Movement parameters of ungulates and scale-specific responses to the environment

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Summary

1. Most studies of animal movements and habitat selection do not recognize empirically that different components of the environment are important to animals at different scales. Often, availability of habitats is defined at one or more arbitrary spatio-temporal scales, but use of those habitats is constrained to one scale. Identification of scalar movement is the first step in developing models to explain why animals select or move to certain parts of their range. We used a non-linear curve-fitting model of movement rates to identify discontinuities in the scales of movement by woodland caribou *Rangifer tarandus caribou* collared with global positioning system (GPS) collars.

2. We differentiated intrapatch from interpatch movements, but were unable to distinguish interpatch from migratory-type movements for most combinations of individual caribou by season. Model fit was stronger for winter than summer movements. We suggest that increased patch heterogeneity during the winter resulted in interseason variation in movements and corresponding model fit.

3. Responses by caribou to the environment were scale-dependent. When we applied logistic regressions, land-cover type, energetic costs of movement, and predation risk differentiated the two scales of movement. Intrapatch movements had a lower cost of movement, were associated with cover types where foraging behaviours probably occurred, and were closer to areas of higher predator risk than interpatch movements.

4. Application of the non-linear model will aid in developing mechanism-based approaches to studying resource selection and animal behaviour.

Key-words: caribou, GPS, habitat patch, heterogeneity, predation risk.

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Introduction

Since the early 1980s, the spatial and temporal scales of animal behaviour and resource selection have received considerable attention (e.g. Johnson 1980; Wiens 1989; Levin 1992; Saab 1999). With the recognition that the observed variability of an ecological system depends on the grain and extent of description, much emphasis has been placed on identifying the appropriate scale or scales of observation. Multiscale, hierarchical study designs have been presented as approaches that can be used to observe the scale-specific responses of animals to the environment (Kotliar & Wiens 1990; Wiens *et al.* 1993; Lima & Zollner 1996). Typically, however, the

scales of study chosen by researchers encompass only the availability of habitats, and those scales are defined arbitrarily or coincide with plant community composition or physiognomy. Few researchers have attempted to stratify observed movements or use of habitats according to the scales at which those behaviours occurred. Most studies conducted at large spatial scales using radio-telemetry or other remote monitoring devices group all animal locations within one behavioural category, *habitat use* (e.g. Poole, Heard & Mowat 2000; Apps *et al.* 2001).

Studies conducted at arbitrarily defined multiple scales may suffer from one or more important limitations. First, an incorrect definition of scale, relative to the perception of space by an animal, may result in the failure to measure responses to variables and variation relevant to the processes of interest. Small-scale processes or patterns may be averaged or large-scale

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variables missed depending on the scope of the measurements (Dunning, Danielson & Pulliam 1992). Secondly, assuming measured responses are scale-independent may result in the erroneous extrapolation of processes or patterns to larger or smaller scales (Gardner *et al*. 1989; Turner 1990). Thirdly, defining availability is ultimately a function of scale (Knight & Morris 1996). Studies that define the patch as an individual unit isolated from neighbouring patch types or beyond the dispersal distance of the organism may be incapable of assessing resource selection (Morris 1992). Fourthly, arbitrary choice of scale may not permit a comparison of scale-specific processes among organisms or studies (Collins & Glenn 1997). Ecologists should begin searching for ways to relate different landscapes or species to one another in common terms (Milne 1991). By successively identifying scale, describing patterns and postulating processes, we can compare animal behaviour and resource selection among species.

Movement paths of individual animals reflect behavioural responses to environmental heterogeneity and may serve as an index of shifts in scale-dependent processes (Kotliar & Wiens 1990; With 1994). Studies of insects have drawn on measures such as fractal pattern, movement rate, length, duration, direction and turning angle to quantify movement paths (Dicke & Burrough 1988; Milne 1991; Turchin 1991; Wiens *et al*. 1995). With few exceptions (e.g. Bascompte & Vila 1997; Bergman, Schaefer & Luttich 2000), those approaches have not been used to understand behavioural patterns of far-moving organisms simply because of the logistical limitations of obtaining continuous, accurate location data (Koenig, Van Duren & Hooge 1996). The recent advent of global positioning system (GPS) collars allows the frequent and accurate relocation of large mammals and the reconstruction of movement paths.

