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Individual responses to novel predation risk and the emergence of a landscape of fear

Thomas A. Perry,[1] Michel P. Laforge,[2,†] Eric Vander Wal,[2]
Thomas W. Knight,[3] and Philip D. McLoughlin[1]

[1]*Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2 Canada*
[2]*Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1B 3X9 Canada*
[3]*Parks Canada Agency, GMNP, Rocky Harbour, Newfoundland and Labrador A0K 4N0 Canada*

Citation: Perry, T. A., M. P. Laforge, E. Vander Wal, T. W. Knight, and P. D. McLoughlin. 2020. Individual responses to novel predation risk and the emergence of a landscape of fear. Ecosphere 11(8):e03216. 10.1002/ecs2.3216

Abstract. Elucidating changes in prey behavior in response to a novel predator is key to understanding how individuals acclimate to shifting predation regimes. Such responses are predicted to vary among individuals as a function of the level of risk to which individuals are exposed, temporal changes in risk, and landscape-mediated changes in perceived risk. We tested how GPS-tracked moose (*Alces alces*, $n = 19$) responded to an emerging risk landscape with the introduction of hunting to a naïve population (large-scale reduction experiment in Gros Morne National Park, Canada). We predicted that predation risk associated with hunters would influence moose habitat selection: Avoidance responses would be stronger during the day when hunting was allowed, and moose would learn to avoid risky locations which would strengthen in successive years for survivors occupying overall riskier home ranges. We found that moose avoided areas associated with a high risk of encounters with hunters but did not alter selection patterns between day and night. We did not find evidence of moose reacting more strongly to emerging risk as a function of risk within their home range. Moose did not increase their avoidance of areas associated with hunter risk across years but over time survivors selected non-hunted refuge areas more frequently. Our results suggest that while moose did not adjust fine-scale habitat selection through time to increased hunting risk, they did adjust selection at broader scales (based on proportions of hunter-free habitat included in home range relative to study area). This finding supports the hypothesis that habitat selection at larger spatio-temporal scales may reflect behavioral responses to a population's most important limiting factors, which may not be apparent at finer scales.

Key words: *Alces alces*; functional response; habitat selection; hunting; landscape of fear; moose.

Received 11 April 2020; accepted 5 May 2020. Corresponding Editor: James W. Cain.

† **E-mail:** m.laforge@mun.ca

INTRODUCTION

Understanding how the costs and benefits of anti-predator behaviors trade off remains enigmatic for most natural populations; however, the consequences of predation risk to prey space use and subsequently population dynamics and community ecology is increasingly becoming a topic of interest (Laundré et al. 2014, Suraci et al. 2016, Gallagher et al. 2017). The return of anti-predator behavioral strategies (Laundré et al. 2001) and subsequent costs to fitness (Creel et al. 2007) in elk (*Cervus canadensis*) following the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park has become a distinguished example of how the risk of predation can affect not only prey behavioral patterns and population dynamics, but also shape landscapes through behaviorally mediated trophic cascades (Ripple and Beschta 2012).

Following this germinal work, the landscape of fear (LOF) has been advanced as a concept to describe the spatial variation in prey perception of predation risk (Laundré et al. 2014, Gaynor et al. 2019). In practice, the LOF is typically applied at the population level by evaluating the collective behavioral response of a group to some construct of perceived predation risk (Bleicher 2017). Despite application in a growing number of predator–prey systems, only recently has research begun to evaluate the mechanisms underlying the LOF at the individual level (Ciuti et al. 2012, Lone et al. 2015), with consequences for understanding the LOF at the population level.

When considering the effects of predation risk on prey animal behavioral patterns, the LOF has only recently begun to evaluate increasingly relevant considerations in animal ecology. First, individuals vary in their propensity to take risks (Møller and Garamszegi 2012). The reaction to perceived risk may be dependent on an individual's immediate circumstances, for example, habitat heterogeneity (Schmidt and Kuijper 2015), distance to refuge (van der Merwe and Brown 2008), or group size (van Schaik et al. 1983), as well as individual state, for example, stress levels (Real and Caraco 1986), body condition (Bleicher and Dickman 2016), and parasitic loads (Raveh et al. 2011). Hence, persistent differences or syndromes in anti-predator responses among individuals should be expected. Secondly, perception of risk is likely to vary as a function of time of day (Kohl et al. 2018), with individuals often undertaking diel migrations to avoid increased predation risk at times when predators are more abundant or active (Courbin et al. 2019). Third, rarely do applications of the LOF concept account for behavioral plasticity within individuals, for example, risk-avoidance behavior over an environmental gradient such as the availability of risk and refuge habitats on the landscape (Hebblewhite and Merrill 2008) with consequences for a functional response in habitat selection (Mysterud and Ims 1998). Finally, the strength of a response to a landscape of fear will likely be dependent on the degree to which habitats used for safety are discrete from habitats used for foraging, with the responses decreasing as foraging and safety habitats intersect (Atuo and O'Connell 2017). Evaluating individual-level response to risk would do much to understand how animals may balance trade-offs in anti-predator behaviors, leading to better predictions of how populations will respond to the presence of predators.

