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Bastille-Rousseau, G., Potts, J.R., Schaefer, J.A. et al. (5 more authors) (2015) Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. Ecography, 38 (10). pp. 1049-1059. ISSN 0906-7590

https://doi.org/10.1111/ecog.01305

This is the peer reviewed version of the following article: Bastille-Rousseau, G., Potts, J. R., Schaefer, J. A., Lewis, M. A., Ellington, E. H., Rayl, N. D., Mahoney, S. P. and Murray, D. L. (2015), Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. Ecography, 38: 1049–1059. , which has been published in final form at http://dx.doi.org/10.1111/ecog.01305. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving (http://olabout.wiley.com/WileyCDA/Section/id-820227.html)

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Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability

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Abstract

Habitat selection is a multi-level, hierarchical process that should be a key component in the balance between food acquisition and predation risk avoidance (food-predation trade-off). However, to date, studies have not fully elucidated how fine- and broad-scale habitat decisions by individual prey can help balance food versus risk. We studied broad-scale habitat selection by Newfoundland caribou (*Rangifer tarandus*), focusing on trade-offs between predation risk versus access to forage during the calving and post-calving period. We improved traditional measures of habitat availability by incorporating fine-scale movement patterns of caribou into the availability kernel, thus enabling separation of broad and fine scales of selection. Remote sensing and field surveys served to create a spatio-temporal model of forage availability, whereas GPS telemetry locations from 66 black bears (*Ursus americanus*) and 59 coyotes (*Canis latrans*) provided models of predation risk. We then used GPS telemetry locations from 114 female caribou to assess food-predation trade-offs through the prism of our refined model of caribou habitat availability. We noted that migratory movements of caribou were oriented mainly towards habitats with abundant forage and lower risk of bear and (to a lesser extent) coyote encounter. These findings were generally consistent across caribou herds and would not have been evident had we used traditional methods instead of our refined model when estimating habitat availability. We interpret these findings in the context of stereotypical migratory behaviour observed in Newfoundland caribou, which occurs despite the extirpation of wolves (*Canis lupus*) nearly a century ago. We submit that caribou are able to balance food acquisition against predation risk using a complex set of factors involving both finer and broader scale selection. Accordingly, our study provides a strong argument for using refined habitat availability estimates when assessing food-predation trade-offs.

Key-words: caribou (*Rangifer tarandus*), conservation biology, habitat selection, mechanistic modelling, step-selection function, migration.

Introduction

Understanding the drivers of antipredator responses and the efficiency by which animals trade-off food versus safety is crucial, since anti-predator behavioural modification can have profound consequences on fitness, and ultimately, population dynamics (Gaillard et al. 2010). Beyond their direct lethal impact, predators can increase physiological stress in prey (Creel et al. 2009) and cause behavioural adjustments that contribute to the net effect of predation (Creel and Christianson 2008, Lima and Bednekoff 1999, Schmitz 2008). These anti-predator behavioural adjustments can also induce a reduction in foraging efficiency (foraging cost of predation; Brown and Kotler 2004), ultimately leading prey to compromise between food and safety. Prey are able to reduce the impact of predation through various behavioural strategies, such as vigilance, grouping, and movement (Lima 1998, Lima and Dill 1990).

Movement is a central process in animal ecology, including in the study of predator-prey interactions (Laundré 2010, Mitchell and Lima 2002, Nathan 2008). Indeed, animals move in response to a variety of competing pressures such as the need to feed, avoid predators, breed, and rear offspring (Brown et al. 1999, Cresswell 2008). These competing demands give rise to trade-offs that individuals must mediate through their space use and movements (Hebblewhite and Merrill 2009, Lima 1998), resulting in distinctive patterns of habitat selection. Numerous studies have tried to unveil potential trade-offs for prey through the process of habitat selection (e.g. Creel et al. 2005, Fortin and Fortin 2009, Hebblewhite and Merrill 2009). Habitat selection is defined as the disproportionate use of a habitat relative to its availability (Johnson 1980, Manly et al. 2002), and elucidating habitat selection determinants remains a central and unifying concept bridging spatial and temporal scales (Mayor et al. 2007, Morris 2003). Indeed, studies often have compared habitat selection across multiple scales (e.g. Dussault et al. 2005, Hebblewhite and Merrill 2009, van Beest et al. 2010). Especially owing to prevalent and rapid environmental change, there is increasing interest in understanding motivations associated with an animal's habitat selection, especially in the context of revealing how such selection may be mismatched with current or future environmental conditions (Middleton et al. 2013, Sih et al. 2011). Indeed, habitat selection is one of the most studied concepts in ecology.

Despite such focused attention, habitat selection studies are frequently limited in the insights they provide, due to: 1) absence of robust information (e.g., qualitative field surveys or predator data), leading to a weak or simplified definition of available forage or predation risk (Hebblewhite and Haydon 2010); 2) restrictive analysis of a single level of selection (Boyce 2006); or 3) trivial or problematic comparison of use versus availability to infer selection (Aarts et al. 2013). Notably, there remain substantive challenges in understanding behavioural processes underlying habitat selection and the animal motivation by which it is governed. This difficulty arises because of non-independent behavioural processes and overlapping motivations across levels of selection, as well as the conditional and statistical nature of 'selection'. This means that previous work often addressed the question of resource selection on the basis of relatively simple (and presumably imprecise) algorithms when defining habitat availability (Beyer et al. 2010). It follows that such an approach may mask actual patterns and drivers of habitat selection at a particular level due to artefacts of finer-scale processes also being considered in the use-availability statistical comparison. Better integration of animal decisions that are quantifiable on the basis of movement ecology should therefore be useful. Here, we propose a refined approach for defining availability that considers finer scale selection patterns and thereby improves the distinction between levels of selection, while also providing insight into motivation underlying such selection.

Caribou (*Rangifer tarandus* L.) offer a unique system for studying food-predation trade-offs in habitat selection, and on the island of Newfoundland, Canada, there are 14 major caribou herds with most exhibiting some degree of migratory behaviour involving the annual use of traditional calving grounds by females. These herds are largely distinct and spatially disjunct at calving (Bastille-Rousseau et al. 2013). Interestingly, during the last 50 years Newfoundland caribou have undergone marked fluctuations in abundance, with populations increasing rapidly during the 1980s to mid-1990s, and declining during the 2000s (Mahoney and Schaefer 2002b, Mahoney et al. 2011).