We modified a previously published technique (Sibly, Nott & Fletcher 1990) to identify scales of movement of far-ranging large mammals over seasons. We present this approach using the movement rates generated from frequent relocations of woodland caribou (*Rangifer tarandus caribou* L.) collected with GPS collars, and compare scales of movement among individuals and seasons.

Based on our animal observations (Johnson 2000), we predicted that the responses of caribou to the environment would be reflected in three spatio-temporal scales of movement that we assumed to correspond with the feeding site, patch and migration. Each of those scales can be defined both by the frequency of movement events and the rate of movement of each event. Caribou make frequent short-distance moves within patches when selecting feeding sites with terrestrial and arboreal lichens (Johnson, Parker & Heard 2001). Caribou move longer distances less frequently when travelling between patches containing accessible forage or to meet other requirements such as predator vigilance (Skogland 1978; Bradshaw *et al*. 1995). Infrequently, caribou move long distances at the scale of

migration to take advantage of plant physiognomy, to avoid environmental conditions (e.g. deep snow) that may limit access to forage, or to reduce the risk of predation (Pruitt 1959; Bergerud, Butler & Miller 1984; Seip 1992). We demonstrate scale-specific variation in the behavioural responses of caribou to vegetation, costs of movement and predation risk and discuss the importance of a multiscale approach to the study of resource selection and animal behaviour.

Methods

IDENTIFYING SCALES OF MOVEMENT: THE MODEL

We adapted a non-linear curve-fitting procedure (Sibly *et al*. 1990) to identify scales of movement. The model accommodates two processes, or behaviours, where typically the frequency of times separating events (for application to foraging bout dynamics, see Gillingham, Parker & Hanley 1997) serves as a measure by which a frequent and less frequent behaviour can be differentiated. We, however, applied data describing the frequency of rates of movement (v_i) generated by successive animal relocations collected with GPS collars:

$$v_i = l_i/t_i, \qquad \text{eqn 1}$$

where l_i represents the distance from location i to location $i + 1$ and t_i represents the time between the acquisition of location i and location $i + 1$.

The non-linear model defines a curve which is fit to a $\log_e$ transformed frequency distribution of movement rates. The model takes the form:

$$y = \log_e(N_s\lambda_s e^{-\lambda_s r} + N_l\lambda_l e^{-\lambda_l r}) \qquad \text{eqn 2}$$

where $_s$ and $_l$ refer to Poisson processes that are assumed to generate small- and large-scale movements, respectively. The predicted number of caribou movements that occur during each discrete interval of movement rates is represented by y. N is the number of small- ($_s$) and large-scale ($_l$) movements that occur at each rate interval, r is the movement rate, and λ represents the probability that an event occurs in the next movement rate interval. A broken stick model (two straight lines) can be fitted to the resulting curve (y) and the point of inflection used to identify visually a threshold splitting the two behavioural processes. A more objective approach involves calculating a scale criterion (r_c) using the parameters from the fitted model:

$$r_c = \frac{1}{\lambda_s - \lambda_l} \log_e \frac{N_s\lambda_s}{N_l\lambda_l} \qquad \text{eqn 3}$$

Sibly *et al*. (1990) fitted the model to the duration of pauses between successive feeding events and thus referred to their threshold as a bout criterion (t_c). We, however, applied the model to movement rates and

therefore refer to the breakpoint value as the scale criterion or r_c. Movement rates of caribou $< r_c$ were considered to be small-scale movements; rates $> r_c$ were large-scale movements.

We modified the original two-process model (Berdoy 1993) to account for a third process that would allow us to assess whether movement rates of woodland caribou occur across three scales of movement (i.e. intrapatch, interpatch, migratory):

$$y = \log_e(N_s\lambda_s e^{-\lambda_s r} + N_l\lambda_l e^{-\lambda_l r} + N_m\lambda_m e^{-\lambda_m r}), \qquad \text{eqn 4}$$

where $_s$, $_l$, and $_m$ now represent small, large and migratory scales of movements, respectively.

