

Linking habitat selection and predation risk to spatial variation in survival

Nicholas J. DeCesare^{1*}, Mark Hebblewhite¹, Mark Bradley², David Hervieux³, Lalenia Neufeld² and Marco Musiani⁴

¹Wildlife Biology Program, Department of Ecosystem and Conservation Science, College of Forestry and Conservation, University of Montana, Missoula, MT, USA; ²Parks Canada, Jasper National Park, Box 10, Jasper, Alberta, Canada; ³Sustainable Resource Development, Government of Alberta, Grande Prairie, Alberta, Canada; and ⁴Faculty of Environmental Design, University of Calgary, 2500 University Dr NW, Calgary, Alberta, Canada

Summary

1. A central assumption underlying the study of habitat selection is that selected habitats confer enhanced fitness. Unfortunately, this assumption is rarely tested, and in some systems, gradients of predation risk may more accurately characterize spatial variation in vital rates than gradients described by habitat selection studies.

2. Here, we separately measured spatial patterns of both resource selection and predation risk and tested their relationships with a key demographic trait, adult female survival, for a threatened ungulate, woodland caribou (*Rangifer tarandus caribou* Gmelin). We also evaluated whether exposure to gradients in both predation risk and resource selection value was manifested temporally through instantaneous or seasonal effects on survival outcomes.

3. We used Cox proportional hazards spatial survival modelling to assess the relative support for 5 selection- and risk-based definitions of habitat quality, as quantified by woodland caribou adult female survival. These hypotheses included scenarios in which selection ideally mirrored survival, risk entirely drove survival, non-ideal selection correlated with survival but with additive risk effects, an ecological trap with maladaptive selection and a non-spatial effect of annual variation in weather.

4. Indeed, we found positive relationships between the predicted values of a resource selection function (RSF) and survival, yet subsequently incorporating an additional negative effect of predation risk greatly improved models further. This revealed a positive, but non-ideal relationship between selection and survival. Gradients in these covariates were also shown to affect individual survival probability at multiple temporal scales. Exposure to increased predation risk had a relatively instantaneous effect on survival outcomes, whereas variation in habitat suitability predicted by an RSF had both instantaneous and longer-term seasonal effects on survival.

5. Predation risk was an additive source of hazard beyond that detected through selection alone, and woodland caribou selection thus was shown to be non-ideal. Furthermore, by combining spatial adult female survival models with herd-specific estimates of recruitment in matrix population models, we estimated a spatially explicit landscape of population growth predictions for this endangered species.

Key-words: ecological trap, habitat quality, resource selection functions, species distribution models, *Rangifer tarandus caribou*, survival, wolves, woodland caribou

Introduction

The relationship between environmental resources and individual fitness is central to ecology and evolution. As framed by niche theory, the fitness of individuals is a

multidimensional function of the abiotic and biotic resources they experience (Hutchinson 1957). This conceptualization of the ecological niche as a fitness gradient across environmental conditions has since offered theoretical foundation for the spatially explicit study of habitat quality as it relates to spatial heterogeneity in resources (Hirzel & Le Lay 2008). However, habitat quality is

*Corresponding author. E-mail: ndecesare@mt.gov

typically estimated according to spatial variation in the distribution or density of species rather than the more difficult to measure variation in demographic vital rates (McLoughlin *et al.* 2010).

The inferred link between density-based habitat models such as species distribution models (Elith & Leathwick 2009) or resource selection functions (Manly *et al.* 2002) and realized fitness benefits hinges on a positive relationship between the average individuals' selection of resources and the benefits conferred by them (Pulliam 2000). Included within this assumption comes a theoretical expectation of animals that adaptively behave in ideal and free distributions (Fretwell & Lucas 1969). Selection of habitats that maximize fitness is expected over evolutionary time (Morris 2003), and such behaviour should collectively incorporate trade-offs between multiple niche dimensions such as food, density, competition and predation (Brown & Kotler 2004). Thus, behavioural observation of species–habitat relationships provides one means of defining and delineating the spatial relationship between habitat and the dynamics of populations and communities (Fryxell & Lundberg 1998).

Population growth rates ultimately represent the mean fitness among individuals (Mills 2012). Using spatial variation in vital rate components of population growth (survival and fecundity), a modest amount of support has been shown for the theoretically positive relationship between selection and demographic benefits (reviewed by Gaillard *et al.* 2010). However, in other systems, ideal or free behaviour by animals may not occur, and selection patterns are often found to poorly reflect underlying habitat quality. For example, territorial behaviour precludes free habitat selection (Fretwell & Lucas 1969) and likely increases occupation of suboptimal habitats, thus obfuscating the selection–demography relationship (Mosser *et al.* 2009). Animals may also have imperfect knowledge of habitat quality, particularly in the face of anthropogenic change (Battin 2004). Resource selection in such systems can portray a 'non-ideal' interpretation of habitat quality where the benefits conveyed by selected habitats are weak or imperfect (Arlt & Pärt 2007), or can reflect ecological traps where animals prefer poor-quality, sink habitats (Battin 2004). Other behavioural constraints such as sociality (Pays *et al.* 2012) or site fidelity (Faille *et al.* 2010) may also prevent ideal and free habitat selection. Lastly, our ability to detect realized benefits of habitat may be complicated by time-lagged effects (Van Horne 1983) or inappropriate treatments of scale (Gaillard *et al.* 2010) when measuring selection patterns.

Despite these complications, species distribution and resource selection models will remain a popular approach to define habitat quality because they facilitate multidimensional modelling of niche relationships with relatively accessible data (Elith & Leathwick 2009). Animals are assumed to behave ideally in such models, and the complex nuances of risk-forage trade-offs and inter-species interactions are integrated into a single selective

response to habitat heterogeneity that presumably maximizes fitness. Researchers have also paired resource selection studies with those of mortality risk due to predators or human causes and have subsequently described habitat quality by adjusting selection predictions with separately modelled risk correlates (e.g. Nielsen, Stenhouse & Boyce 2006). However, it is theoretically unclear how selection and risk are expected to relate, given that if resource selection is adaptive behaviour, selection should inherently balance risk avoidance with other factors. In some cases, selection behaviour has been shown to include avoidance of risk (McLoughlin, Dunford & Boutin 2005; Thomson *et al.* 2006). On the other hand, in maladaptive situations where selection patterns fail to represent underlying quality, one might expect the measurement of risk alone to more accurately convey true demographic habitat quality (Latif, Heath & Rotenberry 2011). Ideally, a demographic test of the importance of either resource selection or predation risk in driving population dynamics should concurrently test the relative effects of each in concert rather than assuming that either acts in isolation.