We develop a refined model of availability to study broad-scale habitat selection, with an emphasis on trade-offs between predation risk and foraging. More specifically, we use a mechanistic model based on a step-selection function that approximates fine-scale movement to create a refined sample of habitat availability. We use this model to study selection of calving grounds (referred as second-order level of selection; Johnson 1980) as well as core areas within the calving grounds (referred as third-order level of selection) in response to vegetation biomass and current predation risk (black bears [*Ursus americanus* L.] and coyotes [*Canis latrans* Say.]). We chose to focus our analysis at the herd level as caribou aggregate into groups during this period. Coyotes are non-native predators that became widespread in Newfoundland in the 1990s. Considering the high amount of caribou calf mortality during calving periods (Trindade et al. 2011) and recent evidence of density-dependent population fluctuations (Mahoney and Schaefer 2002b, Mahoney et al. 2011), we first predicted that predation has a stronger effect on habitat use and that selection of calving grounds would be mostly driven by an expression of predation risk avoidance. Second, we predicted that access to rich foraging sites would be the main factor driving habitat selection at the third order: i.e., the selection of core areas within the calving ground. As a side contribution emanating from our analysis, we compared insights obtained from our mechanistic definition of availability to the traditional approach, and predicted that our refined model would provide insights into the processes underlying caribou decisions vis-à-vis food-predation trade-offs that would not otherwise be evident. We believe that our approach could provide a major shift in how ecologists approach questions related to animal behavioural adjustments in response to the subtle interplay between risks and rewards in their environment.

Material and methods

Study area

Newfoundland is a 108,860-km² island at the eastern extremity of Canada (47°44N, 59°28W to 51°44N, 52°38W), with humid-continental climate and substantial year-round precipitation (Environment Canada 2013). Natural habitat consists mainly of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*), and in some locations substantial areas of bogs and heath or barren habitats. Most of our analyses were based on a Landsat TM satellite imagery, with a resolution of 25 m, classified into 6 different habitat types: wetland habitats (Wetland), barren and other open habitats (Barren), mixed and coniferous open stand (CO), mixed and coniferous dense stand (CD), open water (Water), and a category (Other) comprised of rarer habitats such as broadleaf stands, herbs and bryoids (Wulder et al. 2008). Anthropogenic disturbances are limited in caribou range in Newfoundland but consist of logging, hydroelectric development, and roads. We restricted our analysis to five important migratory herds located south of the main east-west highway that crosses the island (Fig. 1).

Animal capture and monitoring

During 2006-2010, more than 200 caribou were captured, principally during winter, and fitted with global positioning system (GPS) collars that obtained locations every 2 hours. We focused on 114 adult females (271 caribou-years and 384,764 locations) that were followed during 2007-2010 and that resided in 5 distinct herds (Buchans [n=17 caribou], Lapoile [n=19], Middle Ridge [n=28], Pot Hill [n=18] and Gaff Topsails [n=32]). We limited our movement analysis to the crucial, post-migratory period of calving and post-calving (1 May - 1 August) when most caribou neonate mortalities occur. We also used GPS locations of 66 adult male and female black bears (125 bear-years and 96,531 locations) and 47 adult male and female coyotes (59 coyote-years and 18,842 locations) followed during the same period in the vicinity of our study area. Although most of the study area contained radio-collared predators, the central portion of our study area was under-represented in terms of predator locations, most notably for bears. We therefore did not use the density of locations as a measure of predation risk (e.g. kernel density estimate), but rather sought to quantify predation risk via habitat selection approaches.

We used caribou GPS locations to create a 95% bivariate kernel density estimate using an *ad hoc* approach to estimate the smoothing parameter to roughly delineate the areas used during calving and post-calving (hereafter, “calving grounds”) for each herd (see Worton 1989). We then created a general study area of availability that encompassed these five herds that was generally delineated by the Trans-Canada Highway to the north, east and west, and by the coast to the south (Fig. 1). The study area and the herd calving ground delineations represented our two levels of availability (second and third-order selection, respectively; Johnson 1980).

Definitions of availability

1- Random model

Most resource selection analysis involving radio-telemetry is based on the use versus availability design, where availability is sampled from locations drawn within an area assumed to define what actually is available to the animal. However, defining habitat availability has constituted a longstanding challenge in ecology (Beyer et al. 2010). Specifically, ‘availability’ usually is identified by sampling habitats randomly within the defined area and relying on the assumption that accessibility of different habitats is similar across all individuals. This assumption depends on habitat connectivity and animal movement (Dancose et al. 2011), and is less likely to be satisfied at higher orders of selection (Johnson 1980). Our first definition of availability was based on this simple definition (hereafter, "random model"). We generated 5 million random locations within the study area and assigned each location evenly to one of 15,000 virtual individuals. We also generated 1 million random locations within each herd’s calving ground and equally associated them with one of 3,000 virtual individuals. We randomly assigned each location to a specific day and each individual to a specific year (2007-2010 [2009-2010 for Middle Ridge]) corresponding to the radio-telemetry data for each herd. Associating random locations to an individual, day, and year was necessary for subsequent analyses.

2- Mechanistic model

For fine-scale analyses of resource selection, realistic and restrictive definitions of availability based on movement properties have been proposed (Aarts et al. 2013, Fieberg et al. 2010, Fortin et al. 2005, Hjermann 2000, Matthiopoulos 2003), but for broad-scale analyses, alternatives are still limited (see Arthur et al. 1996). Ecologists generally view habitat selection as a hierarchical process; it is well accepted that fine-scale selection is a function of resource availability at the same level, yet availability is defined by broad-scale habitat selection (DeCesare et al. 2012, Mysterud and Ims 1998). The consequence of such a view is that, when inferring motivation behind selection, each level is viewed as independent. This view has been reinforced by the hierarchical habitat selection hypothesis (HSS), proposed by Rettie & Messier (2000), where broad-scale selection reflects the most relevant limiting factors (but see, Dussault et al. 2005, Hebblewhite and Merrill 2009 for a critical discussion of this hypothesis). Use of specific resources, in addition, should be seen as a summation of multiple processes operating at different scales adding to the difficulty of interpreting scale-specific selection. Therefore, inferring motivation behind such patterns often can be challenging (Beyer et al. 2010).

