-38,393.57	1250.77
	Wolf risk + bear risk	5	-39,683.65	3820.93
Summer	Land cover + wolf risk × monitoring year + bear risk × monitoring year	15	-56,851.78	0.00
	Land cover + wolf risk + bear risk $\times$ monitoring year	14	-56,896.19	86.83
	Land cover + wolf risk $\times$ monitoring year + bear risk	14	-56,973.70	241.84
	Land cover + wolf risk + bear risk	12	-57,217.22	724.89
	Land cover + bear risk	11	-57,231.08	750.61
	Land cover + wolf risk	11	-57,355.15	998.75
	Land cover	10	-57,384.77	1055.98
	Wolf risk + bear risk	5	-62,362.62	11,001.68

**TABLE 2** Candidate models used to describe habitat selection by 28 adult female caribou monitored in the Charlevoix region of Québec, Canada (years of monitoring: 2004–2012 and 2017–2020), during each period of risk (winter, spring, calving, and summer).

*Note*: Included are the number of parameters used in each model (k), the log-likelihood (LL), and the difference in Akaike information criterion corrected for small sample sizes (AIC<sub>c</sub>) value between each model and the most parsimonious model ( $\Delta$ AIC<sub>c</sub>).

supporting our hypothesis (Table 3). The relative probability of occurrence of caribou decreased with passing monitoring years in areas with high risks of encounters with bears, and increased in areas of low risk, for all periods (Figure 3d–f).

## DISCUSSION

We sought to assess whether adult female caribou adjusted their antipredator behavior—more specifically their avoidance of areas with high risks of encountering wolves or bears—as they gained experience, with a focus on four particular periods of risk during which predation pressure was likely to be high for adults or calves. With every passing monitoring year, we found an increase in the avoidance of areas where the risk of encountering wolves (for two periods) and bears (for all periods) was high, suggesting that caribou generally became more efficient at avoiding risky areas as they gained experience. During calving and winter, we found no evidence that caribou adjusted their behavior to the risk of encountering wolves as time passed, bringing some nuances in our understanding of caribou responses toward the main predator with which they coevolved. Bear risk

Validation  $(r_s)$ 

Wolf risk  $\times$  monitoring year

Bear risk  $\times$  monitoring year

<b>TABLE 3</b> Selection coefficients ( $\beta$ ) and 95% CI of the most parsimonious models describing habitat selection by 28 female caribou in the Charlevoix region of Québec, Canada, during each period of risk (winter, spring, calving, and summer).										
		Winter Spring		Spring	Calving		Summer			
Variable	β	95% CI	β	95% CI	β	95% CI	β	95% CI		
Wetlands	0.14	0.05 to 0.23	2.01	1.91 to 2.11	1.24	1.15 to 1.34	0.90	<b>0.82</b> to <b>0.97</b>		
>90-year-old conifer stands	1.13	1.06 to 1.19	1.24	1.16 to 1.31	0.02	-0.04 to 0.07	Ref.			
50-90-year-old conifer stands	-0.02	-0.09 to 0.04	-0.21	<b>-0.29</b> to <b>-0.13</b>	-0.46	<b>-0.51</b> to <b>-0.40</b>	-0.43	-0.48 to -0.39		
≥50-year-old mixed-deciduous stands	-0.06	-0.15 to 0.04	Ref.		-0.21	<b>-0.31</b> to <b>-0.12</b>	-0.49	-0.58 to -0.40		
Regenerating stands	-0.73	<b>-0.80</b> to <b>-0.65</b>	0.48	0.40 to 0.56	-1.01	<b>-1.07</b> to <b>-0.94</b>	-0.88	-0.94 to -0.82		
6-20-year-old disturbances	-0.46	-0.53 to -0.39	1.53	1.46 to 1.61	Ref.		0.74	<b>0.68</b> to <b>0.80</b>		
≤5-year-old disturbances	Ref.		1.20	1.11 to 1.28	0.97	0.89 to 1.06	2.57	2.48 to 2.66		
Other	0.57	0.50 to 0.64	0.99	<b>0.91</b> to <b>1.07</b>	-0.09	-0.17 to 0.00	0.29	0.22 to 0.37		
Wolf risk	-1.82	-2.16 to -1.47	-5.07	-5.32 to -4.82	-2.63	-2.93 to -2.33	1.30	1.07 to 1.54		