Here, we separately measure spatial resource selection and predation risk and test each of their relationships with a key vital rate component of population dynamics, adult female survival, for a threatened ungulate, woodland caribou (*Rangifer tarandus caribou* Gmelin). Woodland caribou populations are currently suffering widespread range retraction, population decline and local extirpations (Wittmer, Ahrens & McLellan 2010; Environment Canada 2011). In many cases, the primary source of mortality and ultimately of population declines for caribou is predation from a predator with which they have coexisted over evolutionary time, the wolf (*Canis lupus*, L.; Wittmer, Sinclair & McLellan 2005; McLoughlin, Dunford & Boutin 2005). Generally, one would predict caribou to have adaptive resource selection patterns sufficient to minimize predation risk at sustainable rates (Ferguson, Bergerud & Ferguson 1988; McLoughlin *et al.* 2010). However, widespread anthropogenic disturbances have recently altered the community dynamics of landscapes within which caribou and wolves coexist (DeCesare *et al.* 2010). Landscape changes have also directly altered spatial variation in predation risk, specifically through their effects on wolf resource selection and thus the spatial risk of prey species encountering wolves (Latham *et al.* 2011; DeCesare 2012). Caribou selection patterns are well studied and include avoidance behaviours that minimize predation risk (Rettie & Messier 2000; McLoughlin, Dunford & Boutin 2005), yet widespread declines in populations may imply that observed selection behaviour is maladaptive. This species therefore allows an informative test of the nature of selection- and risk-based relationships to demographic measures of habitat quality in a system where novel conditions may preclude the effective selection of high-quality habitat.

We considered predictions under ideal free selection as a baseline hypothesis for this analysis. Ideal free habitat selection behaviour would result in selection that is correlated with vital rate outcomes (e.g. adult female survival) and assumed to be included in selection patterns is an ideal response (avoidance) to predation risk. We considered four alternative hypotheses for describing different selection and risk relationships to survival outcomes in this system characterized by caribou population declines and human-altered landscapes. We considered a 'predation risk' hypothesis under which spatial variation in risk alone would explain variation in caribou survival without any additional effect of selection. We then combined the effects of selection and risk in two ways, first by including a 'non-ideal selection' hypothesis (Arlt & Pärt 2007) under which selection would remain a favourable but incomplete form of maximizing survival due to an additive effect of predation risk beyond that revealed through selection behaviour alone. Secondly, we considered an 'ecological trap' hypothesis under which an interaction with predation risk would drive maladaptive (negative) relationships between selection and survival (Latif, Heath & Rotenberry 2011). Lastly, we considered a non-spatial 'weather' hypothesis under which variation in survival was driven solely by temporal differences in weather among years rather than by spatial differences in either selection probability or predation risk.

We used Cox proportional hazards modelling (Therneau & Grambsch 2000) to test whether selection was indeed indicative of survival outcomes using a long-term data set for endangered caribou in an area of growing human development impacts, Alberta, Canada. Furthermore, we combined spatially explicit adult female survival estimates with recruitment data at the local population level into demographic models to geographically map growth-based habitat quality in a spatially explicit framework (Franklin *et al.* 2000). Given that population growth rates ultimately represent the mean fitness among individuals (Mills 2012), we extrapolated our models to predict spatial variation in population growth rate according to selection and risk correlates with identify source and sink habitats for this endangered and declining ungulate. This demonstrates the power of this approach for both conceptual and operational definitions of habitat quality based upon demographic data (Hirzel & Le Lay 2008).

Materials and methods

STUDY AREA AND CARIBOU POPULATIONS

We studied woodland caribou survival in 5 spatially distinct local populations (A la Pêche, Little Smoky, Narraway, Redrock-Prairie Creek and South Jasper) within west-central Alberta and eastern British Columbia, Canada (Appendix S1). The large mammal predator-prey community in our study area includes many predators of ungulates such as wolves, grizzly bears (*Ursus arctos* L.),

black bears (*Ursus americanus* Pallas), mountain lions (*Puma concolor* L.), Canada lynx (*Lynx canadensis* L.), coyote (*Canis latrans* Say) and wolverine (*Gulo gulo* L.), as well as multiple species of ungulate prey including woodland caribou, moose (*Alces alces* L.), elk (*Cervus elaphus* L.), white-tailed deer (*Odocoileus virginianus* Z.), mule deer (*Odocoileus hemionus* Rafinesque), big-horn sheep (*Ovis canadensis* Shaw) and mountain goats (*Oreamnos americanus* de Blainville). The study area included large networks of federal and provincial parks and protected areas, but a majority of lands were managed by provincial governments for multiple uses including forestry, oil and natural gas industries. Resource extraction practices have left a substantial footprint in this study area in the form of early-seral stage forestry cut-blocks and linear forest-free corridors such as roads and seismic lines, each of which have been shown to affect caribou space use and resource selection (DeCesare *et al.* 2012b).

ANIMAL CAPTURE AND MONITORING

We deployed a combination of conventional very high frequency (VHF; Lotek Wireless, Newmarket, Ontario, Canada) and global positioning system (GPS; Lotek GPS 1000, 2000, 2200, 3300, 4400 and 7000 models) telemetry collars during 1998–2011 on 468 adult female caribou using helicopter net-gunning. Approximately 24% of the total monitoring time across all individuals included GPS data collected at 1-, 2-, 3-, 4-, or 6-hour intervals, while the remainder (76%) of monitoring time involved aerial telemetry of VHF telemetry collars at a median interval of 52 days. The fate of individuals was recorded with each telemetry location as either alive or dead. Animals that did not die during the study were right-censored and removed from the at-risk pool after their last known alive location in accordance with events such as collar removal, collar battery failure that prevented detection for a period of ≥ 2 years or the end of the study.