To understand the motivation behind caribou migration or other broad-scale habitat selection patterns, researchers might compare locations used by animals to a set of random locations within a larger area. However, mammals, and notably ungulates, are known to display movements that balance both long-term and short-term motivations (Mueller et al. 2011), and therefore a more refined habitat selection analysis should reflect finer-scale decisions that are made when moving within the larger area. As we seek to understand the motivation behind a level-specific behaviour as well as a realistic estimate of habitat availability, we need to control for the influence of fine-scale selection patterns. This can be achieved by refining our definition of availability to consider fine-scale movements. In other words, we examine whether observed spatial patterns result from actual differences in broad-scale space-use, or whether they are simply an artefact of fine-scale movement choices. Refining the definition of availability therefore allows for a more conservative estimate of broad-scale selection that improves the distinction between levels of selection.

To get a more realistic (and restrictive) view of availability that considers fine-scale animal movements, we built a spatially-explicit, mechanistic model that represented between-patch transition in areas that could be occupied by caribou. At a minimum, a suitable model of fine-scale movement should include step lengths and turning angles, but also could incorporate a weighting function representing preference for specific resources (Rhodes et al. 2005). Such a model would therefore include both reduction of movement and biased movement to inform fine-scale selection patterns (Bastille-Rousseau et al. 2010, Moorcroft and Barnett 2008).

We used a spatially-explicit mechanistic model, based on a step-selection function, to provide our second definition of availability (hereafter, "mechanistic model"). We randomly initiated this model within the study area to investigate selection of caribou calving grounds (second-order selection) and to study third-order selection within each of the five calving grounds. This model included movement parameters (step length and turning angles) derived from collared caribou combined with a weighting function translating between-habitat preference in inter-patch movements. Specifically, we estimated habitat-specific step length and turning angle distributions using Weibull and bivariate von-Mises distributions, respectively. The weighting function was calculated by comparing an actual animal step originating in a specific habitat to 100 potential steps based on step length and turning angle distributions. Full details regarding model formulation and estimation of parameters can be found in Potts *et al.* (2014). We initiated 15,000 virtual individuals within the broader areas and 3,000 within each calving ground, which were assigned locations every 2 hours and then processed similarly to locations from the random model.

Predation model

We used a resource selection function (RSFs; Boyce et al. 2002, Manly et al. 2002) to describe the spatial relationship between the probability of occurrence of coyotes and black bears according to landscape attributes. We estimated RSFs by comparing habitat characteristics at observed and random locations with mixed-effects logistic regression models, with the identity of the individual as random factor (i.e. random intercept; Gillies et al. 2006, Hebblewhite and Merrill 2008) to account for spatial autocorrelation and differences in sample size. We drew random locations for a given individual within the 99% utilization distribution evaluated from a Brownian bridge kernel approach (Horne et al. 2007). Random locations were drawn at a density of 2 points per km². Observed and random locations were characterized by dummy variables representing landcover types (with Wetland as the reference category), as well as elevation, slope, and proportion of each habitat category within a 5-km radius (except habitats classified as ‘Water’ and ‘Other’). Proportion of habitat within a buffer was used to account for the presence of a functional response in habitat selection (Moreau et al. 2012, Mysterud and Ims 1998), which may improve model fit, especially over large areas (Aarts et al. 2013). We therefore added an interaction term between coefficients for a specific habitat and its proportion (Aarts et al. 2013, McLoughlin et al. 2010).

The global RSF took the form:

$$w(x) = \exp(\beta_1 x_1 + \ldots + \beta_{\mathrm{u}} x_{\mathrm{uij}} + \beta_{\mathrm{u\_5k}} x_{(\mathrm{u\_5k})\mathrm{ij}} + \ldots + \beta_{\mathrm{u}} x_{\mathrm{u}} * \beta_{\mathrm{u\_5k}} x_{(\mathrm{u\_5k})\mathrm{ij}} + \gamma_{0j}) \tag{1}$$

where $w(x)$ represented the RSF scores, β_{u} was the selection coefficient for resource x_u or for the elevation and the slope, $\beta_{\mathrm{u\_5k}}$ was the selection coefficient for proportion of the resource within a 5-km buffer $x_{(\mathrm{u\_5k})}$, and γ_{0j} was the random intercept for animal j. We tested for collinearity using the variance inflation factor (Graham 2003) and used AICc selection criteria to identify the most parsimonious model (Burnham and Anderson 2002) within the global model and subset of simpler models (Table S1, Supplementary material). We then used k-fold cross validation to evaluate the robustness of RSFs (Boyce *et al.* 2002). An RSF model based on 80% of the data was estimated, withholding the remaining 20% for evaluation. Predicted scores of the model were placed in ten bins of equal size that represented the percentile range of predicted scores. We then determined the frequency of locations in the withheld data (20%) that fell into each bin. To evaluate model performance, we calculated a Spearman rank correlation (r_s) between the frequency of occurrence for the withheld 20% and the ranked RSF-availability bins (Boyce *et al.* 2002). The process was repeated 20 times and we report the average r_s. We used the validated RSFs to build island-wide maps of relative occurrence probabilities, which we used to estimate encounter risk with both predator species. RSFs were calculated using R statistical software (ver. 2.15.0, R Development Core Team 2008) with the package lme4 (Bates et al. 2014) and adehabitatHR (Calenge 2006).

Forage model

To study caribou use of vegetation-rich areas, we created a spatiotemporally dynamic model of forage biomass (similar to Hebblewhite et al. 2008). We considered only food items that have been found in caribou feces during the spring-summer period. This model was based on the five habitat categories, and field vegetation surveys linked to a temporally dynamic forage availability model using MODIS Terra NDVI 250 m every 16 days. Complete details of this model are given in Supplementary material (Appendix S1, Supplementary material).

Statistical analysis

For every set of caribou locations (observed, random, and mechanistic), we extracted habitat category, relative probability of occurrence of black bears and coyotes, and vegetation biomass based on timing of the location. We estimated selection for each habitat by computing resource selection ratios (w_i) and tested for overall selection using a Chi-square test (Manly et al. 2002). We assessed selection for vegetation at a given scale by comparing the yearly between-individual average value of vegetation biomass of each herd with the average value for the set of available locations based on the random and mechanistic models. For locations representing use, confidence intervals around the average provide an indication of individual variation. Similarly, we tested for avoidance of predation by comparing the average probability of occurrence of bears and coyotes for each herd at actual caribou locations with average availability observed from each of our four models of availability.