Moose (*Alces alces*) hunting was initiated in Gros Morne National Park of Canada (GMNP), Newfoundland in 2011 to decrease numbers of hyperabundant moose. This offers a unique quasi-experimental opportunity to test how anti-predator behaviors manifest, over time and on an individual basis, in a predator-naïve moose population. Moose were introduced to Newfoundland early in the 20th century and exist without wolves as a major predator, which were extirpated in the 1930s. Further, since the establishment of GMNP in 1973 hunting had been prohibited in the Park. As a result, the moose population increased to a point of overabundance (some of the highest densities of moose reported in North America, 7 moose/km^2; McLaren et al. 2000), necessitating the need for management through regulated sport hunting (Gros Morne National Park, *unpublished report*). The objectives of the cull, where an estimated 1000 moose were culled from 2011 to 2014, was to reduce moose numbers to counteract overbrowsing of natural vegetation, principally through a direct numerical response. However, there is also the potential for a behaviorally mediated trophic cascade as the introduction of human hunters to the system exposed moose to intense predation risk that was previously absent.

We aimed to test individual-level plasticity and population-level functional responses of moose (n = 19 adult females) to human hunting risk in a system with a newly implemented hunting program. We were specifically interested in how the implementation of hunting as a management tool resulted in changes to the overall spatial distribution of risk across the landscape for moose and how moose selection patterns changed as a result. Specifically, we aimed to test the following predictions developed according to the LOF framework:

(P_1) hunter predation risk would be a significant predictor of moose habitat selection in GMNP;

(P_2) as hunters were restricted to daylight hours, individuals would avoid hunter risk most strongly during the day;

(P_3) as hunters are known to consistently select for easily accessible features, for example, roads, trails, and open habitat types (Lebel et al. 2012), the strength of moose avoidance to hunter risk would strengthen over successive years as individuals learn to recognize and avoid risky features;

(P_4) as moose home ranges vary in their availability (exposure) to hunter risk depending on their placement on the landscape, for example, proximity to roads, the population would demonstrate a functional response in habitat selection, that is, more risk in an individual's home range would result in stronger avoidance of risk by shifting selection to habitats that are perceived as having less risk.

METHODS

Study area

The study area was located in Gros Morne National Park (GMNP; 49°41′22″ N 57°44′17″ W), Newfoundland, Canada. GMNP is influenced by Gulf of St. Lawrence weather patterns producing cool summers and mild winters, with annual precipitation levels between 1200 and 1450 mm (Damman 1983). The region is dominated by balsam fir (*Abies balsamea*) forests interspersed with networks of bogs and rivers (Damman 1983).

Data collection

*Moose telemetry data.—*In March 2011, we captured adult female moose ($n = 19$) from a helicopter using a remote drug delivery system. Animal capture and handling were conducted in accordance with guidelines of the Canadian Council on Animal Care, University of Saskatchewan protocol 20110025. All work was conducted in accordance with Parks Canada Agency Research and Collection permit GMP-2011-7633. We equipped moose with GPS collars (Lotek Engineering, Newmarket, Ontario, Canada) programmed to attempt a GPS fix at 4-h intervals. All GPS locations were screened for large positional outliers and positions collected within 24 h of capture ($n = 132$) were excluded. We limited the time frame of our analyses to correspond to the 2011/12–2013/14 moose hunting seasons in GMNP. There were minor changes to the hunting area boundaries across years; however, these changes did not affect the area where moose were collared, and all moose were accessible to hunters each year of analysis. There were also minor changes to the timing of the hunting season. The initial moose hunting season in Gros Morne National Park began on 11 October 2011 and ran to 8 January 2012 (89 d total, hereafter 2011 hunting season). Season length was extended during the 2012–2013 hunting season to run from 9 October 2012 to 27 January 2013 (110 d total, 2012 hunting season) and pushed forward roughly a week in the 2013–2014 hunting season from 15 October 2013 to 2 February 2014 (110 d total, 2013 hunting season), with an early season beginning in select regions of the park. We thus had to assume that these changes did not affect the spatial or temporal risk affecting moose behavior. Following scheduled collar drop off or animal mortality, data were retrieved periodically throughout the three-year study period resulting in $n = 19$, $n = 11$, and $n = 7$ moose equipped with GPS collars from the 2011–2013 hunting seasons, respectively.

*Hunter kill site data.—*Prior to the beginning of hunting season in GMNP, Parks Canada staff distributed voluntary sampling kits to hunters to collect information on moose kill sites. The predominant methods of hunting in Gros Morne National Park included hunting on foot in search of moose (hunting with dogs or on all-terrain vehicles was not permitted in the Park), calling moose during the rutting period, and sit and wait tactics. Where possible, field staff verified the location of moose kill sites. This resulted in kill location data for $n = 69$, $n = 64$, and $n = 60$ kill sites across the 2011–2013 hunting seasons, respectively. This represented 43% (69/160), 13% (64/490) and 13% (60/463) of total hunter kills in the 2012, 2013, and 2014 hunting seasons, respectively.

Defining hunter risk

To define the landscape of fear in GMNP, we developed resource selection functions (RSFs; Manly et al. 2002) based on moose kill location data collected during the three hunting seasons over which data were collected. RSFs are statistical models that rely on logistic regression to predict the relative probability of selection for a resource unit by an animal on a defined landscape (Boyce et al. 2002). Most studies examining predator risk effects have relied on proxies assumed to capture predation risk, such as distance to anthropogenic features (Proffitt et al. 2010), or open areas (Padié et al. 2015) without capturing spatial events with clear costs of selection (but see Haines et al. 2012, Lone et al. 2014). We defined the probability of a fatal encounter with a hunter for moose across the landscape using logistic regression based on moose kill sites and sites that would be available for moose to be killed, analogous to a population-level RSF (Thomas and Taylor 2006). As we did not estimate the probability of hunter encounter (Hebblewhite et al. 2005) and rather the probability of a fatal encounter, we may have underestimated total predation risk on the landscape. However, our expectations were that the environmental correlates associated with moose kill sites would be perceived as risky across the landscape as there was direct evidence of a cost of selection.