HYPOTHESES OF SPATIAL HABITAT QUALITY

We predicted that the habitat conditions characterized by resource selection functions and predation risk models could have either instantaneous or cumulative effects on the hazard experienced by individuals (Gaillard *et al.* 2010). Thus, we tested two temporal scales of relating spatial variation in selection probability and predation risk to survival. We assessed whether survival outcomes were better predicted according to instantaneous values of the spatial selection probability and risk models encountered with each individual telemetry location, seasonal averages of these spatial models across all locations within a given season or both instantaneous and averaged values.

We then developed five candidate models in accordance with our five hypotheses (Fig. 1), with specific statistical predictions for each: 1) the 'ideal selection' model included only a main effect of resource selection probability on caribou survival, and we predicted a negative relationship between selection probability of a given spatial location and the hazard, or probability of a mortality event at that location; 2) the 'predation risk' model included only a main effect of predation risk on survival and predicted a positive relationship between spatial predation risk and the spatial hazard; 3) the 'non-ideal selection' model included main effects coefficients for resource selection probability and predation risk and predicted that selection would correlate negatively with hazard, while risk would correlate positively, such that risk

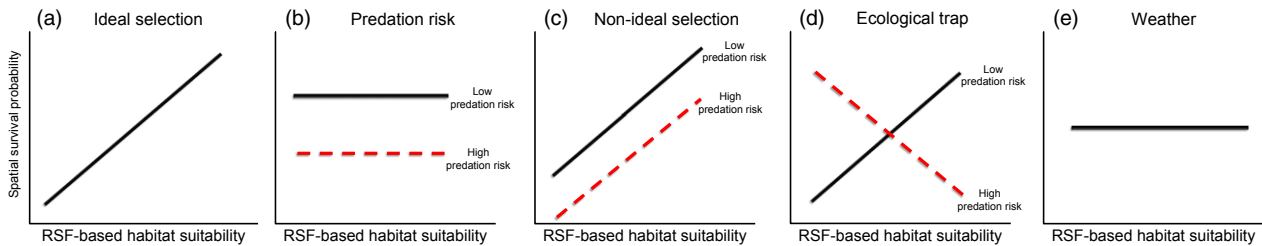


Fig. 1. Relationships between spatial variation in survival probability and predicted habitat suitability according to resource selection functions (RSFs) and spatial models of predation risk of woodland caribou in western Alberta and eastern British Columbia, 1998–2011, under 5 hypotheses of (a) ideal selection of high-quality habitat by caribou, (b) survival patterns driven by predation risk alone, (c) non-ideal selection of high-quality habitat where survival increases with selection but predation risk has additive cost on survival, (d) an ecological trap wherein the relationship between survival and resource selection patterns varies according to the level of predation risk and (e) a non-spatial weather model wherein survival is driven by broad-scale annual variation in weather rather than fine-scale spatial variation.

conveyed an additive effect on the hazard beyond that described by selection patterns alone; 4) the ‘ecological trap’ model included main effects for resource selection probability and predation risk, as well as an interaction term for selection \times predation risk, such that the relationship between selection and survival would vary under different risk scenarios; and 5) the ‘weather’ hypothesis included weather metrics (temperature and precipitation) averaged across the study area for both summer and winter seasons, wherein we evaluated the significance of among-year weather variation as the primary driver of variation in adult survival, as has been shown previously (Jacobson *et al.* 2004). We used Akaike information criteria (AIC) to evaluate the relative support for each hypothesis distinctly during summer and winter seasons.

SURVIVAL ANALYSIS

We used Cox proportional hazards (CPH) modelling to assess the statistical support for each of our hypotheses concerning drivers of adult female caribou survival. Cox proportional hazards models are semi-parametric regression models for survival data that specify a flexible and nonparametric baseline hazard function ($h_0(t)$) of the hazard over time, while at the same time parameterizing a function ($r(x, \beta)$) that describes proportional changes in the baseline hazard with changes in subject covariates (Hosmer, Lemeshow & May 2008). In total, the hazard,

$$h(t, x, \beta) = h_0(t)r(x, \beta), \quad \text{eqn 1}$$

is a function of both changes in the baseline hazard over time and relative differences in hazard according to covariates. The relative effect of a unit change in a given covariate, i , on the hazard is assumed to be constant over time and can be estimated directly from each model coefficient (β_i) according to the hazard ratio (HR),

$$HR_i = \exp(\beta_i), \quad \text{eqn 2}$$

We used a recurrent time of origin based on a biological year where 1st May of each year was set to a time of 1 and 30th April the following year to a time of 365 (Fieberg & DelGiudice 2009). Because individuals were allowed to contribute multiple individual-years to the risk sample, we used robust ‘sandwich’ variance estimation to account for within-individual correlation (Cleves *et al.* 2008). We also stratified CPH analyses by caribou population, which allowed for distinct baseline hazard functions among populations while estimating a single population-averaged

coefficient or response to each covariate (Therneau & Grambsch 2000; Cleves *et al.* 2008). Caribou in our study area are partially migratory, which likely has implications for survival given migratory ungulate life-histories (Hebblewhite & Merrill 2011). DeCesare *et al.* (2012b) used quantitative analysis of migration timing and duration to describe distinct summer and winter seasons for caribou in our study area. Thus, we estimated separate models for summer (1 May–31 October) and winter (1 November–31 April) seasons to accommodate seasonal differences in both resource selection (DeCesare *et al.* 2012b) and predation risk (DeCesare 2012). We used Akaike information criteria (AIC) to evaluate sets of models within each season.

Along with animal fate, each caribou telemetry location was associated with spatial values characterizing caribou resource selection probability and relative risk of wolf predation as well as seasonally averaged weather data. To characterize preferred habitat as typically estimated using species distribution or resource selection modelling approaches, we used a previously developed scale-integrated resource selection functions (SRSFs) to estimate the spatial variation in resource selection probability (DeCesare *et al.* 2012b). These SRSFs were developed separately for each study population and season, as the integrated probabilities of resource use across first-, second- and third-order scales of selection. They used logistic regression to predict the relative probability of use by caribou according to a number of spatial covariates including topographical features (elevation, slope, aspect and topographical position), vegetative features (land cover type, distance to tree line, normalized difference vegetation index and per cent snow coverage) and human disturbance (cut-block and seismic line densities; see DeCesare *et al.* 2012b for more detail).