1.04

-0.37

-0.11

0.94

0.93 to 1.16

-0.43 to -0.32

-0.14 to -0.09

0.50

0.08

-0.31

0.99

u in

Note: For each period, the land cover class with the use/availability ratio closest to 1 was chosen as the reference category (Ref.). Coefficients for which the 95% CI did not include 0 are indicated in bold and are considered to have a significant influence on caribou habitat selection. Bears were excluded from winter models as they are in torpor at that time.

Our results are in relative agreement with those of Mumma et al. (2017), who found that older adult female caribou in British Columbia avoided the risk of encountering wolves more so than younger ones. These results may reflect the capacity of female caribou to "learn" to perceive risks and adjust their antipredator behavior based on their experience with predators and the habitat cues associated with them (Fagan et al., 2013; Gaynor et al., 2019; Laundré et al., 2010). Risk perception in caribou could have become more fine-tuned through life experiences, such as close encounters with predators or through social learning (Griffin, 2004; Kieffer & Colgan, 1992; Laundré et al., 2010). Losing a calf to predation was another likely pathway; for example, Berger et al. (2001) found that female moose that lost their calf to wolves altered their level of vigilance in their subsequent calving period when in contact with cues of wolf presence. In our study area, ~33% of caribou calves died from predation in the first 50 days following their birth, most of them (94%) preyed upon by black bears (Pinard et al., 2012), meaning that most adult females in Charlevoix experienced the death of a calf but survived to learn from the experience. Thus, unsuccessful reproduction events over time could have improved the mothers' ability to recognize and avoid habitat cues associated with their calf's predator, such as patches rich in forbs, grasses, and fruit-bearing shrubs selected by black bears (Brodeur et al., 2008). This adjustment of habitat

-0.04

0.89

-0.11 to 0.03

selection and space use tactics to avoid predation risk was likely adaptive, as in our study area, females adopting safer tactics were shown to have a higher survival rate for both themselves and their calf (Leblond et al., 2016; Leclerc et al., 2014; Losier et al., 2015).

0.29 to 0.72

0.01 to 0.15

-0.36 to -0.25

We expected caribou to show strong behavioral adjustments toward areas used by wolves during winter and calving, when wolves are typically a significant threat to caribou and large ungulates in general (Tremblay et al., 2001). In contrast, their response was to avoid habitat conditions suitable to wolves during these periods, either consistently or less intensively as years went by. This suggests that the level of avoidance expressed by caribou toward wolves at the beginning of their monitoring period may have been sufficient to cope with the predation risk imposed by wolves. There are at least two likely explanations for this. First, as a result of coevolution, caribou could have expressed innate responses to wolves of a sufficient magnitude that no adjustment was required, as observed in other species (Hébert et al., 2019). Such an adapted response would be in line with other antipredator traits in caribou, such as their physiological ability to digest lichens found in old-growth conifer patches (Parker et al., 2005), away from other ungulates and their shared predators (James et al., 2004). Caribou could also have learned to avoid wolf cues from their mother at a very young age, before they were collared. In our study area, Larue et al. (2018)

-0.46 to 0.17

-0.29 to -0.19

-0.48 to -0.37

-0.14

-0.24

-0.42

0.99



**FIGURE 3** The relative probability of occurrence of caribou as a function of years elapsed since the beginning of monitoring (proxy of experience) and different levels of risks of encountering (a–c) gray wolf or (d–f) black bear (bottom row). We used interactions to highlight changes in the selection patterns of caribou toward risky areas over the course of their adult life. The panels represent the response of caribou to the risk of encountering wolves and bears during spring (16 March–24 May), calving (25 May–24 June), and summer (25 June–23 August) periods of risk. The winter period is not represented in this figure, as the interaction between wolf risk and monitoring years was not significant, and bears are in torpor at that time. Relative probabilities of occurrence >0.5 represent a selection of areas suitable to a given predator, whereas values <0.5 represent avoidance. The risk of encounter represents the relative probabilities of occurrence of each predator, which we estimated for every pixel of the study area, based on selection coefficients from predator resource selection functions. Shaded areas represent 95% CIs around estimated probabilities from our models (Animal silhouettes: from Creazilla library; bear silhouette, credit: Natasha Sinegina).

showed that caribou often repeated the habitat selection tactics of their mothers, which they had witnessed as calves. We cannot conclude whether the response of caribou to wolves during winter and calving was innate or acquired early in life (or potentially both); answering this question will require data from individuals followed from birth, paired with genetic information on pedigree and trait heritability.