APPLICATION OF THE MODEL

We applied both the two- and three-process models to 1 year of movement data (Johnson 2000) from five female woodland caribou in the wolverine herd (Heard & Vagt 1998). Those animals live in north-central British Columbia, Canada, and range across 5100 km^2. Terrain varies, from valley bottoms at approximately 900 m to alpine summits at 2050 m and is characterized by numerous vegetation associations resulting from diverse topography, soils and succession. Forest types below 1100 m have been influenced extensively by wildfires and are dominated by lodgepole pine (*Pinus contorta* Dougl. *ex* Loud.), white spruce (*Picea glauca* (Moench) Voss), hybrid white spruce (*P. glauca* × *P. engelmannii*) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt). Between 1100 and 1600 m, a moist cold climate prevails with forest types consisting primarily of Engelmann spruce (*P. engelmannii* Parry *ex* Engelmann) and subalpine fir. Elevations above 1600 m are alpine tundra and are distinguished by gentle to steep windswept slopes vegetated by shrubs, herbs, bryophytes and lichens with occasional trees in krummholz form (Meidinger & Pojar 1991).

Caribou locations were collected with two versions of GPS 1000 collars (small and large battery packs; LOTEK Engineering, Inc. Newmarket, Ontario, Canada). Locations were corrected differentially using N3WIN (V. 2·412, LOTEK Engineering). We scheduled collars equipped with small battery packs to record one location every 3 h for a total of eight locations per day, and collars with large battery packs to record one location every 4 h Saturday–Thursday and every 20 min on every fourth hour for each Friday (60/week).

We applied the model to the five caribou for which we had location data over an entire year (1997–98). Relocations for each animal were divided into four seasons: winter (December 1–March 31), spring (April 1–June 30), summer (July 1–August 31) and autumn (September 1–November 30). We chose the start and end dates of the seasons to match ecological events that may influence the movements and behaviour of caribou. Winter corresponded with the first lasting snowfall; spring with the melting of snow on south-facing slopes and in tree wells and the emergence of green vegetation; summer with the disappearance of snow from the study area and the most active period of vegetative growth; and autumn with the senescence of green plants.

Depending on the number of unique signals acquired by the receiver during a location attempt, and the configuration of the transmitting satellites, differentially corrected GPS locations can be as precise as 3–8 m 95% of the time. We omitted all locations with a horizontal dilution of precision (HDOP = index of satellite configuration) of > 25 and locations generated with three satellites (two-dimensional locations) that were not differentially corrected. The remaining two- and three-dimensional locations were used in the following analyses.

We used rates of movement, as opposed to distances, to standardize variation in sampling interval resulting from the inability of collars to acquire GPS locations for all scheduled attempts, differences in collar schedules, and slight differences in acquisition times. A missed location is the result of the GPS receiver failing to acquire signals from at least three satellites during an attempt and may lead to vegetation and topography-related bias (Dussault *et al.* 1999). Successive relocations of caribou varied from 20 min to 16 h. We developed one-way ANOVA tests for each seasonal combination of sampling intervals to assess the effect of time between relocations (e.g. 20 min vs. 4 h, etc.) on recorded movement rates. Where significant differences were detected, the Tukey HSD for unequal sample sizes was used for *post hoc* comparisons of individual sampling intervals (Spjotvoll & Stoline 1973). Those sampling intervals with similar mean movement rates were pooled for each analysis. To assess the assumption that movement rates are linearly related to distance, regardless of sampling interval, we pooled locations across sampling intervals with similar mean movement rates and fit linear regression models for each of the seasons.

We performed all analyses by individual caribou for each season. Each combination of data was fitted to a one- (analogous to linear regression), two- and three-process model (equations 1, 3). A linear fit is the expected distribution of data collected from a scale-independent process where movement rates occur randomly in space and time (i.e. a negative exponential distribution; Berdoy 1993). As outlined by Sibly *et al.* (1990), we used the sum of squares to test model fit (*F*-statistic). We used Akaike's information criterion (AIC) to identify the most parsimonious and best fitting of the one-, two- and three-process models (i.e. lowest scores). We adopted Burnham & Anderson's (1998) recommendation that all nested models with a difference in AIC of < 2 should be considered good explanatory models. We used repeated-measures ANOVA and the Tukey HSD for unequal sample sizes (Toothaker 1993) to test for differences in r_c values and model fit between seasons. Where seasonal effects were non-significant, we pooled r_c and model fit values

across season and used a one-way ANOVA to test for differences between animals. Model fit was calculated as the change in AIC score between the one-, two- and three-process models. Non-linear regression routines and evaluations were performed in accordance with Bates & Watts (1988). Models were fit using STATISTICA (v. 5·5; non-linear estimation), SPSS (v. 8·0; sum of squares calculations) and S-Plus 2000 (R. 2·0; AIC calculations).