We used previously developed seasonal wolf predation risk models in the same study area to estimate spatial variation in wolf predation risk (DeCesare 2012). These models integrated the probabilities of both encountering a wolf and being killed given an encounter for all ungulate prey species according to similar topographical (slope, topographical position and distance to streams), vegetative (land cover type) and human disturbance (distances to roads, seismic lines and forestry cut-blocks) covariates (see DeCesare 2012 for more detail). We estimated seasonal weather covariates for each year from 1998 to 2012 of maximum daily temperature ($^{\circ}\text{C}$) and precipitation (mm) for the summer season and minimum daily temperature ($^{\circ}\text{C}$) and snow on the ground (cm) for the winter season using Environment Canada’s National Climate Archive data for a weather station within the study area in Jasper, Alberta (52.93 $^{\circ}\text{N}$, 118.03 $^{\circ}\text{W}$).

We conducted two tests of the assumption of proportional hazards for best models. We began with a link test, which re-estimates a CPH model using the linear and squared predicted values, and failure of this test is indicated by a statistically significant coefficient of the squared predictor (Cleves *et al.* 2008). We then plotted the scaled Schoenfeld residuals over time, wherein a nonzero slope over time can indicate a lack of proportionality (Cleves *et al.* 2008).

PREDICTING DEMOGRAPHIC HABITAT QUALITY

To visually depict the continuum of habitat quality according to drivers of seasonal survival probabilities, we predicted cumulative seasonal survival probabilities from the best seasonal model under input conditions characterizing both low (5th percentiles of seasonal average) and high (95th percentile) values of each covariate. We also spatially extrapolated model predictions for each population, j , by estimating seasonal survival rates to the end of each season ($S[t_e]$) as a function of each pixels' attribute data according to:

$$S_j(t_e|x) = (S_{0,j}[t_e])^{\exp(x\beta_s)} \quad \text{eqn 3}$$

where $S_{0,j}[t_e]$ is the baseline cumulative survival probability per population to the last day of each season, with different baseline estimates according to strata, j , or in this case populations (Cleves *et al.* 2008).

We used matrix population models to combine spatial survival estimates from eqn 3 with average recruitment estimates from age ratio surveys into population growth rates (DeCesare *et al.* 2012a) or the mean fitness of individuals within each population (Mills 2012). Because the annual period was divided equally into two seasons, we divided recruitment estimates in half to distribute the recruitment component of population growth equally across seasonal models. These additional steps allowed us to spatially estimate population growth as a function of two commonly measured covariates, as well as to extrapolate a raster of habitat quality across the study area as quantified with predicted population growth rates, with immediate conservation implications.

Results

Model selection results indicated strong support for the non-ideal selection hypothesis that both resource selection and predation risk were important and non-interacting predictors of the relative mortality hazard for adult female caribou (Table 1). Though ΔAIC was <2 for the ecological trap model for both seasons, the interaction term of selection and risk did not appreciably reduce model deviance and received no statistical support in either summer ($P = 0.708$) or winter ($P = 0.935$) seasons (Appendix S2). When comparing nested models that differ in only a single parameter, the general rule of models with $\Delta\text{AIC} < 2$ being equally supported is not valid (Arnold 2010). Thus, the interaction term characterizing an ecological trap can be considered an uninformative parameter (Arnold 2010). While increases in resource selection probability did correlate favourably with decreased hazard during both seasons, the ideal selection model was strongly inferior to one including a separate,

Table 1. Model selection results including the number of parameters (k) and ΔAIC comparing relative support for five hypotheses and a null model testing spatial patterns of adult female woodland caribou survival during each of summer and winter seasons in west-central Alberta and eastern British Columbia, 1998–2011

Model	k	AIC	ΔAIC
Summer			
H1. Ideal selection (selection)	1	1153.792	35.79
H2. Predation risk (risk)	1	1192.389	74.39
H3. Non-ideal selection (selection + risk)	2	1118.002	0
H4. Ecological trap (selection + risk + s*r)	3	1119.828	1.83
H5. Weather (temp + precip)	2	1215.407	97.41
Null	0	1213.797	95.80
Winter			
H1. Ideal selection (selection)	1	866.892	8.98
H2. Predation risk (risk)	1	884.598	26.69
H3. Non-ideal selection (selection + risk)	2	857.910	0
H4. Ecological trap (selection + risk + s*r)	3	859.901	1.99
H5. Weather (temp + snow)	2	890.619	32.71
Null	0	889.459	31.55

additive effect of predation risk on the hazard beyond that accounted for by selection alone. In accordance with our predictions for the non-ideal selection hypothesis, resource selection probability was negatively related to the mortality hazard (i.e. positively to survival) during both summer ($\beta = -34.364$, $P < 0.001$) and winter ($\beta = -22.509$, $P < 0.001$) seasons, and predation risk was positively related to the hazard (i.e. negatively to survival) in both summer ($\beta = 20.227$, $P < 0.001$) and winter ($\beta = 6.096$, $P < 0.001$) models (Table 2).

There was univariate support for relationships between the mortality hazard and both seasonal average and instantaneous measures of resource selection probability and predation risk, though in multivariable models only a single scale remained significant for each (Table 2). In the best summer model, the seasonal average resource selection value for each individual-year was most predictive of hazard, while in the best winter model, the instantaneous, or per location, value of resource selection probability was most predictive. Predation risk was most predictive when measured instantaneously during both seasons. Weather parameters such as maximum temperature ($P = 0.182$) and precipitation ($P = 0.266$) during summer and minimum temperature ($P = 0.476$) and snow ($P = 0.313$) during winter did not have significant effects on the hazard as measured using seasonal averages for each year (Appendix S2).