Habitat covariates for the model predicting likelihood of lethal encounter between hunters and moose included landcover with a 30 × 30 m spatial resolution. We reduced habitat type to two classifications: open habitats (which included wetland, rocky areas, lichen, and conifer scrub) and closed habitats (conifer, mixedwood, and broadleaf forest). We quantified the proportion of open and closed habitat in a buffer of 100 m radius surrounding each used (hunter kill) and available (random) location. This helped account for the fact that moose likely did not die in the exact spot where they were shot. We also quantified distance to nearest road, as well as distance to nearest linear feature, which included hiking trails, power lines, and snowmobile trails. We also used elevation data to generate an estimate of terrain ruggedness using the *terrain* function in package raster (Hijmans 2019). We dropped elevation itself from our analyses however, as it was correlated with distance to roads, and we predicted that distance to roads would be a more significant predictor of hunting success than elevation. All analyses were performed in R version 3.6.1 (R Core Team 2019). All spatial analyses were conducted using R package raster v. 3.0-2 (Hijmans 2019).

The resource selection function model follows the binomial logistic regression equation:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k) \qquad (1)$$

where $w(x)$ is the relative probability of selection as a function of covariates x_1 to x_k and β_1 to β_k are the values of resource selection coefficients estimated from fixed-effects logistic regression. We followed a used/available design where used kill locations were compared to a sample of 10,000 randomly generated available points (Barbet-Massin et al. 2012) generated within GMNP's permissible hunting area for that year/combination of years (corresponding to the second order of selection; Johnson 1980). A list of a priori candidate models containing landscape covariates relevant to hunter selection patterns (Lebel et al. 2012) were evaluated using Akaike's information criterion (AIC; see Table 1).

We were interested in how moose hunting pressure changed through time. We assumed that a risky landscape in year one would be associated with risk in year two, therefore, we produced hunter risk models at three temporal scales, one incorporating only the first year of hunting data, the second including years 1 and 2, and finally a model using all three years of data. These models were then used to generate a map of hunter risk in each year, including carryover effects from previous year(s). These maps were then used to quantify hunter risk in moose resource selection models.

Moose habitat selection and hunter risk

Modeling animal resource selection provides the basis for quantifying predator and prey space-use patterns and for predicting the effects of a LOF. Predicting how animals may use risky habitat is traditionally modeled using resource selection functions (e.g., McLoughlin et al. 2010). Typically, these models have focused on providing population-level (mean) estimates of resource selection. More recently methods that incorporate random, or conditional, effects in the traditional RSF framework have enabled the estimation of both population- and individual-level responses to resource variables of interest (Gillies et al. 2006, Dzialak et al. 2011*a*, *b*). This framework has been extended to provide a

Table 1. Candidate models and Δ Akaike's information criterion (ΔAIC) for resource selection function models describing relative probability of moose being killed by hunters in Gros Morne National Park in the first three years since hunting first began in the park.

Model	Covariates	Δ AIC − Year 1	Δ AIC − Year 1 + 2	Δ AIC − Year 1–3
Full	Open habitat + terrain ruggedness + distance to roads + distance to linear features	0	0	0
Anthropogenic	Distance to roads + distance to linear features	3.40	19.96	43.77
Roads	Distance to roads	25.79	68.30	50.78
Natural	Open habitat + terrain ruggedness	87.24	175.23	185.11
Null	None	138.60	262.42	306.37

means to evaluate consistent individual differences in animal selection patterns within populations (Benson et al. 2015, Leclerc et al. 2016), an application of conditional estimates commonly employed in behavioral ecology (Dingemanse and Wolf 2010). We take a similar approach to explore how variation in predation risk influences individual prey resource selection strategies across a changing gradient of predation risk.

To define available habitat in our models, we generated 95% kernel home ranges for each moose using R package adehabitatHR v. 0.4.16 (Calenge 2006) using the ad hoc smoothing parameter (href). Random points (1:1 ratio used: available) were then generated within the home range to define available habitat for each individual, corresponding to a third-order analysis sensu Johnson (1980). Covariates included in the analyses included proportion of landcover types within a 100 m buffer based on 30 × 30 m Landsat imagery, elevation, hunter risk, year, and whether the location was within the allowable hunting zone.

To fit our RSF models, we used a Bayesian framework to fit generalized linear mixed-effects models using package MCMCglmm v. 2.29 (Hadfield 2010). Bayesian regression models use Markov Chain Monte Carlo sampling to yield robust parameter estimates and credible intervals based on the highest posterior distribution and therefore provide more exact measures of confidence than often imprecise standard errors derived using a frequentist approach (Hadfield 2010). Our model included random intercepts for year plus individual nested in year. Including random intercepts for individuals allowed us to account for differences in sample sizes among individuals (Gillies et al. 2006). We included the random intercept for year to assign used and available points to the correct year within the model.

For our models, we used uninformative priors for fixed effects that were normally distributed with mean = 0 and a large variance (10^8). We fixed the residual variance at 1 as recommended for binary response GLMMs (Hadfield 2010). We specified an inverse-Wishart distributed prior for random effects with variance = 1 at the limit and low belief parameter nu = 0.002. Using a low value for nu reflected the lack of prior information in our models (Reid and Sun 2010). We ran models for 150,000 iterations with a burn-in period of 50,000 and thinning interval of 100.