Lastly, to gain insight into the behavioural motivation behind migration, we assessed trade-offs between vegetation and predation faced by caribou at the second-order level of selection. We used the following linear model:

$$Biomass\ (x) = \beta_0 + \beta_{Bear} * x_{Bear} + \beta_{Coyote} * x_{Coyote} + \beta_{Interaction} * x_{Bear} * x_{Coyote} \qquad (2)$$

where $Biomass(x)$ represents the vegetation biomass in a given location, β_0 represents the intercept, $\beta_{Predators}$ represents the slope between the risk from a predator $x_{Predators}$ and biomass. A positive and statistically significant coefficient β indicates that caribou would face a trade-off between the specific cause of predation and forage. An interaction between bear and coyote relative probability of occurrence was added to account for the presence of non-linearity in the influence. We estimated this model using the actual set of locations, but also using the availability models generated within the general study area based on the random and mechanistically simulated models. We used bootstrapping to get more robust standard error estimates for the two availability models, since these models are biased due to arbitrary determined sample sizes. More precisely, we performed these regressions with a sub-sample of the random and mechanistic datasets of available locations, sampling the same amount of individuals as the actual data (n=271 individual-years). We repeated these steps 1000 times and used the average standard errors in confidence interval calculation.

Results

Predator occurrence and vegetation abundance

For both black bears and coyotes, AICc model selection showed that the global model with all habitat categories and presence of functional responses was most parsimonious (AICc weights > 0.99, Table S1). Both black bears and coyotes displayed a functional response in habitat selection, where preference for most habitats decreased as the proportion of a given habitat in the area surrounding a location increased as revealed by the negative coefficient for interactions terms. This response was stronger for coyotes than for bears in the selection of Barren and Wetland habitats (Table 1). The two predators responded differently to elevation and slope, with black bears avoiding sites with higher elevations, but selecting sites with steeper slopes, and coyotes displaying the opposite pattern, with selection favouring higher elevation and low slope. K-fold cross-validation indicated these models were robust, with r_s= 0.979 for black bears and r_s = 0.930 for coyotes.

During the same period, Wetland and Coniferous Open supported the highest vegetation biomass, followed by Barren and Coniferous Dense (Table 2). Correlations between increases in NDVI Modis Tera satellite index and vegetation growth were strong (average conditional $R^2 = 0.346$). As revealed by the magnitude of the slopes, changes in NDVI had the strongest impact on changes in vegetation growth in Wetland and Barren habitats, while having smaller influence in Coniferous Dense (Table 2). Complete details of the spatio-temporal vegetation model are given in Appendix S1.

Habitat selection

Based on the random model of availability, female caribou (except for Pot Hill) displayed selection for Barren and Wetland habitats at both second- and third-order levels. Conversely, caribou tended to avoid Coniferous Open and Dense stands as well as Water, at both scales. Surprisingly, the Pot Hill herd displayed the opposite pattern, with preference for Coniferous Open stands and general avoidance of other habitats at both scales (Table 3). Patterns of selection were qualitatively similar to those from the mechanistic sampling model, although the proportion of statistically significant selection ratios across habitats decreased from 68% to 53%. This decrease in statistical significance would lead to different inferences regarding selection due to the more conservative nature of the comparison between used- and mechanistically defined availability locations.

Response of caribou to forage and predation

Three herds displayed selection for sites with higher forage when choosing their calving grounds based on the 2nd-order mechanistic definition of availability; all herds displayed selection based on the random 2nd-order model. All herds also displayed selection for vegetation when moving within the calving grounds based on the 3rd-order random model, but only one herd (Gaff Topsails) displayed selection based on the 3rd-order mechanistic model. Interestingly, the mechanistic model of availability indicated greater access to forage than the random model, a pattern that was consistent across scales. This indicates that no matter where caribou were moving, interpatch movement rules were already providing access to sites with greater forage, but that the choice of calving grounds and core areas within caribou calving grounds reinforced this selection (Fig. 2).

Only two herds (Buchans and Gaff Topsails) appeared to reduce risk of encountering coyotes by migrating to their calving grounds. These two herds and the Middle Ridge herd were also able to further reduce risk when moving within their calving grounds. Individuals from two herds (Buchans and Lapoile) appeared to reduce risk of encountering bears when migrating to their calving ground but when considering carefully their potential exposure based on their fine-scale movement (mechanistic model), all herds except Pot Hill appeared to reduce predation risk from bears via second-order selection. Three herds also enhanced risk reduction when choosing core areas within calving grounds. In all cases, the mechanistic model of availability showed higher risk of predation than the random model, indicating that fine-scale movements could increase risk for caribou (Fig. 2).

Trade-offs between predation risk and forage

If areas with high forage availability are associated (positively correlated) with an increased risk of predation, caribou will face a trade-off between the two. In general, available locations with higher forage biomass based on the random or mechanistic models were associated with higher risk of predation from both bears and coyotes (positive coefficient, Fig. 3). However, caribou were also exposed to higher risk from both predators in their actual use of habitat, most notably regarding the relationship between foraging sites and black bear predation risk (Fig. 3).

Discussion

Using an extensive dataset of telemetry locations of caribou and their predators, we studied broad-scale habitat selection of five caribou herds with an emphasis on the trade-offs between food acquisition and predation risk. We found that caribou movements are oriented mainly toward increased access to forage and also reduction of encounter risk with bears, and to a lesser extent, coyotes. This was somewhat contrary to our original predictions in that we expected third order selection would be driven by an avoidance of predation risk. Our refined definition of habitat availability, based on a mechanistic model of caribou movements, provided different insights into the food-predation trade-off faced by caribou and allowed us to consider behavioural motivation as a driving level-specific force behind habitat selection. The fact that this refined analysis revealed patterns of forage selection and predator avoidance that would not have been revealed using more traditional approaches, speaks to the subtle factors underlying caribou movements and the need to better identify what is considered as ‘available’ in use-availability studies. Ultimately, our findings reveal how prey can integrate multiple levels of selection to balance the importance of predation risk on foraging behaviour.

Our results showed that most caribou herds selected calving grounds on the basis of the foraging opportunities that they provide. This observation was reinforced by evidence of habitat selection at the movement paths between habitat patches (as shown by the difference in vegetation exposure between our two models of availability). Following Rettie and Messier’s (2000) hypothesis that a hierarchy in limiting factors matches the hierarchy in habitat selection, it appeared that foraging access was likely to be an important limiting factor for some herds during the critical period of calving and post-calving, with the cost of lactation for ungulate females and associated increasing need in foraging (Hamel and Côté 2008). However, predation risk avoidance was not as clear given that some herds were more responsive to risk exposure than were others, perhaps reflecting local differences in cause-specific predation risk across the broader caribou population. For instance, recent coyote colonization in Newfoundland may explain why caribou tended to display less avoidance of this predator. Lastly, we contend that our approach offers transparent and conservative results regarding selection because the analyses summarized individual selection and then pooled the individual responses into herds rather than a more uniform (and less appropriate) multi-herd pooling.