Predictions of seasonal survival rates varied from 0.660 to 0.996 during summer and from 0.820 to 0.985 during winter according to low (5th percentile) and high (95th percentile) seasonally averaged resource selection and predation risk values among collared individuals (Fig. 2). This amounted to a predicted range in annual survival

Table 2. Cox proportional hazards coefficients, standard errors, Wald statistics (z) and probability values for best summer and winter 'non-ideal selection' models of the effect of resource selection probability and predation risk on the relative hazard, or probability of mortality, for adult female woodland caribou, west-central Alberta and eastern British Columbia, 1998–2011

Parameter	β	SE	z	P
Summer				
Resource selection probability, seasonal average	-34.36	5.98	-5.75	<0.001
Predation risk, per location	20.23	2.91	6.95	<0.001
Winter				
Resource selection probability, per location	-22.51	6.15	-3.66	<0.001
Predation risk, per location	6.10	1.61	3.79	<0.001

from 0.541 to 0.981 between relatively hazardous areas with low selection probability and high risk and relatively safe areas with high selection probability and low risk, respectively. Spatially extrapolating the Cox proportional hazards models allowed the integration of baseline survival probabilities, relative selection probabilities and relative predation risk into spatial depictions of survival-based habitat quality (Fig. 3). Furthermore, in combination with average calf/cow ratio recruitment estimates, these models allowed projection of population growth rate predictions in both environmental and geographical space as a function of these two biologically fundamental axes of species niches (Fig. 4).

Link tests of both summer ($P = 0.720$) and winter ($P = 0.990$) models showed insignificant squared predictors,

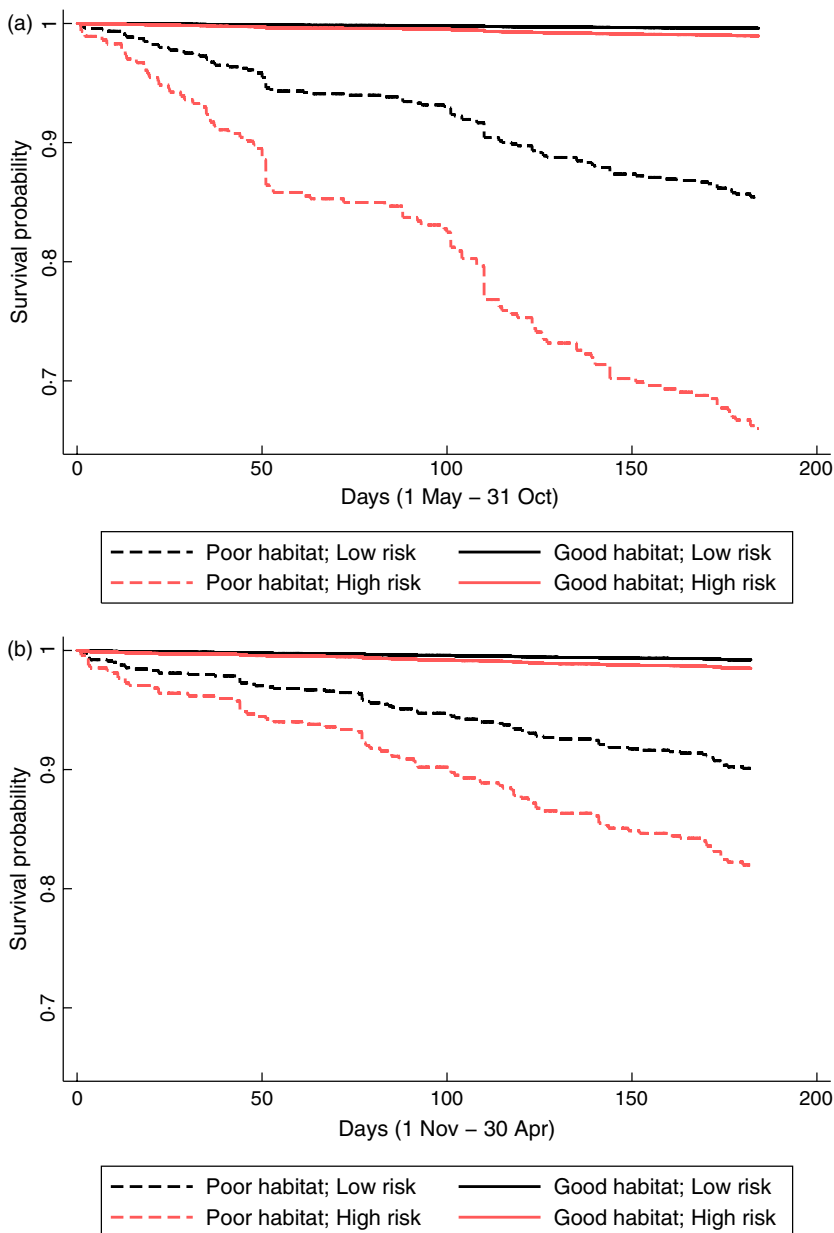


Fig. 2. Predicted seasonal survival rates according to varying conditions of high and low resource selection probabilities and wolf predation risk of adult female woodland caribou survival during (a) summer and (b) winter seasons in west-central Alberta, 1998–2011.

and generally suggested that both models were specified correctly with little evidence for omitted variables. Scaled Schoenfeld residuals did not vary systematically over time and generally supported meeting the assumption of proportional hazards for both summer and winter models (Appendix S3).

Discussion

Resource selection and species distribution models hinge on an assumption that animals select habitat ideally and freely to maximize fitness with respect to forage, risk and other niche dimensions. While such models have been predictive of vital rates in some cases (McLoughlin *et al.* 2006), other research in systems with high predation risk or recent anthropogenic change has revealed breakdowns between habitat selection and realized quality (Battin 2004). We tested first whether resource selection models were predictive of adult female survival for woodland caribou. Indeed we found positive relationships between the predicted values of a scale-integrated resource selection function and the probability of survival across both winter and summer seasons (Appendix S2). This result supported our ideal free habitat selection hypothesis that selection was indicative of benefits to

survival conferred by habitat. However, the subsequent addition of predation risk into models strongly improved explanation of spatial patterns of adult survival, suggesting that predation risk offered an additive source of hazard beyond that which was detected through resource selection alone. Similar to non-ideal selection originally posed by Arlt & Pärt (2007), we interpret this result to indicate a flaw in resource selection, such that predation risk was not avoided in a matter representative of its impact on survival.