We divided location data between day/night according to the mean monthly sunset and sunrise times. For both day and night, we created five a priori candidate models to test our predictions involving the influence of hunter predation risk on moose habitat selection patterns (P_1–P_3; see Table 2). We evaluated the fit of all models using Deviance Information Criterion (DIC) with lowest values indicating more plausible model explanations (Hadfield 2010). We first evaluated four candidate models with different fixed-effect parameters:

1. The risk model was only composed of the hunter risk covariate as a fixed effect to explain moose selection patterns.
2. The natural model included all six habitat variables (wetland, conifer, mixed-wood, rock, and lichen) and elevation.
3. The landscape model included the natural model, with the addition of our hunter risk covariate.

Table 2. Candidate models to assess resource selection and hunter risk avoidance by moose (n = 19) in Gros Morne National Park, NL, from 2011 to 2014.

Model	Fixed effects	Random slopes	ΔDIC, day	ΔDIC, night
Risk	Hunter Risk	1	1504.9	824.1
Natural	Wetland + Broadleaf + Conifer + Mixed-wood + Rock + Lichen + Elevation	1	378.7	321.8
Landscape	Natural + Hunter Risk	1	113.4	135.4
Refuge	Landscape + Year × Refuge†	1	9.8	2.4
Individual response	Landscape + Year × Refuge†	Hunter Risk × Year + Hunter Risk × (Year × ID)	0	0

Notes: Δ deviance information criterion from the top model presented for resource selection for both day and night. All models were fit with random intercepts for year and moose ID nested in year.

† Refuge refers to a binary variable of whether locations were located within the permissible hunting zone.

4. The refuge model included the landscape model in addition to the interaction between year and a refuge variable (whether individuals were outside the permissible hunting zone).

If the covariate for hunter risk was included in the most parsimonious model, we then evaluated an individual response model by incorporating random slopes (Hebblewhite and Merrill 2008) for hunter risk to the model. We fit random slopes for both year (to evaluate changes in risk-avoidance behavior across years), and ID nested in year to fit individual moose responses across years. This enabled us to test if individual responses to hunter predation risk would improve model fit (P_4).

To evaluate the behavioral plasticity of individuals across a gradient of risk, that is, an individual's functional response in selection of risky habitat, we estimated the mean coefficient to hunter risk for each individual moose (estimated using random slopes for individual-years) and plotted estimates as a function of mean risk within an individual's home range (Fig. 1a, b).

RESULTS

Hunter RSFs

The top RSF model for all three sets of hunter kill location data (year 1, years 1 + 2, and years 1–3) showed similar patterns, with hunter kill sites generally not occurring in open areas or areas far from roads and linear features. Hunters also killed moose in areas associated with low terrain ruggedness, although this was not significant using only the first year of data. Distance to roads did not change significantly with the addition of more years of data, although the strength of selection for linear features did decline when all three years of data were considered, suggesting that hunters may have had to travel further from linear features to find/kill moose in the third year of hunting (Table 3). These RSFs were then used to quantify risk to moose from hunters in our moose RSFs.

Moose RSFs

A total of 21,764 GPS locations were used to generate moose resource selection functions, with a total of 10,825 points occurring during the day and 10,939 points at night. Due to scheduled GPS release (n = 5), hunter mortality (n = 5) and other mortality (n = 2), the total sample size declined through time, resulting in a sample size of n = 19, n = 11 and n = 7 individual moose in the 2011–2013 hunting seasons, respectively.

Moose avoided wetlands and areas with high elevation during both day and night, while selecting for forested areas and lichen. Moose also marginally selected for rocky areas at night (Table 4). Consistent with P_1, moose significantly avoided areas associated with hunter risk during both the day (β [90% credible interval] = −2.450 [−2.931, −1.964]) and at night (−1.978 [−2.429, −1.576]). All individuals avoided areas associated with high hunter risk, however the relationship was not significant for 7/37 (19%) of ID × year combinations during the day and 11/37 (30%) of ID × year combinations at night (Fig. 1a, b). Estimates for each individual/year were determined by summing the value of the fixed effect for hunter risk, along with the corresponding random slope to hunter risk for both year and year × ID combination. Significance was determined by summing the lower and upper 90% credible interval bounds for the three parameter estimates.

We failed to detect a significant difference in selection for areas associated with hunter risk between day and night. While the estimate for hunter risk avoidance was higher during the day than at night, the 90% credible intervals for the two estimates overlapped, suggesting no difference in selection at night versus during the day, counter to P_2. Individual-level responses did differ in magnitude, however, with greater avoidance during the day than at night—the slope of the correlation between random effects for hunter risk during the day and at night was significantly less than one (a change of one unit in selection during the day resulted in a change of 0.65 [SE = 0.06] at night; Fig. 2).

Counter to P_3, we did not find any difference across years in moose avoidance for areas associated with high hunter risk, as random slopes for hunter risk in all three years and for both day and night had 90% credible intervals that overlapped 0 (and consequently, each other; Table 4; Fig. 1c, d). We did, however, find that moose resource selection switched to use a greater proportion of habitat that was outside of the allowable hunting zone across years (Table 4), suggesting moose were altering behavior at broader spatial scales (e.g., at the landscape scale as opposed to within home range). This may also have been as a result of individuals with a greater proportion of their home range within the allowable hunting area being harvested disproportionately by hunters.