The Buchans herd appeared to be the most effective at avoiding predation, which is interesting given that it is the herd that undergoes the longest annual migration to calving grounds (Mahoney and Schaefer 2002a). This suggests that migratory caribou may face a trade-off between migration distance and its expected benefit in terms of reduced predation risk and increased foraging opportunities (Gunn et al. 2012); such a trade-off is likely to exist in terrestrial species given the high costs associated with migratory behaviour (Alerstam et al. 2003). Considering the observed variability in Newfoundland caribou migratory movements (Rayl et al. 2014), it appears that this trade-off may lead to variable migratory behaviour across herds. Some ungulates such as elk (*Cervus elaphus* L.) and caribou exhibit partial migration with some populations migrating and others being sedentary (Festa-Bianchet et al. 2011, Hebblewhite and Merrill 2009, Middleton et al. 2013), but results from Rayl *et al.* (2014) as well as those herein reveal a likely gradient of migratory behaviour in Newfoundland caribou. Bergerud et al. (2008) concluded that migration for caribou herds in North America was associated with wolf (*Canis lupus* L.) avoidance because migrating females typically had access to lower quality forage than sedentary males. In addition, elsewhere in caribou range, movements away from tree line likely reduce risk of wolf predation (Bergerud et al. 2008). However, the relatively small size of Newfoundland island may impose spatial constraints on migrating caribou compared to other populations, thereby reducing their ability to escape predation by wolves (historically) or other carnivores (currently). Indeed, migration in Newfoundland caribou may have originated both as a predation- and foraging-oriented behaviour, which is supported by the observed behaviour among female caribou in this study, almost a century after wolves were extirpated from the island.

During the past 50 years, caribou herds on Newfoundland have undergone marked changes in abundance, with population sizes being notably low during the 1960s and 1970s, increasing rapidly during the 1980s to mid-1990s, and declining precipitously following the mid-late 1990s (Mahoney and Schaefer 2002b, Mahoney et al. 2011). These fluctuations seem to be driven by a combination of factors, including decadal trends in winter severity, density-dependent nutrition during summer, and predation on neonates (Bastille-Rousseau et al. 2013, Schaefer and Mahoney 2013). However, if migratory behaviour or habitat selection are mismatched with current predation risk and forage availability, then reductions in productivity and survival are expected (Hebblewhite and Merrill 2011, Middleton et al. 2013). To date, this potential source of caribou population decline in Newfoundland had yet to be fully tested.

Our results do not support this hypothesis but rather show that habitat selection is driven by improved foraging opportunities and predation risk reduction, implying that food has been limiting, at least during the period of decline (see Fryxell and Avgar 2012, Fryxell and Sinclair 1988). It seems that fine-scale interpatch movements may have increased caribou exposure to predation risk while also providing increased access to forage. It is understood that most prey species, notably ungulates (Creel et al. 2005), avoid forage-rich areas when such areas also confer higher risk (leapfrog effect; Laundré 2010, Sih 1998). Because Newfoundland caribou do not avoid such habitats, this disconnect may explain why high calf predation seems to be the main proximate factor limiting the Newfoundland caribou population (Mahoney and Weir 2009). It follows that low calf survival ultimately may be driven by risk-prone foraging by parturient females under high nutritional stress.

Refining the definition of availability to study behavioural trade-offs

Habitat selection studies usually describe an animal as using certain areas within a rather specific and narrow set of rules. Yet, this approach can be problematic because it fails to provide an appropriate mechanism explaining habitat use patterns relative to what is actually available to the animal (Aarts et al. 2013). We showed how a mechanistic model of availability, mimicking fine-scale inter-patch movements, can be used to study broad-scale selection and thereby improve our understanding of how caribou trade off food acquisition versus predation risk. Our mechanistic model allows us to draw inferences about multiple and perhaps paradoxical motivations, as was evident by the revelation that female caribou make habitat-related decisions on the basis of foraging opportunities despite resultant increase in predation risk. Specifically, we would have missed that caribou are able to adjust their movements to reduce bear predation risk; such an interpretation would not have been possible in the absence of our mechanistic model, since we would not have detected that the majority of the herds displayed bear avoidance. Accordingly, we suggest that our model offers an improvement over the random model by restricting habitat availability to areas that are potentially usable by an individual on the basis of its movement decisions. Other approaches have been proposed in this vein (see notably Avgar et al. 2013), but our approach is unique in that we used a mechanistic model of movement capturing fine scale selection to study broader scale patterns. Spatially-explicit modelling therefore allowed us to isolate the selection process occurring at a specific level, clarifying inferences about the motivation behind selection and providing a refined understanding of how caribou handle food versus safety trade-offs across levels of selection. Therefore, we infer that this refined assessment of habitat availability will open up additional opportunities for testing new hypotheses related not only to predator-prey interactions but to the general behavioural process of habitat selection in relation to the several competing behavioural motivations underlying such selection.

Acknowledgements

This project was a component of the Newfoundland & Labrador Caribou Strategy, 2008-2013. This study was partly funded by the Institute for Biodiversity, Ecosystem Science & Sustainability and the Sustainable Development & Strategic Science Division of the Newfoundland & Labrador Department of Environment & Conservation and also the Safari Club International Foundation (SCIF). GBR was supported by a scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC). MAL and JRP were funded by NSERC Discovery and Accelerator grants. MAL also gratefully acknowledges a Canada Research Chair and a Killam Research Fellowship. We thank the Sustainable Development & Strategic Science Division and the Wildlife Division of the Newfoundland & Labrador Department of Environment & Conservation for providing the telemetry data as well as the government personnel involved in the black bear, coyote, and caribou captures and monitoring over the last four decades. We thank K. Morgan, F. Norman and K. Lewis for preparing the telemetry data, L-P. B.-Rousseau for help in processing Modis NDVI imageries, and E. Downey and M-C. Roy-Avilan for fieldwork assistance. Lastly, we thanks N. Courbin for fruitful discussion and C. Soulliere, T. Fuller and J. Organ for comments on a draft manuscript.

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Table 1. Mixed-effects RSFs for black bears and coyotes, Newfoundland, 1 May - 1 August, 2008-2010. Parameter estimates (β), standard errors (SE), and variance estimates of the random intercept are presented.

