Relating predation mortality to broad-scale habitat selection

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Summary

1. Few studies have related metrics of fitness to broad-scale, multivariate patterns of resource selection.

2. Our objective was to relate long-term predation-mortality patterns for adult woodland caribou [*Rangifer tarandus caribou* (Banfield)] from Alberta, Canada (1991–2002), with patterns of multivariate habitat selection.

3. We first compared probabilities of radio-tracked caribou dying ($n = 55$) from predation in habitats within the home range, controlling for habitat availability, with that expected from habitat selection probabilities for the same animals during life. We then compared survival rates of caribou ($n = 141$) possessing dissimilar patterns of habitat selection using a Cox proportional hazards regression model.

4. Patterns in habitat-specific predation mortality differed significantly from expected given probabilities of habitat selection during life ($P < 0.0001$). Cox regression indicated that mortality rates of caribou due to predation were affected significantly by and can be predicted from patterns of selection ($P = 0.02$).

5. Our results strongly suggest that uplands (primarily mixed deciduous and coniferous forest) present caribou with higher than expected levels of predation risk, and that caribou can avoid predation by maximizing selection of peatlands (open, conifer-dominated bogs and fens).

6. Approaches presented in this study may be useful for ecologists interested in assessing the influence of mortality factors on broad-scale, multivariate resource selection. Linking metrics of fitness to multivariate resource selection will enable us to ask questions of evolutionary ecology once restricted to only the finest ecological scales.

Key-words: Cox regression, habitat selection, predation, survival, woodland caribou.

Introduction

Maximizing fitness is often assumed when organisms demonstrate disproportionate resource selection (Rosenzweig 1981; Morris 2003). Testing this assumption has been easiest at the finest scales of selection (Johnson 1980), whereby individuals select for a discrete resource and fitness consequences based on decisions are measured (e.g. reproductive success in relation to selection of a nest site). However, as the scale of resource selection expands over space and time,

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resource selection by individuals becomes a multivariate, rather than discrete, phenomenon (Johnson 1980; Senft *et al.* 1987; Orians & Wittenberger 1991), complicating the relationship between fitness and resource selection. Relating fitness measures to multivariate resource selection has received little attention in ecology.

Ecological systems are less suited to experimental manipulation at broader scales. Here, natural experiments comparing multivariate space-use with specific ecological patterns (e.g. habitat-specific predation risk) or processes related to survival and reproduction (e.g. mortality due to predation) offer the most practical means by which to advance our knowledge of how resource selection relates to fitness. Research of this nature remains rare, however, especially for species for

which study requires considerable fieldwork over large areas and long periods of time.

In this study we relate predation mortality to multivariate habitat-selection patterns of woodland caribou, a species thought to be limited primarily by predation from wolves [*Canis lupus* (Linnaeus)] (Seip 1992). Although our main goal was to further our understanding of caribou ecology, our motivation was also to present a methodology for ecologists interested in assessing the influence of mortality factors on broad-scale, multivariate resource selection. We present two approaches to relate predation mortality to multivariate habitat selection, using location and mortality data collected as part of a long-term (1991–2002) radio-tracking study from Alberta, Canada. The first compares probabilities of radio-tracked caribou dying from predation in habitats within the home range, controlling for habitat availability, with that expected from habitat-selection probabilities for the same animals during life. The second compares survival rates of caribou showing dissimilar patterns of habitat selection. Consistent with the hypothesis that woodland caribou avoid predation by selecting for peatlands (treed bogs and fens) over uplands (primarily deciduous and coniferous stands of forest), where densities of predators and alternate prey [like moose, *Alces alces* (Linnaeus)] are higher (review in James 1999), we predict: (1) patterns of habitat selection at the moment of death due to predation differs from habitat selection during life, with decreased selection for peatlands and increased selection for uplands, and (2) caribou that select more peatlands and less uplands relative to other caribou avoid predation at a higher rate.