We did not detect a functional response of moose avoidance of areas associated with hunter risk as a function of mean risk within the individual's home range during the hunting season. Mean risk in the home range was not correlated with the random slope for habitat associated with hunter risk ($P = 0.59$ and 0.93, respectively, for day and night; Fig. 3), providing no support for P_4.

DISCUSSION

Our goal was to test if hunting could be implemented as an effective way of altering moose habitat selection patterns to an emerging landscape of risk, and to quantify how individuals responded to this novel risk. Our results provide mixed support for moose reacting to an emergent landscape of risk in response to the introduction of hunting in a previously un-hunted national park. Moose avoided areas associated with a high risk of being killed by hunters, suggesting that introducing hunting likely resulted in a risk response by moose and avoidance of risky areas. Moose also increased use of hunting-free refugia over successive years of the study, suggesting a change in the location of moose ranges in response to hunting pressure. We did not, however, find evidence of increasing avoidance of risky areas across years, nor did we find a significant difference between selection for risky habitats between day and night, likely due to an absence of heterogeneity of risk within moose home ranges.

Hunter risk was the most significant factor explaining moose habitat selection (P_1, Table 4); however, counter to P_3 we failed to detect an increase in the avoidance of risky areas across years (Fig. 1c, d). This suggests that moose were either already wary of humans and that hunting did not result in an increased avoidance of risky areas, or that they acclimated their behavior very quickly in the first year of hunting. Hunting is known to cause changes in ungulate space use and movement (Marantz et al. 2016). Behavioral avoidance of hunters can emerge either via natural selection due to removal of risk-prone phenotypes (Ciuti et al. 2012), learning, or both (Thurfjell et al. 2017). Ciuti et al. (2012) found differences in selection behavior of individual elk that ended up being killed during the hunting season versus those that survived. In the same population, Thurfjell et al. (2017) found that older individuals were more cautious than younger individuals suggesting that learning in addition to selection played a role in elk avoidance of hunters. We found little evidence of female moose learning to avoid areas associated with increased hunter risk. It may be that three years of hunting was an insufficient amount of time for moose to learn to avoid habitats associated with hunters, as the elk in the previous study continued to learn to avoid hunters up to 10 yr of age. Moose are also less social than many other ungulate species, and there is evidence that suggests that less social species may not have the ability to learn about novel predators as they get older (Bleicher et al. 2016). We may also have failed to detect an increase in avoidance of risky areas because female moose were already wary of humans. Lone et al. (2015) found that male red deer (*Cervus elaphus*) that were shot during the hunting season did adjust habitat selection patterns; however, females did not, with the authors of the study suggesting that females with calves may already be cautious prior to the onset of hunting. Avoidance of risky areas had the largest effect size in our models; therefore, individuals may not have needed to