	Black bear		Coyote	
Variables	β	SE	B	SE
Water	-1.103	0.035	-1.395	0.050
Barren	-0.113	0.032	-0.257	0.049
Coniferous Dense (CD)	0.799	0.024	0.331	0.038
Coniferous Open (CO)	0.570	0.017	0.195	0.028
Other	0.641	0.051	0.288	0.091
Elevation	-0.178	0.010	0.081	0.023
Slope	0.243	0.009	-0.105	0.012
Wetland within 5 km	0.050	0.014	-0.248	0.022
Barren within 5km	0.112	0.013	-0.255	0.023
Coniferous Open within 5km	-0.031	0.017	-0.345	0.025
Coniferous Dense within 5km	-0.074	0.016	-0.552	0.023
Wetland within 5km * Wetland	-0.146	0.014	-0.135	0.029
Barren within 5km * Barren	-0.264	0.020	0.023	0.030
Coniferous Open within 5km * CO	0.012	0.014	-0.076	0.023
Coniferous Dense within 5km * CD	-0.159	0.015	-0.350	0.032
Random effect	Variance: 1.168		Variance: 1.506	

Table 2. Relative abundance indices of vegetation biomass from vegetation surveys by landcover type. The slope and coefficient of determination (conditional R^2) represent the relationship between vegetation biomass and NDVI values. See Supplementary Information 1.

Habitat	Index of biomass	Slope	Conditional R^2
Barren	0.734	0.908	0.389
Wetland	1.000	0.912	0.465
Coniferous Open	0.990	0.902	0.380
Coniferous Dense	0.458	0.821	0.151

Table 3. Selection ratios (± 95% CI) of 134 caribou from five caribou herds, Newfoundland, 1 May - 1 August, 2007-2010. Interpretation of selection ratios are relative to one: Values higher than one indicate selection for a given resource whereas values lower than one indicate avoidance of the resource. Selection ratios were computed at two different levels: second-order and third-order (within calving grounds), using the general random model of availability and a mechanistic model of availability. Chi^2 values indicating overall presence of selection are also given. Statistically significant values (α=0.05) are presented in bold.

Random model

Herd	Level	Water	Barren	Wetland	Coniferous Open	Coniferous Dense	Other	Chi2
Buchans	3rd-order	**0.264 ± 0.178**	**1.971 ± 0.376**	**1.531 ± 0.262**	**0.700 ± 0.129**	**0.622 ± 0.276**	0.929 ± 2.238	**82.476**
	2nd-order	**0.242 ± 0.163**	**3.366 ± 0.642**	**1.700 ± 0.291**	**0.603 ± 0.111**	**0.652 ± 0.290**	**0.251 ± 0.605**	**157.178**
Lapoile	3rd-order	**0.308 ± 0.201**	**1.377 ± 0.278**	**1.236 ± 0.222**	0.971 ± 0.154	**0.458 ± 0.275**	0.87 ± 1.244	**37.046**
	2nd-order	**0.257 ± 0.167**	**3.103 ± 0.626**	**1.589 ± 0.285**	**0.738 ± 0.117**	**0.368 ± 0.221**	0.71 ± 1.015	**130.663**
Middle Ridge	3rd-order	**0.414 ± 0.191**	**2.215 ± 0.862**	**1.492 ± 0.219**	**0.817 ± 0.121**	0.877 ± 0.445	2.724 ± 3.158	**51.602**
	2nd-order	**0.497 ± 0.229**	1.027 ± 0.400	**2.061 ± 0.303**	**0.809 ± 0.120**	**0.509 ± 0.258**	1.075 ± 1.247	**68.687**
Pot Hill	3rd-order	**0.337 ± 0.236**	0.488 ± 0.892	**0.680 ± 0.269**	**1.171 ± 0.071**	0.826 ± 0.322	1.225 ± 2.171	**24.023**
	2nd-order	**0.224 ± 0.157**	**0.051 ± 0.093**	**0.431 ± 0.171**	**1.634 ± 0.099**	0.832 ± 0.324	0.463 ± 0.820	**133.777**
Gaff Topsails	3rd-order	**0.147 ± 0.138**	1.119 ± 0.288	**1.372 ± 0.250**	1.016 ± 0.142	0.898 ± 0.348	0.392 ± 0.804	**42.535**
	2nd-order	**0.125 ± 0.118**	**2.117 ± 0.545**	**1.558 ± 0.284**	**0.861 ± 0.121**	0.843 ± 0.326	0.346 ± 0.710	**81.911**

Mechanistic model

Herds	Scale	Water	Barren	Wetland	Coniferous Open	Coniferous Dense	Others	Chi2
Buchans	3rd-order	0.663 ± 0.445	**2.137 ± 0.408**	**1.493 ± 0.255**	**0.605 ± 0.112**	**0.572 ± 0.254**	1.031 ± 2.486	**79.488**
	2nd-order	0.601 ± 0.404	**3.412 ± 0.651**	**1.610 ± 0.275**	**0.533 ± 0.098**	**0.630 ± 0.280**	0.315 ± 0.760	**144.079**
Lapoile	3rd-order	0.633 ± 0.412	**1.396 ± 0.281**	1.180 ± 0.212	0.866 ± 0.138	**0.457 ± 0.274**	0.954 ± 1.364	**21.728**
	2nd-order	0.638 ± 0.416	**3.144 ± 0.634**	**1.506 ± 0.27**	**0.653 ± 0.104**	**0.356 ± 0.214**	0.892 ± 1.275	**115.613**
Middle Ridge	3rd-order	1.005 ± 0.464	**2.289 ± 0.891**	**1.420 ± 0.209**	**0.703 ± 0.104**	0.877 ± 0.445	3.819 ± 4.428	**42.600**
	2nd-order	1.232 ± 0.568	1.041 ± 0.405	**1.952 ± 0.287**	**0.715 ± 0.106**	**0.492 ± 0.250**	1.352 ± 1.567	**62.433**

Pot Hill	3rd-order	0.882 ± 0.617	0.561 ± 1.026	**0.673 ± 0.267**	**1.080 ± 0.065**	0.862 ± 0.336	1.622 ± 2.876	6.656
	2nd-order	**0.556 ± 0.389**	**0.051 ± 0.094**	**0.408 ± 0.162**	**1.444 ± 0.087**	0.805 ± 0.314	0.582 ± 1.031	**90.992**
Gaff Topsails	3rd-order	**0.356 ± 0.335**	1.148 ± 0.295	**1.312 ± 0.239**	0.898 ± 0.126	0.864 ± 0.334	0.448 ± 0.919	**15.654**
	2nd-order	**0.311 ± 0.292**	**2.145 ± 0.552**	**1.476 ± 0.269**	**0.761 ± 0.107**	0.815 ± 0.315	0.435 ± 0.893	**52.952**