Non-ideal selection may be a symptom of recent, human-induced changes to spatial patterns in predation risk (Latham *et al.* 2011; DeCesare 2012), where a potential lag may occur between present survival outcomes of changed conditions and their selective pressures on evolving animal behaviour (Van Horne 1983). Non-ideal selection may also result from non-free selection by animals, such as caribou, with other constraints such as sociality (Pays *et al.* 2012) or site fidelity (Faille *et al.* 2010). In either case, predation risk represents an additive covariate of spatial survival probability beyond that detectable through selection patterns alone. We found no support for an ecological trap in this system; predation risk induced a constant proportional decrease in survival while not interacting with the generally positive selection

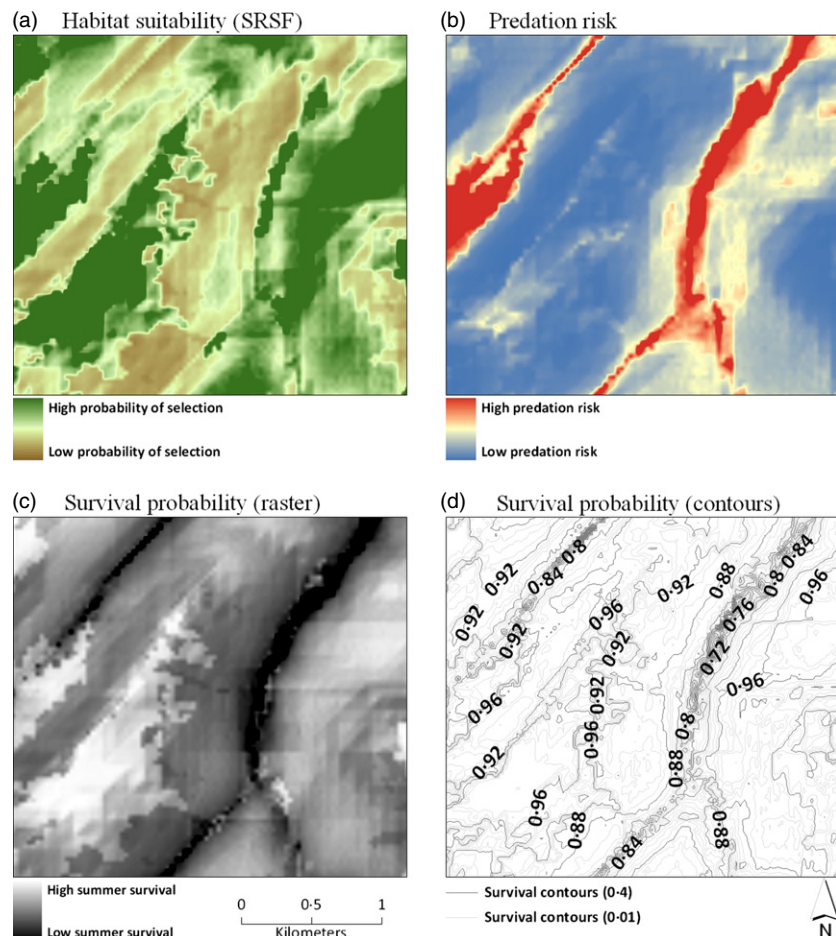


Fig. 3. Spatial predictions of two input surfaces [(a) a scale-integrated resource selection function (SRSF) and (b) a wolf predation risk model] and a Cox proportional hazards model incorporating both the SRSF and predation risk into both (c) raster and (d) contoured spatial predictions of adult female woodland caribou survival for an example portion of the study area in west-central Alberta, 1998–2011.

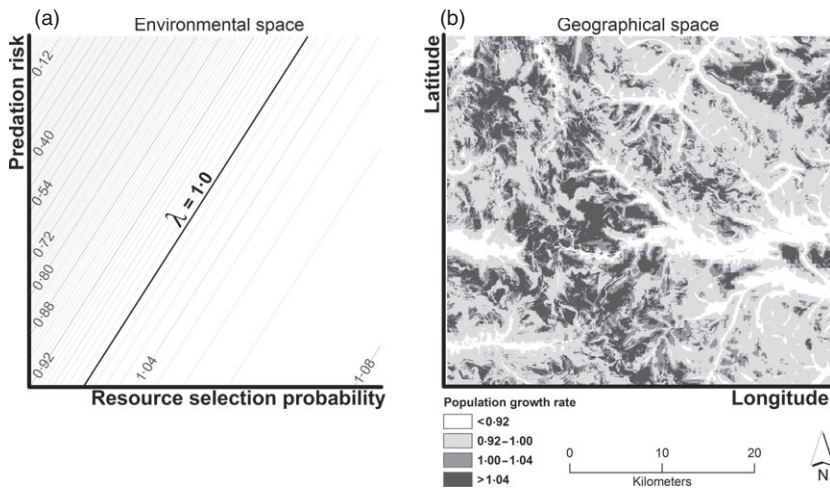


Fig. 4. The relationship between local variation in predicted resource selection function probability values, wolf predation risk and woodland caribou population growth achievable under such conditions across both (a) environmental space and (b) geographical space (*sensu* Hirzel & Le Lay 2008) for an example range of environmental and geographical conditions for woodland caribou in west-central Alberta, 1998–2011. Note: predictions are based on a 6-month summer spatial model of adult survival and half of the non-spatial annual recruitment estimate, and thus are representative only of the summer season contribution to annual population growth.

relationship. Ecological traps are often found where novel and risky conditions mimic those of high-quality habitat, and as a result adaptive cues underlying habitat selection, decisions become maladaptive (Schlaepfer, Runge & Sherman 2002). Woodland caribou do not show active selection of risky areas, but rather have exhibited behavioural avoidance of risk across many study areas (Rettie & Messier 2000; McLoughlin, Dunford & Boutin 2005). Rather than novel sources or cues of risk, our results may simply reflect higher overall levels of risk in the same risky places, thus causing an imbalance between risk avoidance and other niche dimensions shaping caribou selection.

Theoretically, animals may use local variation in density to distribute themselves in a manner that facilitates equivalent fitness across all levels of habitat quality (Fretwell & Lucas 1969). This may preclude efforts to measure habitat quality as a function of adult survival as we do here because equal survival among individuals could be attainable across varying levels of inherent habitat quality as mediated by density. However, caribou in our study area are known to occur at substantially lower densities than historically observed (ASRD & ACA 2010). Furthermore, because there is no evidence of negative density dependence on adult survival in declining woodland caribou populations (Wittmer, Ahrens & McLellan 2010; DeCesare *et al.* 2011), we expect few density-induced effects on local variation in survival.