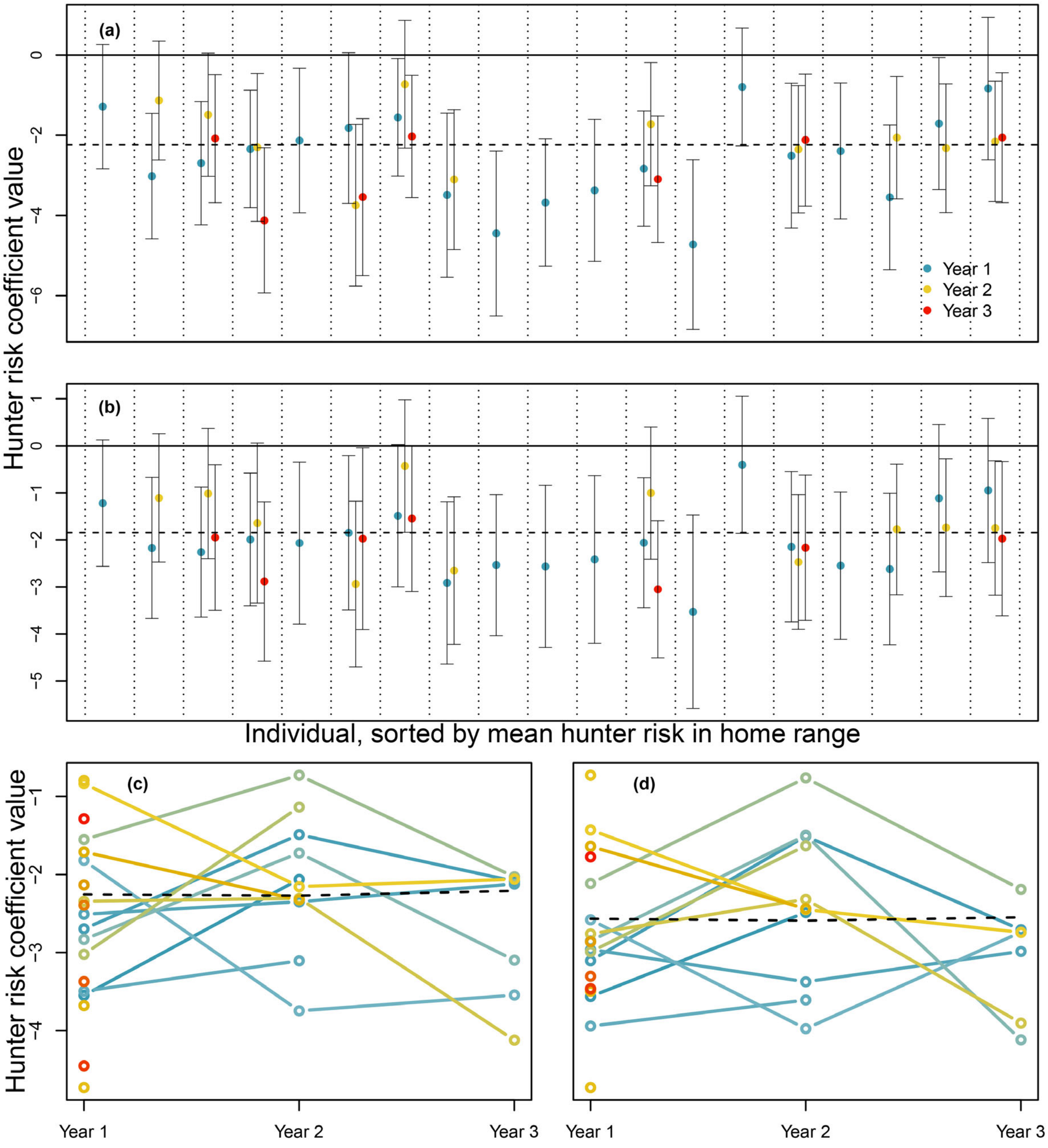

Fig. 1. Total selection of areas associated with hunter risk for moose (*Alces alces*, n = 19) for three years after

(Fig. 1. *Continued*)
start of hunting in Gros Morne National Park, NL. Estimates represent the value of the fixed effect for hunter risk from each model (represented by the dashed lines), plus the associated random slope for year and the random slope for each individual year × individual ID. Panels (a) and (b) show confidence intervals as the sums of the absolute values of the difference between the estimate and the lower and upper confidence intervals of all three terms. Panel (a) represents habitat selection during the day, panel (b) at night. Individuals are sorted by mean level of hunter risk within the home range and are separated by dotted vertical lines. Blue symbols represent the first year of hunting, yellow symbols represent the second year of hunting, and red symbols represent year 3. Solid horizontal lines represent no selection or avoidance, dashed horizontal lines represent the mean population (fixed effect only) response. Panels (c) and (d) show the same data but by individual across years to better represent changes in random slopes through time. Panel (c) represents selection during the day, and panel (d) represents selection at night. Each color represents a unique individual. If moose were learning to avoid hunters through time, the prediction would be for moose to have lower selection for risky areas across years.

Table 3. Beta coefficients and 95% confidence interval for resource selection function model predicting probability of moose (*Alces alces*) being killed by hunters in Gros Morne National Park, NL.

Parameter	Year 1	Year 1 + 2	Years 1–3
Intercept	−6.396 (−7.421, −5.370)	−5.830 (−6.495, −5.165)	−4.622 (−5.042, −4.202)
Open habitat	−1.160 (−1.98, −0.341)	−1.264 (−1.819, −0.710)	−1.246 (−1.701, −0.792)
Distance to roads	−1.481 (−2.014, −0.948)	−1.602 (−2.029, −1.174)	−1.550 (−1.883, −1.218)
Distance to linear features	−1.679 (−2.564, −0.794)	−1.612 (−2.184, −1.040)	−0.339 (−0.638, −0.040)
Terrain ruggedness	−0.300 (−1.138, 0.538)	−0.627 (−0.997, −0.257)	−0.870 (−1.182, −0.557)

Note: Since perceived risk from hunters was predicted to carry over into subsequent years, we modeled risk additively for each year of our study by incorporating each year's hunting data sequentially.

Table 4. Coefficients and 90% credible intervals of fixed effects and random effects of year for Markov Chain Monte Carlo generalized linear mixed-effects models describing moose (*Alces alces*, $n = 19$) habitat selection and risk-avoidance behavior in Gros Morne National Park, NL, from 2011 to 2014.

Parameter	Day	Night
Intercept	0.040 (−0.119, 0.114)	−0.106 (−0.222, 0.004)
Wetland	−1.772 (−1.912, −1.613)	−1.194 (−1.338, −1.062)
Broadleaf	1.333 (1.049, 1.604)	0.944 (0.664, 1.185)
Conifer	1.040 (0.653, 1.367)	1.094 (0.737, 1.419)
Mixed-wood forest	1.306 (1.068, 1.523)	0.628 (0.398, 0.865)
Rock	0.205 (−0.320, 0.678)	0.386 (−0.074, 0.799)
Lichen	0.926 (0.731, 1.109)	0.707 (0.547, 0.927)
Elevation	−0.154 (−0.191, −0.118)	−0.123 (−0.156, −0.088)
Hunter risk	−2.450 (−2.931, −1.964)	−1.978 (−2.429, −1.576)
In hunt	0.432 (0.326, 0.537)	0.503 (0.395, 0.597)
Year 2012†	0.055 (−0.077, 0.181)	0.189 (0.045, 0.305)
Year 2013†	0.318 (0.181, 0.476)	0.443 (0.307, 0.587)
In hunt × year 2012	−0.256 (−0.399, −0.106)	−0.352 (−0.504, −0.208)
In hunt × year 2013	−0.387 (−0.552, −0.225)	−0.520 (−0.679, −0.359)
Random slopes for hunter risk—years‡		
2011	−0.019 (−0.325, 0.395)	0.052 (−0.269, 0.475)
2012	−0.001 (−0.378, 0.398)	−0.044 (−0.376, 0.330)
2013	−0.006 (−0.349, 0.433)	−0.063 (−0.386, 0.318)

† Reference category: 2011.
‡ Random slopes for each year × ID combination were also computed but not shown (see Figures).