MODEL EFFECTIVENESS AND ECOLOGICAL INFERENCE

We developed logistic regressions to assess whether the scales determined by the non-linear model represented ecologically meaningful relationships of caribou to the environment. We compared measures for cover type (vegetation), predation risk and the costs of movement. Logistic analyses were conducted only for winter when we had collected detailed information on foraging behaviours by following caribou on the ground (Johnson *et al.* 2001). Geographic information system (GIS) analyses were conducted with IDRISI (v. 4·1, v. 2, v. 32; Clark Laboratories 1999).

Cover type. We used LANDSAT V Thematic Mapper satellite imagery and terrain resource information management (TRIM) elevation data to classify the geographical area used by all collared caribou. We identified 13 cover types of unique vegetative and topographical association (Johnson 2000). Cover types included stands of primarily deciduous trees (aspen/cottonwood); poor productivity sites dominated by pine and an abundant understory of terrestrial lichen (pine terrace); wetter more productive growing sites dominated by pine (pine); spruce stands (spruce); mixed stands of pine and spruce (pine–spruce); patches of mixed pine and black spruce, and pure black spruce (pine–black spruce/black spruce); poorly drained areas with few conifers (wetland); permanent and ephemeral water bodies (lakes/rivers); mid-elevation forest types composed of subalpine fir, spruce, and pine (mid-elevation coniferous); ecotone areas bordering alpine cover types and dominated by shrubs and dwarf conifers (Krummholz); alpine areas with an extensive cover of dwarf birch (*Betula glandulosa* Michx.) and willow (*Salix reticulata* L.) (alpine–shrub), grasses (*Festuca altaica* Schreb.) (alpine–grass) and few vascular plants consisting mainly of exposed rock and lichen (alpine–little vegetative cover).

Distance to predation risk. We used VHF and GPS collars to monitor the movements and feeding habits of 19 wolves (*Canis lupus* L.) from eight packs between 1996 and 1999. After excluding individuals travelling together or multiple relocations at den or kill sites, 200 relocations and seven kill sites were considered independent and located within the range of the collared caribou. Selection of habitat by wolves was inferred

through a comparison of relocations and kill sites to random locations drawn from the 95% minimum convex polygon of wolf relocations. We centred an error buffer with a radius of 125 m on all wolf relocations and extracted the proportion of each cover type (Leptich, Beck & Beaver 1994). Because wolves select certain habitats for hunting vs. other behaviours (Kunkel & Pletscher 2000), we arbitrarily weighted kill sites (where predation was confirmed) to have twice the influence as nonkill relocations (where wolf presence was a potential risk to caribou).

We used logistic regression to determine which cover types were most associated with wolves, and therefore associated with high risk of predation (Mladenoff, Sickley & Wydeven 1999). Predation risk is defined as the probability of encountering or being captured by a predator during some time period (Lima & Dill 1990). The significant positive coefficients of the logistic regression were used to develop a spatial surface describing the weighted distance of every cell (i.e. GIS pixel) to high-risk cover. This operation involved three steps: (1) for each cover type with a positive coefficient, we generated a GIS surface where every 25×25-m cell in the study area was assigned a risk value equal to the shortest distance to that cover type; (2) each risk value was then multiplied (weighted) by the inverse of the coefficient produced from the logistic regression; and (3) the risk values of all cells were averaged to produce one surface representing the overall proximity to risk for each cell within the study area. The greater these values, the greater the distance to high-risk cover types, and the lower the risk of predation for the animal.

Costs of movement. We used equations developed by Fancy & White (1987) to model the energy expended by a 100-kg female caribou moving across variable terrain. We used a digital elevation model (DEM) generated from TRIM data to estimate whether an animal was moving up or down slope, the mean slope of the movement path, and the change in elevation between caribou relocations (25×25-m pixel resolution, British Columbia Ministry of Crown Lands 1990). The energy costs ($kJ \times kg^{-0.75}$) of walking on a horizontal snow-covered surface were calculated as the distance travelled multiplied by the cost per km (1.696 kJ/kg $\times$ km^{-1}) corrected for sinking depths in snow of 12–47 cm ($(0.02416 \times e^{0.0635}) + 1$) (Fancy 1986). The net energy costs of moving uphill were calculated as the mean cost of lifting 1 kg of body weight (1.957 kJ/kg $\times$ m^{-1}) adjusted for slope of terrain, multiplied by the total vertical distance ascended. Energy recovered during downhill movements was calculated as the efficiency of recovery (0.412 kJ/kg $\times$ m^{-1}) corrected for slope, multiplied by the potential energy stored while lifting 1 kg of body weight 1 m (9.79 kJ) and total vertical distance (Fancy 1986).