Methods

STUDY AREA

The study area encompassed five ranges of a meta-population of woodland caribou in north-east Alberta, Canada (Fig. 1). The region is part of the western boreal plains of North America, and is naturally fragmented into well-drained uplands and treed bogs and fens (peatlands) in low-lying areas. Bradshaw *et al.*
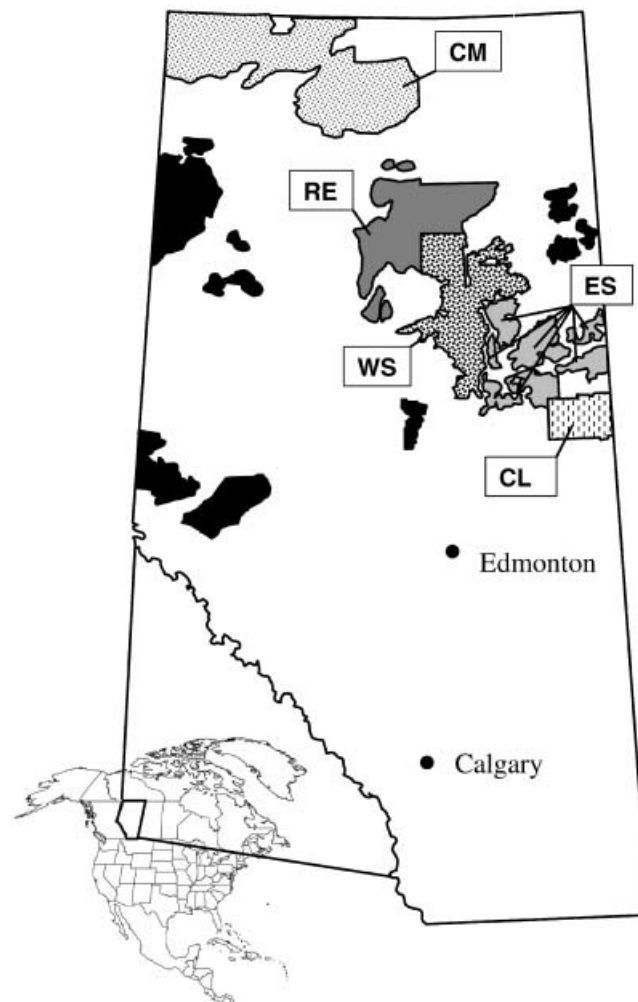

Fig. 1. Distribution of the metapopulation of woodland caribou in Alberta, Canada. Ranges sampled in this study include the Caribou Mountains (CM), Red Earth (RE), West Side of the Athabasca River (WS), East Side of the Athabasca River (ES), and the Canadian Armed Force's Cold Lake Air Weapons Range (CL). Shading and patterns refer to woodland caribou distribution. Unstudied caribou ranges are filled in black.

(1995) provides a detailed description of the landscape typical of boreal caribou range in north-east Alberta. Predation rates on caribou likely differed throughout the study area owing to varying densities of wolves, caribou, moose and other alternate prey species, and the extent of natural and anthropogenic disturbances (e.g. fire, forestry and petroleum development), which may influence caribou–wolf dynamics (James 1999; James & Stuart-Smith 2000; Dyer *et al*. 2001).

LOCATION AND MORTALITY DATA

From 1991 to 2002, we equipped 195 caribou (169 females, 26 males) with very high frequency (VHF) radio collars to obtain location and survival data (Lotek Engineering Inc., Newmarket, Ontario, Canada). We captured and marked all animals according to procedures described by Stuart-Smith *et al*. (1997) following Animal Care Protocol no. 230001 of the University of Alberta. We relocated caribou at minimum once every 2–4 weeks using fixed-wing aircraft and global positioning system (GPS) receivers. The average number of relocations obtained from sampled caribou was 95·0 (SD = 53·7), collected over a mean of 4·1 years (SD = 2·2). Mortalities were investigated by helicopter as soon as possible after detection. We attributed cause of death to predation only if: (1) clear sign at the mortality site indicated predation had occurred, or (2) condition of a carcass indicated an animal unlikely to die of other causes. Using these criteria, we attributed 55 mortalities to predation (McLoughlin *et al*. 2003).

HABITAT COMPOSITION

We first calculated home ranges of caribou from relocation data to define boundaries of available habitat to individuals. We used 95% fixed kernel estimates of home ranges (Seaman & Powell 1996), created with the Animal Movement extension (Hooge & Eichenlaub 1997) of ArcView 3·2 (Environmental Systems Research Institute, Inc. 1998).