In this study, instantaneous variation in predation risk was found to be a better predictor of survival than the seasonal average risk exposure for each individual. This suggests that the most relevant variation in risk occurs locally or at fine scales, though the significance of seasonal average risk levels at the univariate level does lend some support to a cumulative risk effect (*sensu* Christianson & Creel 2010). With regard to RSF predicted values, seasonally averaged values per individual were more predictive of survival outcomes during summer, whereas instantaneous RSF values were more predictive during winter. This may reflect a greater role of

predation risk in driving winter survival and forage in driving summer survival in Alberta, though an opposite pattern has also been suggested for woodland caribou in British Columbia (Wittmer, McLellan & Hovey 2006).

We focused on adult survival due to its high influence on population growth in ungulates, particularly those in declining populations, though recruitment may also explain much variation in ungulate population growth rates (Johnson *et al.* 2010). In a previous study concerning one of the populations included here, DeCesare *et al.* (2012a) found that 54% and 43% of the variation in annual population growth rates were explained by variation in adult survival and recruitment, respectively. Demographic evaluation of habitat quality has shown both similar (Arlt & Pärt 2007) and discordant (Martin 1995) patterns of quality with respect to different vital rates. Thus, our spatial function of habitat quality (Fig. 4) as driven by adult female survival may not adequately account for important habitat components of juvenile survival. Complete representation of environmental and spatial gradients of fitness should integrate measures of habitat quality according to other life-history parameters as well (Martin 1995; Coulson *et al.* 2003). While detailed study of calf survival in woodland caribou has been rare, predator-caused mortality is typically an important source of mortality for juvenile ungulates (Griffin *et al.* 2011). The additive effect of predation risk may be even greater in driving overall quality of habitats after accounting for spatial variation in recruitment.

Predicted seasonal survival rates from our models suggest a wide range in habitat quality experienced by individuals according to their space use and underlying gradients of selection probability and risk of predation. Though Wald statistics suggested similar statistical evidence of the effect of both selection probability and predation, we used outer 5th and 95th percentiles of seasonal averages to frame the observed bounds of selection probability and predation risk experienced by individuals. This approach suggested that variation between low and high selection probability more strongly dictated survival

probability (Fig. 2). Predation risk induced a constant proportional decrease in survival probability across gradients in selection probability (Fig. 1c), though this translated to a small absolute effect on survival probability in favourable habitat and a large absolute effect in poor habitat (Fig. 2). Because animals within this study area are partially migratory, both the resource selection results of DeCesare *et al.* (2012b) and those of this study are subject to a lack of precision when estimating average summer models from data including both migratory and sedentary individuals. Future work might improve on this approach by studying or accounting for differential survival-based landscapes during particular seasons when behavioural strategies such as migration create intrapopulation variation (Hebblewhite & Merrill 2011).

Ultimately, we used Cox proportional hazards modelling to facilitate the translation of resource selection and predation risk patterns into an estimate of habitat quality founded on adult female survival. This achieved the high standard of translating gradients of environmental resources into a multidimensional, demography-based model of the gradient in caribou niche space (*sensu* Hirzel & Le Lay 2008). Furthermore, this technique allowed the extrapolation of vital rate predictions across geographical space (Figs 3 and 4), with great potential for conservation or management applications (Franklin *et al.* 2000). Such a spatial model of demographic habitat quality may be used to inform critical habitat under endangered species legislation or may be linked with landscape scenario models to forecast relationships between landscape conditions and population viability (Heinrichs *et al.* 2010). However, we caution that the ability of our model to describe or predict population dynamics would likely be improved by additional inclusion of spatial, habitat-induced variation in other important vital rates such as fecundity and juvenile survival. Overall, this work indicates both the strength and the limitation of commonly conducted resource selection or species distribution modelling. We found that density and/or selection did indeed relate positively to survival, yet were found to incompletely represent spatial variation in adult survival and survival-based depictions of habitat quality.

Acknowledgements

Capture protocols were approved by the University of Montana Institutional Animal Care and Use Committee (Animal Use Protocol 059-09MHWB-122209), University of Alberta Animal Care Committee (Protocol SCHM-2005-61) and Parks Canada Animal Care Committee (JNP-2009-4052). Financial and other support for our research programme was provided by the Alberta Conservation Association, Government of Alberta Department of Sustainable Resource Development, British Columbia Ministry of the Environment, Canadian Association of Petroleum Producers, Canadian Forest Products, Foothills Research Institute, Montana Institute on Ecosystems (as supported by NSF EPSCoR Grant EPS-1101342), National Aeronautic and Space Agency (NASA; under award No. NNX11AO47G), NSERC, Petroleum Technology Alliance of Canada, Parks Canada, Royal Dutch Shell Canada, University of Alberta, University of Calgary, University of Montana, West Central Alberta Caribou Committee, Weyerhaeuser Company and World Wildlife Fund. Any opinions, findings and conclusions, or recommendations expressed do

not necessarily reflect the views of the funding entities listed above. We thank J. Berger, L. S. Mills, A. Mysterud, D. Pletscher, N. Yoccoz and three anonymous reviewers for helpful reviews of previous versions of this manuscript. We also thank A. Dibb, J. Ficht, S. Hazenberg, D. Hobson, K. Lisgo, L. Morgantini, L. Neufeld, W. Peters, S. Robertson, M. Russell, F. Schmiegelow, M. Sherrington, S. Slater, K. Smith, D. Stepnisky, B. Weckworth, M. Wheatley, J. Whittington and J. Wilmshurst for their invaluable assistance with data collection and project management.