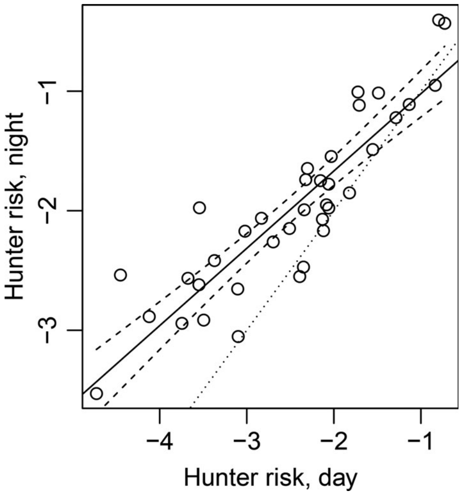

Fig. 2. Fixed effect for hunter risk plus summed random slopes for moose (*Alces alces*, $n = 19$) selection of habitat associated with hunter risk at night versus during the day. Selection at night was significantly correlated to selection during the day (slope = 0.65, SE = 0.06, $P < 0.001$, adjusted $R^2 = 0.786$, solid line; dashed line represents 95% confidence interval). A slope less than one (dotted line) suggests that individual moose had a greater response to hunter predation risk during the day than at night.

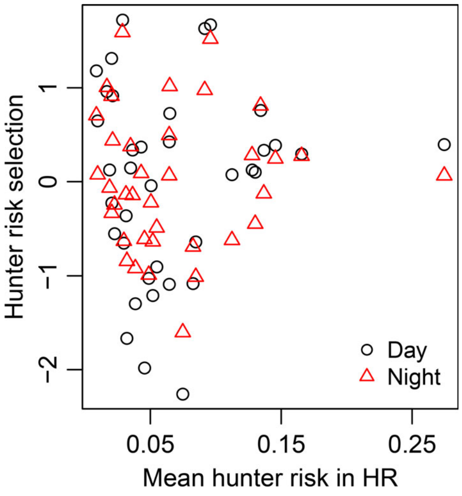

Fig. 3. Random slope of moose (*Alces alces*, $n = 19$) for selection for areas associated with hunter risk for individual moose/years as a function of the mean of hunter risk in the individual's seasonal home range during the day (black circles) and at night (red triangles). No functional response was evident, as hunter risk did not change significantly as a function of mean risk within the home range at either time of day (β day = 1.65, SE = 3.06, $P = 0.59$, adjusted $R^2 = -0.02$; β night = 0.21, SE = 2.25, $P = 0.93$, adjusted $R^2 = -0.03$).

further decrease avoidance of risky areas across years.

Moose may have sought refuge as opposed to attenuating risk. We found that selection for refuge habitat increased across years. Proffitt et al. (2013) found that during the hunting season, elk selection of areas with restricted public hunting was higher than selection for security habitat, for example, areas where hunting was permitted but access was low. Female moose in our population may have reacted similarly to the onset of hunting and prioritized the selection of refuge habitat as opposed to altering selection patterns to avoid risk in areas where hunting was permitted. This suggests that moose in this population may have responded behaviorally at a broader spatial scale to variation in risk, suggesting that factors influencing selection by moose may have been more relevant at the landscape scale (e.g., Johnson 1980s 2nd order) of selection as opposed to within the home range (Rettie and Messier 2000). Alternatively, female moose may have increased vigilance rates as opposed to habitat selection patterns, as was the case in female elk and bison (*Bison bison*) in Yellowstone National Park in response to the reintroduction of wolves (Laundré et al. 2001).

Our hunter risk model was primarily driven by landscape variables that varied over broad spatial scales (distance to roads and linear features) which resulted in the landscape of risk being relatively homogenous at the scale of individual moose ranges. This suggests that the landscape of risk for moose in our system is likely quite coarse-grained (Tolon et al. 2009). With increased risk, individuals respond at different spatial scales (Padié et al. 2015), either by altering habitat selection within their home range (Padié et al. 2015), altering areas used within their home range (Marantz et al. 2016) or by changing the location of home ranges to increase use of refuge habitat (Tolon et al. 2009, Proffitt et al. 2010). As the degree of heterogeneity in the physical landscape is a precursor for spatial variation in predation risk and associated behavioral trade-offs in prey (Atuo and O'Connell 2017, Gaynor et al. 2019), our prediction that moose would exhibit demonstrable temporal responses to risk in a largely homogenous landscape may have been misjudged. The coarse-grained landscape of fear for moose may be an alternate explanation for why we saw little evidence of an increased response across years to hunter risk, as individuals may not have been able to alter fine-scale habitat selection in response to pressure from hunters.

Moose may have adjusted the location of their home ranges in response to hunting, but this increased avoidance may have gone undetected as hunters also altered their hunting locations across years. Our model indicates that hunters used sites farther from linear features in the third year of hunting (Table 3). As wolves re-established in Yellowstone National Park, the landscape of fear re-established in a heterogeneous manner, with female elk and bison farther from the reintroduction site increasing vigilance rates in later years as wolves expanded into previously wolf-free areas (Laundré et al. 2001). In our case, moose may have responded to increased hunting risk by using areas farther from linear features, but this increased avoidance may have gone undetected in our models as hunters also shifted their behavior and increased risk in locations that were previously considered safe, or at least lower risk.