Aerial photography was used to classify the landscape into patches of 'peatlands' and 'uplands' (Vitt *et al*. 1996). We classified polygons into peatlands only where ≥ 50% of a polygon was composed of fen or bog classes. Remaining habitat was classed as uplands, with the exception of a third habitat class describing the ecotone (natural edge) between peatlands and uplands (2500 m buffer separating peatlands from uplands). Habitat composition of home ranges was determined using the Spatial Analyst extension for ArcView.

DATA ANALYSIS

All analyses were conducted within the home range [i.e. at the third order of selection (Johnson 1980)]. We first asked whether probabilities of caribou dying from predation (predation risk) in available habitats would be reflected in probabilities of resource selection, controlling for habitat availability (Approach 1). We defined predation risk by developing a predation-event probability function [*sensu* a multivariate resource selection probability function, RSPF (Manly, McDonald & Thomas 1993)], following the maximum likelihood method presented by Arthur *et al*. (1996). Arthur *et al*.'s model was developed originally to assess resource selection when availability differs over time and/or among individuals. We adopted the technique to estimate habitat-specific predation risk from our sample of caribou mortalities, where dead caribou possessed unique availabilities of habitat within their home range. Our function was described by a set of $j = 1$ to H relative predation risk indices, $\hat{b}_j$, where H is the number of available habitats. Parameters of this function summed to 1·0, and described the probability that a predation event would occur in habitat j, based on equal availability of all habitat types. Probabilities of predation events were expected to be non-randomly distributed among habitats when $\hat{b}_j \neq 1/H$.

The probability function was estimated from equations:

$$\hat{w}_k = \sum_{i=1}^{D} \frac{\dfrac{\sum_{i=1}^{D} o_{ik}}{A_{ik}}}{\sum_{j=1}^{H} A_{ij}\hat{b}_j} \qquad \text{eqn 1}$$

and

$$\hat{b}_k = \frac{\hat{w}_k}{\sum_{i=1}^{D} \hat{w}_j} \qquad \text{eqn 2}$$

where the subscript k indicates a particular habitat type from the set $j = 1$ to H, o_{ik} is the observation of death in type k (either 0 or 1) for individual $i = 1$ to D, A_{ik} is the proportional availability of habitat k for individual i, and $\hat{b}_k$ is the estimated predation risk index for habitat k. The values of $\hat{b}_j$ were determined through iteration (Arthur *et al*. 1996). From any starting set of $\hat{b}_j$, eqn 2 was used to calculate new values for $\hat{b}_j$, which were substituted back into eqn 1 and the process repeated until $\hat{b}_j = w_j$ for all j.

To assess habitat selection, we again applied eqns 1 and 2, but here we defined o_{ik} as a measure of habitat use: the proportion of a dead caribou's relocations within habitat k collected while it was alive. The set of $\hat{b}_j$-values now described the probability that a caribou would select a habitat during a selection event, provided equal availability of all habitats (i.e. a conventional RSPF).

We then tested the null hypothesis that predation events and selection events would occur in each habitat with the same probability. We used a χ^2 analysis to test for the goodness-of-fit between calculated sets of predation probabilities (observed) and selection probabilities (expected). The sample size of the χ^2 test was determined by the number of caribou in the analysis ($n = 55$), and the test statistic calculated using proportions of $\hat{b}_j$ multiplied by n (see, e.g. similar approach in

Neu *et al.* 1974 and White & Garrot 1990). Degrees of freedom (d.f.) = $H - 1$, and we used $\alpha = 0.05$. Standard errors (SE) were calculated for values of $\hat{b}_j$ from the formula presented for proportions in Neu *et al.* (1974).

Zar (1996: 560–562) presents a multiple comparisons test for proportions that is analogous to the Tukey test. As every set of $\hat{b}_j$ summed to 1·0, we adopted this test for comparing values of $\hat{b}_j$ between index sets. This required an angular (arcsine) transformation of each sample of $\hat{b}_j$ as proportions between 0·0 and 1·0 form a binomial rather than a normal distribution. We used $\hat{b}_j' = \arcsin\sqrt{\hat{b}_j}$, and converted values to range from 0 to 90 degrees (Table B.24 in Zar 1996). The multiple comparison procedure is very similar to that of the Tukey test; however, the critical value is $q_{\alpha,\infty,k}$ and SE of the two samples being compared is presented, in degrees as:

$$ SE = \sqrt{\frac{(180°/2\pi)^2}{n + 0.5}} \qquad \text{eqn 3} $$

when *n* is the same size. We used *n* equal to the number of individuals upon which each sample of $\hat{b}_j$ was based (i.e. 55).