References

- Arlt, D. & Pärt, T. (2007) Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology*, **88**, 792–801.
- Arnold, T.W. (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, **74**, 1175–1178.
- ASRD & ACA (Alberta Sustainable Resource Development and Alberta Conservation Association). (2010) Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta: update 2010. *Alberta Wildlife Status Report No. 30 (Update 2010)*. Alberta Sustainable Resource Development, Edmonton, Alberta, Canada 88 pp.
- Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, **18**, 1482–1491.
- Brown, J.S. & Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, **7**, 999–1014.
- Christianson, D. & Creel, S. (2010) A nutritionally mediated risk effect of wolves on elk. *Ecology*, **91**, 1184–1191.
- Cleves, M., Gould, W., Gutierrez, R. & Marchenko, Y. (2008) *An Introduction to Survival Analysis Using Stata*, 2nd edn. Stata Press, College Station, USA.
- Coulson, T., Kruuk, L.E.B., Tavecchia, G., Pemberton, J.M. & Clutton-Brock, T.H. (2003) Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution*, **57**, 2879–2892.
- DeCesare, N.J. (2012) Separating spatial search and efficiency rates as components of predation risk. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4626–4633.
- DeCesare, N.J., Hebblewhite, M., Robinson, H.S. & Musiani, M. (2010) Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation*, **13**, 353–362.
- DeCesare, N.J., Whittington, J., Hebblewhite, M., Robinson, H., Bradley, M., Neufeld, L. *et al.* (2011) The role of translocation in recovery of woodland caribou populations. *Conservation Biology*, **25**, 365–373.
- DeCesare, N.J., Hebblewhite, M., Bradley, M., Smith, K.G., Hervieux, D. & Neufeld, L. (2012a) Estimating ungulate recruitment and growth rates using age ratios. *Journal of Wildlife Management*, **76**, 144–153.
- DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L. *et al.* (2012b) Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, **22**, 1068–1083.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.
- Environment Canada (2011) *Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (Rangifer Tarandus Caribou)*, Boreal Population, in Canada: 2011 Update. Environment Canada, Ottawa, Canada.
- Faille, G., Dussault, C., Ouellet, J.-P., Fortin, D., Courtois, R., St-Laurent, M.-H. *et al.* (2010) Range fidelity: the missing link between caribou decline and habitat alteration? *Biological Conservation*, **143**, 2840–2850.
- Ferguson, S.H., Bergerud, A.T. & Ferguson, R. (1988) Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia*, **76**, 236–245.
- Fieberg, J. & DelGiudice, G.D. (2009) What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology*, **90**, 1687–1697.
- Franklin, A.B., Anderson, D.R., Gutiérrez, R.J. & Burnham, K.P. (2000) Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs*, **70**, 539–590.
- Fretwell, S.D. & Lucas, H.L. Jr (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16–36.
- Fryxell, J.M. & Lundberg, P. (1998) *Individual Behavior and Community Dynamics*. Chapman & Hall, New York, USA.

- Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. *et al.* (2010) Habitat–performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2255–2265.
- Griffin, K.A., Hebblewhite, M., Robinson, H.S., Zager, P., Barber-Meyer, S.M., Christianson, D. *et al.* (2011) Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology*, **80**, 1246–1257.
- Hebblewhite, M. & Merrill, E.H. (2011) Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. *Oikos*, **120**, 1860–1870.
- Heinrichs, J.A., Bender, D.J., Gummer, D.L. & Schumaker, N.H. (2010) Assessing critical habitat: evaluating the relative contribution of habitats to population persistence. *Biological Conservation*, **143**, 2229–2237.
- Hirzel, A.H. & Le Lay, G. (2008) Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, **45**, 1372–1381.
- Hosmer, D.W., Lemeshow, S. & May, S. (2008) *Applied Survival Analysis: Regression Modeling of Time to Event Data*. Wiley, New York, New York, USA.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–427.
- Jacobson, A.R., Provenzale, A., von Hardenberg, A., Bassano, B. & Festa-Bianchet, M. (2004) Climate forcing and density dependence in a mountain ungulate population. *Ecology*, **85**, 1598–1610.
- Johnson, H.E., Mills, L.S., Stephenson, T.R. & Wehausen, J.D. (2010) Population-specific vital rate contributions influence management of an endangered ungulate. *Ecological Applications*, **20**, 1753–1765.
- Latham, A.D.M., Latham, M.C., Boyce, M.S. & Boutin, S. (2011) Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications*, **21**, 2854–2865.
- Latif, Q.S., Heath, S.K. & Rotenberry, J.T. (2011) An “ecological trap” for yellow warbler nest microhabitat selection. *Oikos*, **120**, 1139–1150.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*. Kluwer, Boston, Massachusetts.
- Martin, T.E. (1995) Avian life history Evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101–127.
- McLoughlin, P.D., Dunford, J.S. & Boutin, S. (2005) Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology*, **74**, 701–707.
- McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1449–1454.
- McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010) Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, **79**, 4–12.
- Mills, L.S. (2012) *Conservation of Wildlife Populations: Demography, Genetics, and Management*. John Wiley & Sons, Oxford.
- Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1–13.
- Mosser, A., Fryxell, J.M., Eberly, L. & Packer, C. (2009) Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, **12**, 1050–1060.
- Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006) A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, **130**, 217–229.
- Pays, O., Fortin, D., Gassani, J. & Duchesne, J. (2012) Group dynamics and landscape features constrain the exploration of herds in fusion-fission societies: the case of European roe deer. *PLoS ONE*, **7**, e34678.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Rettie, W.J. & Messier, F. (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466–478.
- Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**, 474–480.
- Therneau, T.M. & Grambsch, P.M. (2000) *Modeling Survival Data: Extending the Cox Model*. Springer, New York, USA.
- Thomson, R.L., Forsman, J.T., Sardá-Palomera, F. & Mönkkönen, M. (2006) Fear factor: prey habitat selection and its consequences in a predation risk landscape. *Ecography*, **29**, 507–514.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.
- Wittmer, H.U., Ahrens, R.N.M. & McLellan, B.N. (2010) Viability of mountain caribou in British Columbia, Canada: Effects of habitat change and population density. *Biological Conservation*, **143**, 86–93.
- Wittmer, H.U., McLellan, B.N. & Hovey, F.W. (2006) Factors influencing variation in site fidelity of woodland caribou (*Rangifer tarandus caribou*) in southeastern British Columbia. *Canadian Journal of Zoology*, **84**, 537–545.
- Wittmer, H.U., Sinclair, A.R.E. & McLellan, B.N. (2005) The role of predation in the decline and extirpation of woodland caribou. *Oecologia*, **144**, 257–267.

Received 2 April 2013; accepted 2 September 2013

Handling Editor: Atle Mysterud

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Study area figure.

Appendix S2. Cox proportional hazards model coefficients, standard errors, Wald statistics (z) and probability values for all models evaluated.

Appendix S3. Schoenfeld residual plots for summer and winter univariate Cox proportional hazards models.