Data treatment. We stratified caribou relocations by movement rate according to r_c. The mid-point of each

vector between successive relocations was calculated and a circular buffer with a diameter equal to the distance between those two relocations was generated. We assumed that the circular buffer represented the potential area over which a caribou may have ranged between relocations and that it accommodates bias associated with the failure of the GPS collars to acquire signals from at least three satellites at each attempt. The buffer was superimposed on each data layer (cover type, predation risk, cost of movement) and the mean value or, for cover type, the percentage of each cover type within that buffer, was extracted for analysis.

We developed a logistic regression for each animal; scale served as the dichotomous dependent variable, and 13 cover types, cost of movement, and predation risk were the independent variables. We used AIC to rank and identify the cover-type variables that were most reliable for making inferences about the movement processes (Burnham & Anderson 1998). This method is best suited for a small subset of a priori hypotheses, but the large number of cover types and interanimal variability led us to use a best subsets approach. We ranked all cover-type regressions from lowest AIC score to highest. For those with a difference in scores of less than two from the lowest we calculated Akaike weights (w), which serve as a normalized measure, and summed the ws for each cover type (Burnham & Anderson 1998). Cover types that occurred frequently or with low AIC scores would therefore have a large summed w-value. Those cover types with a w greater than 0·15 were retained and used with the other two independent variables (predation risk, cost of movement) for final regression comparisons.

We used log likelihood χ^2 tests, non-cross-validated classification accuracy and Nagelkerke R^2 values to assess the reliability of the logistic regressions (Menard 1995). We used the likelihood ratio test to evaluate individual coefficients. Leverage statistics and Pearson standardized residuals served to diagnose animal relocations that fit the model poorly or had a large influence on model coefficients. Independence of residuals was assessed using Durbin–Watson tests of the linear equivalents of the logistic models (logit transform) (Neter, Wasserman & Kutner 1990). Independent variables were log-ratio transformed to reduce the effects of collinearity (Aebischer, Robertson & Kenward 1993). Statistical analyses were performed with STATISTICA (v. 5·5). We considered tests to be statistically significant at an α of 0·05.

Results

FITTING THE NON-LINEAR MODEL: DISTINGUISHING SCALES OF MOVEMENT

Influence of sampling interval on movement rate. GPS collars collected 841 movement intervals with a duration of 20 min, 989 with a duration of 3 h, 2655 with a duration of 4 h, 61 with a duration of 6 h, 493 with a duration of 8 h, 27 with a duration of 9 h, 199 with a duration of 12 h, 16 with a duration of 15 h, and 82 with a duration of 16 h. Analysis of variance revealed significant differences in mean movement rates among sampling intervals for winter ($F_{8,2559} = 3·74$, $P < 0·001$), spring ($F_{8,1533} = 4·30$, $P < 0·001$), summer ($F_{5,598} = 12·31$, $P < 0·001$) and autumn ($F_{5,643} = 5·47$, $P < 0·001$). *Post hoc* analyses, however, revealed only significant differences for 20 min vs. longer sampling intervals (other interval comparisons: $P > 0·834$ winter, $P > 0·358$ spring, $P > 0·927$ summer, $P > 0·451$ autumn). Consequently, only those data with a sampling interval ≥ 3 h and ≤ 16 h were used in subsequent analyses where the majority (81%) had a duration of 3 or 4 h. For those, data of ≥ 3 h and ≤ 16 h significant linear relationships existed between distance travelled and movement rate for the winter ($F_{1,2170} = 6504·9$, $P < 0·001$, $r^2 = 0·75$), spring ($F_{1,1311} = 4642·6$, $P < 0·001$, $r^2 = 0·78$), summer ($F_{1,501} = 1439·2$, $P < 0·001$, $r^2 = 0·74$) and autumn ($F_{1,532} = 1748·0$, $P < 0·001$, $r^2 = 0·77$).