All individuals avoided areas associated with increased hunter risk, but there was individual variation in the response to that risk. We did not, however, find evidence of a functional response in moose avoidance of risky areas as a function of increased risk in the home range (Fig. 3). By contrast, wild boar (*Sus scrofa*) did show a functional response in use of protected areas during the day to avoid hunters (Tolon et al. 2009). If, however, risk was distributed homogeneously within individual home ranges it was likely more difficult for individuals to adjust their space-use tactics in response to risk and may have made it more difficult for us to detect a functional response. Individual differences in the response to risk may have depended on individual experience, or other non-exclusive factors, such as propensity to take risk (Ciuti et al. 2012), proximity to refuge (e.g., Tolon et al. 2009), ability to move home range (Padié et al. 2015), and differences in age (Lone et al. 2015), body condition (McNamara 1997), and local density (Guariento et al. 2015).

We failed to detect diurnal and nocturnal behavioral differences in moose avoidance of hunter risk, instead finding similarly strong avoidance of hunter risk both during the day and at night (Fig. 2). Temporal differences in space-use patterns have been illustrated as a mechanism for ungulates to reduce the likelihood of predator encounter in predator-risky areas, particularly in those areas with a foraging benefit (Godvik et al. 2009, Kohl et al. 2018). The absence of a difference in predator avoidance strategies between day and night may simply be a result of risky areas providing no incentive, for example, increased foraging opportunities, for moose at any time period. Moose strongly selected for all forest types, that is, mixed-wood, broadleaf, and conifer, during both day and night across all three years of study, suggesting foraging and cover (Dussault et al. 2005) requirements were not affected by hunter risk. As moose were not explicitly faced with a trade-off between foraging needs and risk avoidance within heterogeneous habitat types (e.g., predator-sensitive food hypothesis; Creel et al. 2009), moose likely avoided predator-risky areas without any consequence to survival or reproductive success.

In our study, we assumed that the landscape of fear was correlated with the risk of death from hunting, as opposed to being based on more direct proxies of fear such as giving up densities (Brown 1999, Kotler et al. 2004, van der Merwe and Brown 2008) or vigilance rates (Brown 1999, Laundré et al. 2001, Creel et al. 2014). Given that these hunting events resulted in mortality, we think we generated an accurate representation of the landscape of fear perceived by moose; however, our method for estimating predator risk assumes that prey are given the opportunity to learn and respond to predator risk. In non-human predators, hunting attempts are successful on average between 8% and 26% of hunts (reviewed by Laundré et al. 2010), meaning that for most predator encounters the prey escapes and is given the opportunity to learn. In our system over the course of the study, the average hunter success rate was estimated at 53% (Government of Newfoundland, *unpublished data*). As hunter encounter was more likely than not to end in mortality, moose learning most likely occurred based on an individual's association of conspecific kill locations with human olfactory or auditory (e.g., voices, gunshot) cues, as opposed to the experience associated with a failed hunting attempt. We did not measure the number of failed hunting attempts. If a high proportion of failed hunting attempts occurred in different habitat/locations compared to successful ones, this would result in a different distribution of risk and therefore a different landscape of fear. We suggest future research using similar methodology incorporate the use of both kill site locations, in addition to information that includes failed harvest attempts to more accurately generate the landscape of fear.

Over the course of our study, a total of seven moose were killed, five of which were killed by hunters, which impacted the overall robustness of our study. The loss of sample moose over successive years of study resulted in analysis of a nonrandom subset of our initial sample, which created the risk of biasing our results toward the remaining sampled moose. Given that some of the moose in our sample were killed by hunters, it is possible that the increase in selection for refuge over the years could be due to a bias in hunter harvest, where individuals with greater distance to refuge were more likely to be killed and removed from our sample in subsequent years. If proximity to refuge was in fact the underlying factor that resulted in our finding of increased selection for refuge over the years, we acknowledge this is an alternative, but interesting result. For example, this conclusion outlines the importance of consumptive effects on changing the distribution of individuals across a landscape.

Hyperabundant cervids can have important consequences on ecosystems, and hunting may provide a means to mitigate these impacts, especially in systems with a dearth of natural predation pressure. Selective foraging by cervids can alter vegetation abundance and dynamics resulting in a change in community composition (Côté et al. 2004). Moose are hyperabundant in certain areas of Newfoundland and browse heavily on balsam fir and hardwood species unchecked by any significant predators (McLaren et al. 2004). The concept of hunting for fear has been introduced as a means to manage ungulate populations by inducing a fear response to elicit a change in species' distribution to divert them from certain areas (Cromsigt et al. 2013). Our results suggest that while moose may not be able to attenuate their exposure to risk at fine spatial scales, they do appear to have the ability to find refuge from hunting areas in order to nullify their risk from hunters.

ACKNOWLEDGMENTS

We thank Jim Rettie and Steve Simpson for helping to launch this research project and contribute to fieldwork and study design, and Beth Pollock and John Neville for assistance with animal captures. S. Taylor, S. Gerrow, and D. Whitaker, GMNP, provided invaluable assistance by providing GPS data, assisting with fieldwork, and sharing their knowledge of the Gros Morne National Park ecosystem. A. Rodgers, Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, and R. Brook, University of Saskatchewan, provided advice and constructive criticism throughout the project. We would like to thank all of the hunters who voluntarily assisted in data collection; this project would not have been possible without their contributions. Funding was from Parks Canada Agency (PM), the Natural Sciences and Engineering Research Council (NSERC) Canada, Discovery Grant 371535-2009 (PM), and the Canada Foundation for Innovation Leader's Opportunity Fund 25046 (PM). We would like to acknowledge valuable comments from S. Webb and one anonymous reviewer on a previous draft of this manuscript. All experiments complied with current laws of the country in which the experiment was performed.

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