Female caribou selected  $\leq$ 5-year-old disturbances that were also selected by bears, which corroborates previous studies conducted in the same study area. Dussault et al. (2012) and Leblond et al. (2016) interpreted this behavior as maladaptive, caused by a lack of opportunities to adjust to the high predation pressure imposed by black bears. Contemporary bear densities are much higher than those encountered historically (Lamontagne et al., 2006), and

caribou could be more naive toward bears, at least during their early life, due to a lack of historical exposure to bears. However, our findings challenge the notion that this naivety persists throughout their lifespan. Instead, our results suggest that experience acquired over the course of their lives may have allowed caribou to adjust their behavior to this novel predator and partially compensate for the lack of innate responses toward bears (as conceptually suggested by Sih et al., 2010). The effect of experience on the response of prey to novel predation conditions has been suggested in different species in both laboratory and field studies (e.g., common bully, Gobiomorphus cotidianus: Kristensen & Closs, 2004; northern brown bandicoot, Isoodon macrourus: Bytheway & Banks, 2019) and is believed to be crucial in explaining how prey species may cope with rapid changes in predation pressures

induced by human activities (Sih et al., 2011). In addition, caribou may be less efficient at predicting the location of bears, an opportunistic predator in this system, despite attempting to spatially separate themselves from predators and alternate prey to reduce predation risk (e.g., James et al., 2004; Peters et al., 2013). Studies have shown that bears exhibited a wide range of behavioral responses, with most individuals selecting areas with abundant vegetation such as mixed forest stands and linear features, and a smaller fraction of the population seeking habitat components used by caribou (Bastille-Rousseau et al., 2011; Latham et al., 2011; Rioux et al., 2022). These individuals may have been responsible for the bulk of the predation on caribou calves observed in our study area (Leclerc et al., 2014; Pinard et al., 2012).

Prey facing multiple predators may have to prioritize the avoidance of one over another, when avoiding all of them is impossible. Previous research in the same study area showed that female caribou that strongly avoided wolves were found in areas favorable to bears, and vice versa (Leblond et al., 2016). This outcome stemmed from the distinct habitat preferences of wolves and bears combined with the abundance of habitat patches suitable to both predators in the landscape, preventing caribou from avoiding both wolves and bears at the same time. This offers a potential explanation for our observed reduction in caribou's avoidance toward wolves during the calving period. Given that female caribou improved their avoidance of bears, they may have had to lessen their avoidance of wolves due to a lack of suitable alternatives in this highly disturbed landscape. This would seem like a good compromise, as females that adopted an intermediate strategy of avoidance toward both predators during calving demonstrated higher probabilities of survival for their calves (Leblond et al., 2016).

By monitoring individuals over a long period of time (3-8 years), we were able to assess behavioral adjustments made by caribou during their adult life. This is an important contribution and a superior design compared with studies contrasting responses of individuals from different age groups. Indeed, older age groups may contain less risk-prone individuals due to their typically higher mortality rate compared with risk-averse individuals (Mumma et al., 2017), which may in turn bias results toward a greater risk avoidance by older individuals. There remains a possibility that the more risk-prone individuals in our study system died early compared with the more risk-averse individuals (i.e., survival selection bias), which was raised as a methodological concern in a similar study by Perry et al. (2020). We partially controlled for this influence in our analyses by allowing intercepts to vary across individuals, meaning that all individuals, on average, whether they were averse or prone to risk,

showed evidence of adjustment to risk throughout their life. We also note that in our study, we lost track of most individuals owing to a collar drop-off rather than the death of individuals, making our analyses less sensitive to the potential censoring of risk-prone individuals with increasing monitoring years.