It was conceivable that chances of dying from predation would be related to individual-based RSPFs of caribou (Approach 2). We assessed this by comparing the RSPFs of those caribou that died due to predation with those that survived during the period of study using a multivariate Cox proportional hazards model (Cox 1972). The model is especially suited to situations like ours whereby survival and death are 'staggered' events (i.e. individuals are followed and die or survive over different intervals of time). If survival is not staggered, a multivariate analysis of variance (MANOVA) or multivariate logistic regression approach may be used to test for differential survival in response to the RSPF. For simplicity, we assumed underlying habitat availabilities and associated predation risks were constant through time, allowing us to consider only 'right'-censored (staggered) data. If this were not the case, the Anderson–Gill or multiplicative hazards derivation of the Cox regression, which accommodates both left- and right-censored data, would be appropriate (Anderson & Gill 1982; Therneau & Grambsch 2000).

In the proportional hazards model, the cumulative survival function $S(t)$, which defines the probability of surviving longer than time *t* (we used years and fractions thereof), is expressed as a hazard function, which is the derivative of the survivor function over time (i.e. instantaneous probability of death):

$$ h(t) = dS(t)/dt \qquad \text{eqn 4} $$

The proportional hazards model is:

$$ h(t) = h_0(t)e^{[\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p]} \qquad \text{eqn 5} $$

where $h_0(t)$ is the baseline hazard function, *e* is the base of the natural logarithm, β_1 to β_p are regression coefficients, and x_1 to x_p are model covariates (for review see Cox 1972; but also Cox & Oakes 1984). We wanted our covariates to describe the RSPF of each caribou. However, since values of $\hat{b}_j$ summed to 1·0 and were thus collinear, we developed a vector of $H - 1$ linearly independent contrasts between pairs of $\hat{b}_j$-values to enter as synthetic covariates into the regression (i.e. $\hat{b}_{upland} - \hat{b}_{peatland}$ and $\hat{b}_{peatland} - \hat{b}_{edge}$), similar to Arthur *et al.*'s (1996) incorporation of $\hat{b}_j$ into a MANOVA. In addition, because we a priori expected survival to differ among ranges (McLoughlin *et al.* 2003), we included the range in which a caribou lived (Fig. 1) as a categorical covariate coded as a set of deviation contrasts with four estimable parameters. The full regression model included effects of range and the two synthetic covariates. Since known fate (death due to predation or survival) was required for unbiased estimates of predation mortality, we limited our analysis only to those caribou for which fate was known to be death from predation (*n* = 55), or survival until collars were removed or slipped (*n* = 86). Caribou that died of any other cause, known or unknown, were excluded from analysis. Hence, survival in the regression analysis should be interpreted as 'survival from predators', rather than total survival. We were unable to test for a sex or age effect, as few males (*n* = 16) were included in the remaining sample, and caribou were only field-aged as 'adult'.

If none of the covariate models was statistically significant at $\alpha = 0.05$, then the null (baseline) model of survival was to be selected as the final model; however, if one or more models fits significantly better than the null model, we used Akaike's information criterion (AIC) to select the model that optimized goodness-of-fit and parsimony (Burnham & Anderson 2002). AIC is defined as the sum of -2 times the log likelihood ($-2 \log L$) plus two times the number of estimable parameters (degrees of freedom) of the model in question. When we explored results from reasonable alternative models (i.e. $0 < \Delta_i$ AIC < 2·0), we used model-averaging to combine results from similarly parameterized models (Burnham & Anderson 2002) including model-averaged estimates of SE (i.e. unconditional SE) that can be used to bootstrap variation in model predictions. We determined cumulative survival (and SE) using mean model covariates, and from this estimated annual average survival $[\sqrt[t]{S(t)}]$ and predation mortality rates $[1 - \sqrt[t]{S(t)}]$, where $S(t)$ is taken to the *t*th root and *t* is equal to the maximum number of years considered. We presented cumulative survival rates in graphical form grouped by range to illustrate dissimilar effects of predation on caribou. Our analyses were conducted using model-building tools provided in SPSS, Inc. (2003).