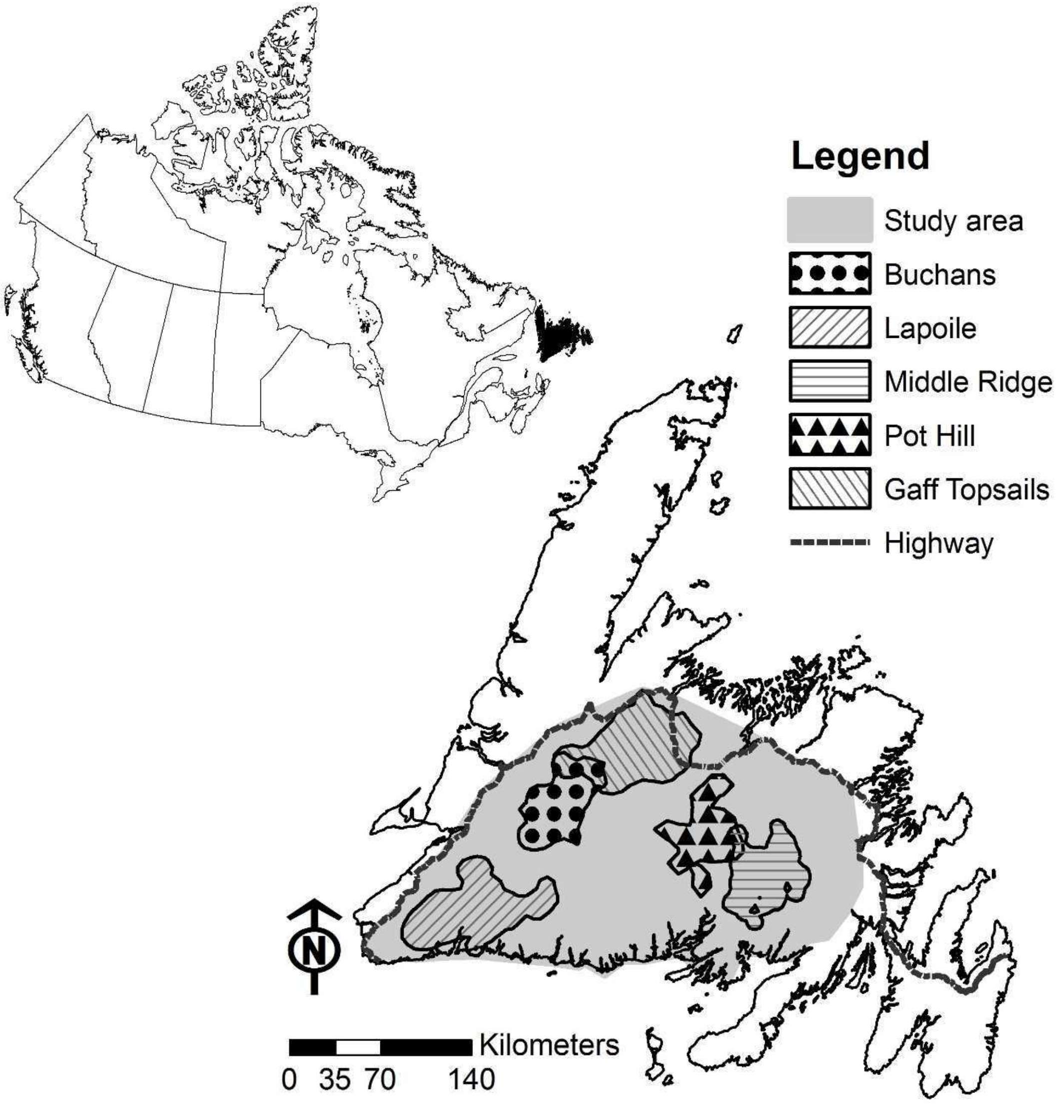
Figure legends

Figure 1. Calving grounds and the larger study area for five caribou herds in Newfoundland, Canada. These delineations were used to define habitat availability.

Figure 2. Average (± 95% C.I.) exposure to forage biomass, coyote encounter risk and bear encounter risk for female caribou from five herds, Newfoundland. Actual exposure (Use) is compared to availability represented by two scales of movement: (i) Selection of a calving ground (2nd-order)) and (ii) movement within calving-ground (3rd-order)). Availability at each scale was also defined using two approaches; (i) a random model (Random) and (ii) simulated locations based on mechanistic modelling of fine-scale movement (Mechanistic). Overall, selection is inferred when use is higher than availability while avoidance is inferred otherwise.

Figure 3. Linear models between vegetation biomass and predation risk from bear, coyote and the interaction of the two showing potential trade-offs for caribou when choosing their calving grounds. Models estimates are given with 95% confidence intervals. Models were performed using the actual caribou locations (Use), but also using random sample of availability (Random) within the study area and a simulated sample based on a mechanistic model (Mechanistic) of fine scale movement for caribou.

Figure 1


Legend
Study area
Buchans
Lapoile
Middle Ridge
Pot Hill
Gaff Topsails
Highway
N
Kilometers
0
35
70
140