Two-process model. The two-process non-linear model fit the $\log_e$ frequency distribution of movement rates for caribou well ($P < 0·001$) for most combinations of caribou by season, suggesting differentiation of large-scale from small-scale processes (Table 1). A typical fit of the non-linear model to the $\log_e$ frequency distribution of caribou movement rates is shown in Fig. 1. In that example, the two-process model (equations 2, 3) calculated a scale criterion (r_c) of 2·18 m min^{-1} for caribou 042B. The two-process model did not fit the movement data for caribou E41A during the summer (Table 1). In that instance, examination of the $\log_e$ frequency vs. movement rate plot revealed a linear relationship, whereas the other caribou-season combinations illustrated non-linear relationships with distinct scale criteria.

The failure to fit a two-process model to caribou E41A during the summer (i.e. empty cell) required us to test seasonal differences in r_c and model fit for the five caribou for winter, spring, and autumn and to compare the four seasons while excluding data for E41A. Average r_c values did not statistically differ between seasons ($F_{2,8} = 0·881$, $P = 0·451$, $F_{3,9} = 2·25$, $P = 0·152$) or individual caribou ($F_{4,14} = 0·891$, $P = 0·495$). There was, however, considerable variation, with average differences among animals being greatest for caribou 042B (2·96 m/min ± 0·33 SE) and 1D2B (6·78 ± 2·78 m/min) and among seasons between winter (2·6 ± 0·29 m/min) and summer (8·24 ± 3·14 m/min). The AIC scores illustrated differences in fit between the one- and two-process models. With the exception of caribou 042B during the summer, the AIC scores for the two-process models were 2 points less than the one-process models (Table 1). Significant differences in fit were not apparent for the three season comparison (i.e. excluding summer; $F_{2,8} = 2·76$, $P = 0·123$), but were significant for the four-season comparison (i.e. excluding caribou E41A; $F_{3,9} = 8·48$, $P = 0·006$). *Post hoc* analyses of

Table 1. Scale criteria (r_c) calculated using a two-process model (equations 2 and 3) and used to differentiate small- and large-scale movements for five caribou across four seasons in north-central British Columbia; results illustrate comparison to a one-process model. Scale criteria (r_c) were calculated as m/min, AICΔ represents the difference between the Akaike's information criterion scores for the two and one-process models, and NF (no fit) represents r_c values that could not be calculated because of poor model fit. Models were all statistically significant ($P < 0{\cdot}001$)

Season	Caribou	r_c	N	R^2		F		AICΔ
				Two Pro.	One Pro.	Two Pro.	One Pro.	
Spring	042B	3·72	42	85·0	65·8	66·17	50·07	30·49
	1D2B	8·70	38	88·2	81·2	79·18	98·16	13·82
	772B	1·89	61	87·4	65·6	103·61	59·63	57·44
	B91A	3·19	65	88·7	74·2	144·44	113·07	49·63
	E41A	2·81	59	87·7	68·5	105·85	68·41	51·41
Summer	042B	2·77	49	77·0	74·4	39·35	71·22	1·37
	1D2B	13·80	48	86·9	81·7	77·18	109·03	5·99
	772B	2·83	81	83·1	74·8	105·63	125·38	31·71
	B91A	13·54	79	87·6	84·0	166·48	256·53	16·04
	E41A	NF	57	NF	79·7	NF	86·42	NF
Autumn	042B	3·17	43	88·1	64·9	79·49	42·93	42·64
	1D2B	2·45	35	92·6	75·5	109·28	58·95	37·81
	772B	4·55	121	86·2	79·7	199·06	255·51	42·97
	B91A	4·43	70	84·7	76·7	144·89	184·50	25·40
	E41A	5·46	39	88·6	86·0	103·79	175·34	3·00
Winter	042B	2·18	80	89·0	67·5	159·28	84·95	82·61
	1D2B	2·18	38	87·8	52·4	66·17	22·53	47·73
	772B	2·87	81	89·3	72·6	172·74	114·29	72·28
	B91A	2·13	55	87·5	69·7	96·02	66·89	44·62
	E41A	3·62	24	95·8	81·0	159·46	60·97	32·14
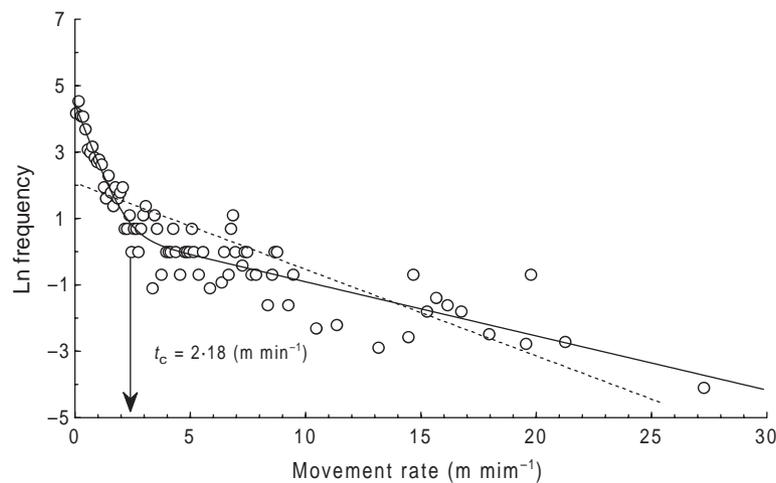
Fig. 1. Example of $\log_e$ frequency distribution of movement rates by caribou 042B during winter (December 1997–April 1998). A non-linear two-process model was fit (equation 2) and the scale criterion (equation 3; r_c) was calculated using the parameters of the fitted equation. For comparison, a linear regression (dashed line) serves as the null model of a nonscalar response.