Results

Caribou were most likely to die from predation in peatlands, followed by uplands and edge, based on equal availability of all habitats (Fig. 2). Relative mean probabilities of predation occurrence, as determined by eqn

Table 1. Cox proportional hazards regression models describing the survival of caribou from predators, Alberta, Canada (1991–2002). Models are ordered according to descending AIC scores. Significance of models compared to the null are indicated by χ^2 statistics and *P*-values. The parameter Δ_i AIC refers to the change in AIC between model *i* and the most parsimonious model, *R*. AIC weights are defined as: $e^{\left(-\frac{1}{2}\Delta_i\text{AIC}\right)} \Big/ \sum_{r=1}^{R} e^{\left(-\frac{1}{2}\Delta_i\text{AIC}\right)}$, which sum to 1·0 (Burnham & Anderson 2002). We use UP to refer to the contrast $(\hat{b}_{\text{upland}} - \hat{b}_{\text{peatland}})$ and PE to refer to $(\hat{b}_{\text{peatland}} - \hat{b}_{\text{edge}})$

Model	(−2 log *L*)	χ^2	d.f.	*P*-value	AIC	Δ_i AIC	AIC weight
Null	491·44	–	0	–	491·44	4·52	0·04
UP + PE	487·40	4·5	2	0·10	491·40	4·48	0·04
PE	489·03	2·6	1	0·11	491·03	4·11	0·04
UP	487·60	4·1	1	0·04	489·60	2·68	0·09
Range*	480·87	10·8	4	0·03	488·87	1·94	0·13
Range + UP + PE*	476·69	15·3	6	0·02	488·69	1·77	0·14
Range + PE*	478·42	13·7	5	0·02	488·42	1·50	0·17
Range + UP*	476·92	15·1	5	0·01	486·92	0·00	0·35

*Models averaged for final interpretation of results, whereby coefficients included in the average were weighted by AIC weights (Burnham & Anderson 2002).
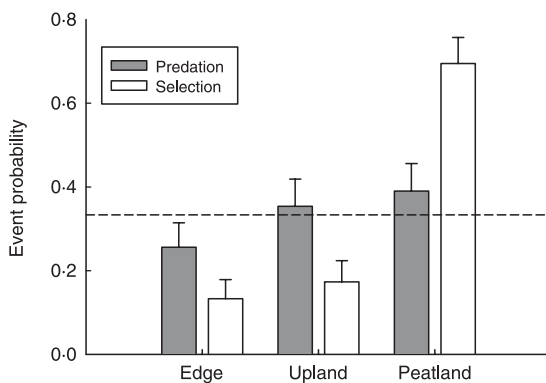

Fig. 2. Habitat-specific probabilities of mortality events and selection by woodland caribou in Alberta, 1991–2002, assuming equal availability of habitat types. Random probabilities (0·33) for a habitat type are indicated by a dashed line. Error bars are ± 1·0 SE.

2, were 0·39, 0·36, and 0·25 for peatlands, uplands and edge, respectively, although differences within the set were not significant (all *P* > 0·05). Predation patterns appeared to be influenced by habitat-selection patterns when caribou were alive (Fig. 2). Here, strong significant differences were detected between peatlands and uplands (*q* = 8·3, *P* < 0·001) and peatlands and edge (*q* = 9·1, *P* < 0·001). Mean probabilities of selection were 0·69, 0·17, and 0·13, for peatlands, uplands and edge, respectively. Patterns of predation risk significantly differed from what was expected given probabilities of habitat selection during life (χ^2 = 24·0, d.f. 2, *P* < 0·0001). The large χ^2 statistic resulted primarily from significantly higher than expected chances of dying in uplands (*q* = 3·2, *P* < 0·05), and lower than expected chances of dying in peatlands (*q* = 4·6, *P* < 0·01).