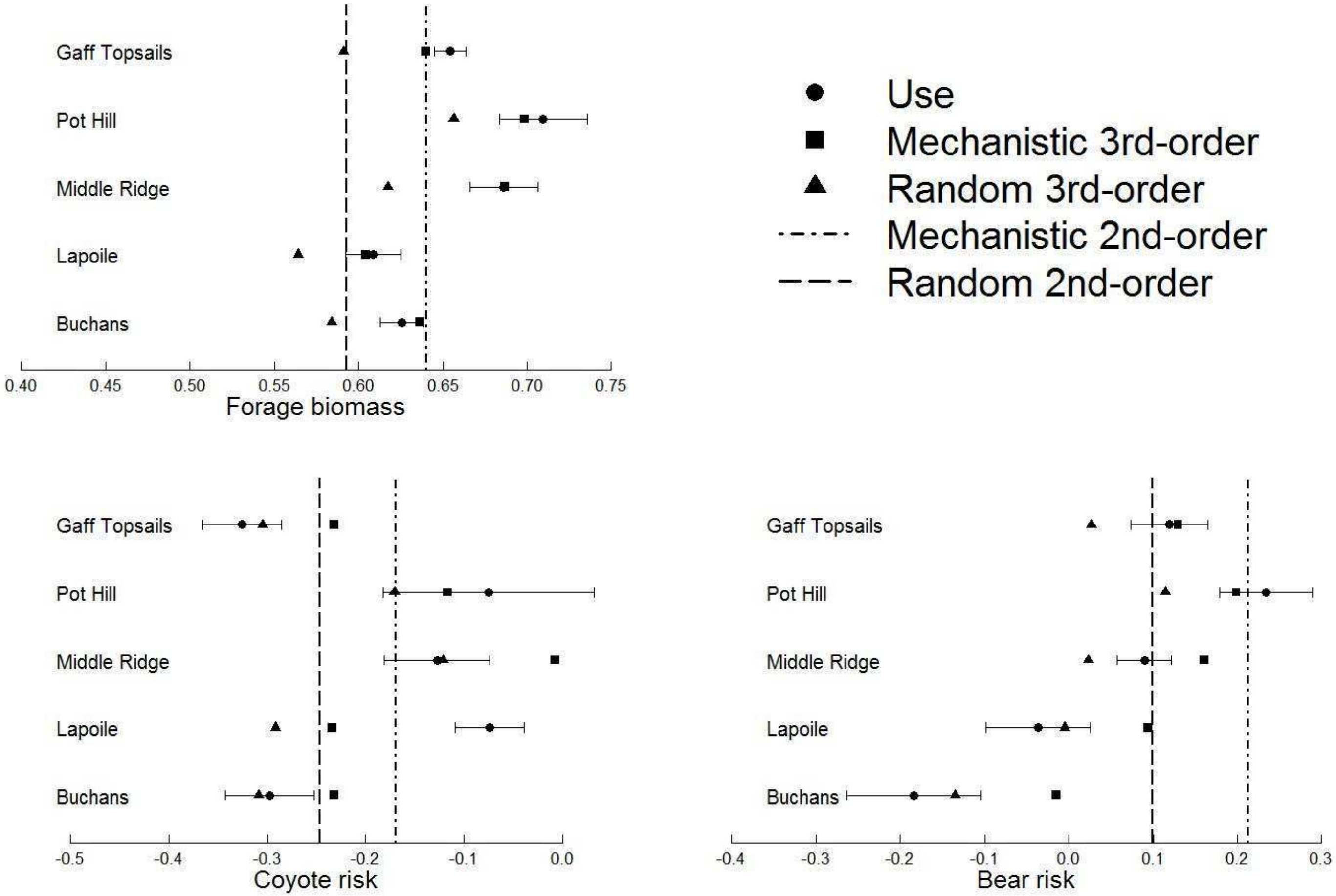
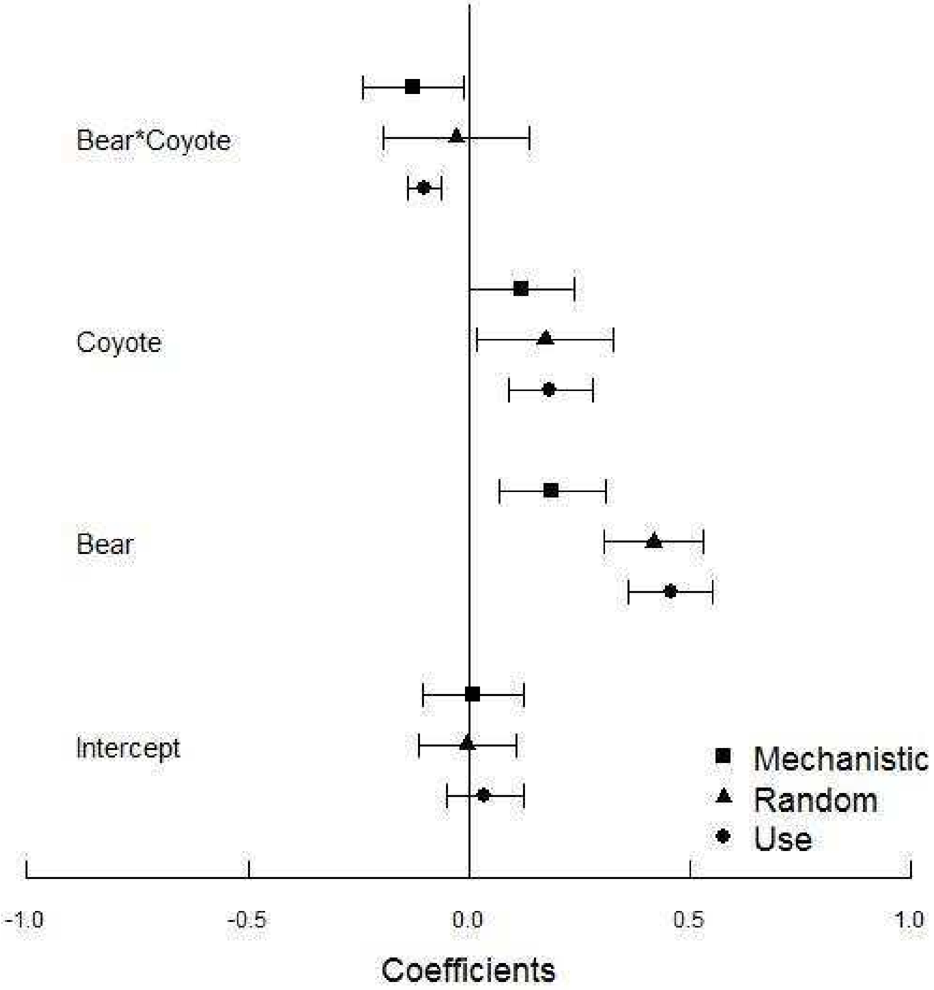

Gaff Topsails
Pot Hill
Middle Ridge
Lapoile
Buchans
0.40 0.45 0.50 0.55 0.60 0.65 0.70 0.75
Forage biomass
● Use
■ Mechanistic 3rd-order
▲ Random 3rd-order
-·-· Mechanistic 2nd-order
— — Random 2nd-order
Gaff Topsails
Pot Hill
Middle Ridge
Lapoile
Buchans
-0.5 -0.4 -0.3 -0.2 -0.1 0.0
Coyote risk
Gaff Topsails
Pot Hill
Middle Ridge
Lapoile
Buchans
-0.4 -0.3 -0.2 -0.1 0.0 0.1 0.2 0.3
Bear risk

Figure 2

Figure 3


Bear*Coyote
Coyote
Bear
Intercept
■ Mechanistic
▲ Random
● Use
-1.0
-0.5
0.0
0.5
1.0
Coefficients