Knowing the age of individuals would have allowed us to test for more detailed predictions. For example, it is plausible that behavioral adjustments would show nonlinear relationships with age, for example, a faster rate of adjustment early in an individual's life and a slower rate thereafter (Culler & Girden, 1951). For example, a single encounter with a new predator was enough for juvenile fence lizards (*Sceloporus undulatus*) to develop an effective antipredator response (Robbins & Langkilde, 2021). Unfortunately, age estimates based on tooth wear were not reliable enough to allow for such analyses. Nevertheless, the fact that a signal consistent with our hypothesis was observed at the population level supports the existence of behavioral adjustments to risk with passing years in adult caribou, irrespective of their age.

Several factors must be considered when evaluating predation risk for prey, in addition to the relative probabilities of spatial co-occurrence with predators (Lima & Dill, 1990). For instance, in our study area, bear densities were about 50 times higher than those of wolves, making the absolute probability of encountering a "static" bear much greater than the probability of encountering a "static" wolf. Of course, wolves are also much more mobile than bears, meaning that the actual rate of encounter between caribou and both predators may depend on a complex interaction between local densities, movement rates, and habitat composition. Without robust, spatially explicit estimations of bear and wolf densities, we were unable to map these variations. The inclusion of recent predator density data in our models would improve our understanding of caribou antipredator behaviors in a multi-predator system (e.g., Fryxell et al., 2020). Nevertheless, our assessment of the relative predation risk imposed by bears and wolves, via their respective relative probability of occurrence, offers a sound-albeit incomplete-picture of the behavioral compromises that female caribou need to make to survive and keep their calf alive.

Finally, we recognize that other factors, such as individual differences (e.g., boldness; Thurfjell et al., 2017), range fidelity (Kreling et al., 2021), and historical exposure to natural (Lafontaine et al., 2019) and human disturbances (Leclerc et al., 2014), may have contributed to explain the behavioral adjustments to predation risk we found. Future work should aim not only at integrating some of these mechanisms, but also at relating the individual differences in behavioral adjustments to their impacts on reproductive success and survival, to determine whether females that adjusted their antipredator behaviors were also more likely to survive, or have their calf survive.

### CONCLUSIONS

The conservation of boreal caribou presents a significant challenge due to the substantial predation pressure they face, which is anticipated to amplify in the coming decades owing to the growing impact of the logging industry on boreal landscapes in conjunction with the projected intensification of climate change (Leblond et al., 2022). Our study provides empirical support that caribou may adjust their behavior as they gain experience with predation risk. These results are consequential for caribou conservation, as well as wildlife conservation in general, because they suggest that experience may allow prey to cope with predation risk during their lifetime. This is particularly relevant in areas submitted to novel conditions benefiting predators, such as increasingly disturbed landscapes. Provided that behavioral adjustments to predation risk are heritable and confer fitness advantages to the individuals that show the greatest adjustments (which is likely considering the known benefits of predator avoidance on the survival of large mammals; DeCesare et al., 2014; Leclerc et al., 2014; Losier et al., 2015), such behaviors could lead to local adaptations at the population level, an avenue that will need to be explored in future studies. That being said, the current rate of habitat degradation in caribou ranges across Canada could outpace the rate at which caribou could potentially adjust to changes in the landscape of fear. In the interim, conservation measures aiming at reducing predation pressure and protecting remnant predator-free areas will be key for the conservation of the species.

### **AUTHOR CONTRIBUTIONS**

Laurie Derguy contributed to formal analysis, investigation, methodology, validation, and writing—original draft. Mathieu Leblond contributed to conceptualization, funding acquisition, investigation, methodology, project administration, supervision, validation, and writing review and editing. Martin-Hugues St-Laurent contributed to conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, and writing—review and editing.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data (Derguy et al., 2024) are available from Dryad: https:// doi.org/10.5061/dryad.02v6wwq5c. The caribou location data can be made available upon request; it is considered sensitive information. Requests should be directed to the wildlife division of the Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs at donneescaribous@mffp.gouv.qc.ca.

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### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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