Model selection using AIC suggested four models with relatively strong support (Table 1), whereby the difference between each candidate model and the null (baseline model) exceeded 2·0 AIC units (Burnham &

Anderson 2002). The model-averaged regression model, weighted by AIC weights (Table 1), was expressed with regression coefficients as:

$$h(t) = h_0(t)e^{[-0\cdot777(R_1)+0\cdot724(R_2)-0\cdot322(R_3)+0\cdot571(R_4)+0\cdot887(\hat{b}_u-\hat{b}_p)-0\cdot133(\hat{b}_p-\hat{b}_e)]}$$

eqn 6

where Range$_1$ to Range$_4$ (R$_1$–R$_4$) is a four-parameter vector coded as {1000}, {0100}, {0010}, {0001} and {0000} for ranges CL, CM, ES, RE and WS (Fig. 1), respectively; $\hat{b}_u = \hat{b}_{\text{upland}}$ and $\hat{b}_p = \hat{b}_{\text{peatland}}$. Unconditional, model-averaged estimates of SE of parameters in eqn 6 were: 0·757 (Range$_1$), 0·365 (Range$_2$), 0·463 (Range$_3$), 0·368 (Range$_4$), 0·333 ($\hat{b}_{\text{upland}} - \hat{b}_{\text{peatland}}$), and 0·343 ($\hat{b}_{\text{peatland}} - \hat{b}_{\text{edge}}$).

Equation 6 can be applied to predict survival and mortality for caribou as follows. Consider a sample of caribou in CL, with habitat selection functions predicting $\hat{b}_k$ of 0·2, 0·6, and 0·2 for uplands, peatlands and edge, respectively. For a period of 3·6 years, for instance, eqn 6 would predict *h*(*t*) = 0·121, where $h_0(t)$ = 0·396 (not shown). Converting to *S*(*t*) we find that caribou with this selection function could expect to survive (avoid predation) the period at a rate of 0·886 (SE = 0·044), at an average annual rate of 0·967 (mortality rate = 0·033/ year). If the resource selection functions for uplands and peatlands were reversed, however, such that $\hat{b}_{\text{upland}}$ = 0·6 and $\hat{b}_{\text{peatland}}$ = 0·2 ($\hat{b}_{\text{edge}}$ remains at 0·2), the caribou would only expect to avoid predation at a rate of 0·771 (SE = 0·089) with mean average annual survival and mortality rates of 0·930 and 0·070, respectively.

Using means of final model covariates, overall cumulative survival – in the absence of all other mortality except for predation – was estimated to be 0·555 (SE = 0·053) over 5·71 years. This translated into average annual survival and predation mortality rates of 0·902 and 0·098, respectively. Among ranges, predation was relatively severe for caribou in CM and RE, with lesser impacts for caribou in ES, WS and CL (Fig. 3).
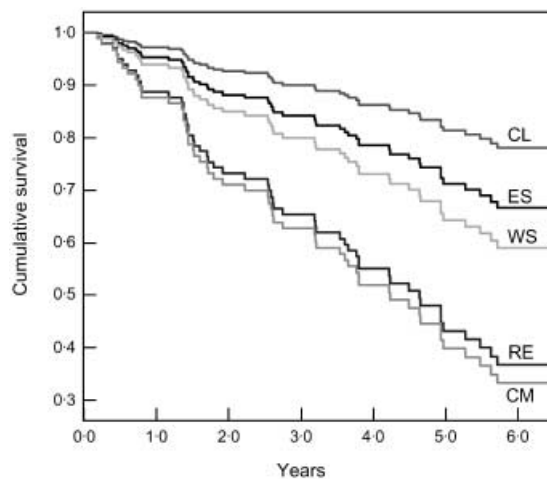
Fig. 3. Cumulative survival for caribou among ranges (Fig. 1) using covariate means for the weighted-average Cox proportional hazard model: Range $+ (\hat{b}_{upland} - \hat{b}_{peatland}) + (\hat{b}_{peatland} - \hat{b}_{edge})$.

Discussion

Our results suggest strongly that uplands present caribou with higher than expected levels of predation risk (Fig. 2). Further, caribou can avoid predation by maximizing selection of peatlands (eqn 6). These results support our predictions and are consistent with the hypothesis that woodland caribou avoid predation by spatially separating themselves from areas where densities of wolves and alternate ungulate prey species, such as moose, are higher (i.e. uplands).

Although caribou, on average, avoided uplands during life (Fig. 2), all caribou did use uplands at some point in time and in a few cases animals actively selected uplands. Given the relatively higher risk of predation encountered by caribou in uplands, why is avoidance of uplands not absolute? Caribou may simply need to traverse uplands to access adjacent peatlands, although higher densities of alternate ungulate prey species in uplands suggests that forage resources may also be more abundant in uplands compared to peatlands (James 1999). In addition, caribou have been known to use uplands where old-growth stands of pine offer access to arboreal lichens, which may become important during winter (Rettie & Messier 2000). Use of uplands by caribou may thus present a trade-off between energy intake and predation risk, a phenomenon that has been well documented both theoretically (e.g. Lima & Dill 1990; McNamara & Houston 1990) and empirically (e.g. Gilliam & Fraser 1987; Abrahams & Dill 1989). This is only conjecture, however, and our data are insufficient to explore this idea further.

Given differences in survival in each caribou range, one could presume that wolf density differs among ranges, with higher densities of wolves found in CM and RE. Relatively higher amounts of natural and anthropogenic disturbance in CM, RE and ES, compared to CL and WS, may underlie higher densities of wolves in the north if disturbance also results in higher alternate ungulate

prey densities (Seip 1992). Such disturbances may also affect predation rates by altering the functional response of wolves to caribou, for example in areas where linear features increase access of wolves to caribou (James 1999; James & Stuart-Smith 2000; Dyer *et al*. 2001).

Our data do not allow us to conclude with certainty that caribou having resource selection functions that favour peatlands experience higher fitness than caribou that use more edge or uplands. Although we possess sound data on survival, information on reproduction is also needed to address this problem fully. A more direct approach to testing the selection-fitness assumption would be to relate lifetime net reproduction, R_0, to resource selection, rather than mortality, because R_0 is a direct measure of Darwinian fitness. Of course, determining R_0 for a sample of caribou would be difficult, although this may not be the case for other species. A more practical alternative may entail a study similar to the one presented in this paper, whereby finite recruitment and mortality for some period of time are both included as dependent variables of interest. Here, finite recruitment and mortality from all natural sources for individuals exhibiting similar patterns of multivariate resource selection may be linked together to calculate contributions to the finite rate of population growth, λ [$\lambda = (1 - M)/(1 - R)$, where M and R refer to finite mortality and recruitment rates, respectively (applied to moose and caribou; Hatter & Bergerud 1991; McLoughlin *et al*. 2003)]. Finite population-growth rate, related to R_0 as $\lambda = R_0^{1/T}$, where T is generation length in intervals of time, may also be construed as a measure of the average fitness among individuals in the population. If λ, or expected contributions to λ, can be calculated for animals exhibiting different selection patterns, conclusions as to the relationship between fitness and multivariate habitat selection may be drawn.

For caribou in this study, however, these additional analyses may be unnecessary. Consider that almost all female caribou in this study (> 90%) tested positive for pregnancy upon capture and are known to give birth at similarly high rates (McLoughlin *et al*. 2003). One major component of fitness in long-lived animals such as caribou is the number of opportunities for reproduction, which is a direct function of survival, and caribou recruitment and adult survival have been observed previously to vary in concert (Bergerud 1988). Although we could not determine if female caribou showing greater selection for uplands had higher calf survival, we know that they did not have higher pregnancy rates and did suffer higher mortality. It is probable, therefore, that caribou selecting for relatively greater amounts of upland habitat possess lower overall fitness.

Little, if any, effort has been directed at relating metrics of fitness to habitat selection when selection is considered to be a multivariate phenomenon. Most theory in habitat selection derives from hypotheses that assume discrete choices of resource selection have clear demographic consequences (Rosenzweig 1981; Morris 2003). For most long-lived species, however,

it is extremely difficult to measure demographic consequences (survival, reproduction) in response to time spent in only one habitat type; rather, demographic responses are estimable only over spatial and temporal scales for which habitat selection is best described in multivariate terms (e.g. multi-annual movements, home range). In this study we present methods to evaluate demographic consequences of broad-scale, multivariate habitat selection. Although we restrict our analysis to survival from predation, our methods are equally applicable to estimates of total survival and, with some modification in technique (e.g. use of Poisson or multiple linear regression rather than Cox regression), estimates of parameters such as mating success or lifetime reproductive success. Linking fitness measures to multivariate resource selection will enable us to ask questions of evolutionary ecology once restricted to only the finest ecological scales.

Acknowledgements

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