seasonal effects revealed differences between winter and summer ($P = 0{\cdot}003$). Because of seasonal effects in model fit we were not justified in pooling and performing interanimal comparisons.

Three-process model. The three-process model fitted most combinations of caribou by season poorly or not at all. In several instances, the r_c values designed to separate the between-patch from migratory movements were large negative or positive numbers or the model failed to converge. In other instances, inspection of the fitted curves indicated that the non-linear models overfitted data. This outcome was characterized by one of the two r_c values being slightly less and the other slightly greater than the two-process r_c and no apparent breakpoint in the plotted data. Visual inspection of fitted data was sufficient to assess model fit and therefore we did not calculate inferential statistics.

Table 2. Statistical summary of logistic regression models using cover type, cost of movement, and predation risk to differentiate large- from small-scale movements for four caribou of the Wolverine herd in north-central British Columbia (December 1997–April 1998)

Variables retained in model	β^{1}	χ^2	P
Caribou 042B: $\chi^2 = 96\cdot92$, d.f. = 6, $P < 0\cdot001$; $n = 580$, $R^2 = 0\cdot28$; Class. accuracy = 88·6% (small scale = 98·0%, large scale = 30·0%)			
Lakes/rivers	0·052	8·55	0·004
Alpine–little vegetative cover	−0·064	6·48	0·011
Mid-elevation coniferous	0·008	3·90	0·048
Pine	−0·195	0·04	0·843
Cost of movement	0·002	77·27	< 0·001
Predation risk	0·014	0·69	0·407
Caribou 1D2B: $\chi^2 = 34\cdot53$, d.f. = 6, $P < 0\cdot001$; $n = 368$, $R^2 = 0\cdot28$; Class. accuracy = 95·1% (small-scale = 99·4%, large-scale = 11·1%)			
Krummholz	0·151	6·25	0·012
Spruce	−0·022	2·02	0·155
Lakes/rivers	0·036	1·99	0·158
Alpine–grass	0·208	1·02	0·313
Cost of movement	0·002	19·04	< 0·001
Predation risk	0·114	4·22	0·040
Caribou 772B: $\chi^2 = 38\cdot17$, d.f. = 11, $P < 0\cdot001$; $n = 605$, $R^2 = 0\cdot11$; Class. accuracy = 85·8% (small-scale = 99·4%, large-scale = 0%)			
Lakes/rivers	0·076	8·13	0·004
Pine–spruce	0·131	5·51	0·019
Pine terrace	−0·052	4·01	0·045
Mid-elevation coniferous	0·020	3·31	0·069
Alpine–little vegetative cover	−0·148	3·13	0·077
Wetland	0·065	2·80	0·095
Aspen/cottonwood	−0·188	2·44	0·119
Alpine–shrub	0·099	0·77	0·379
Pine	−0·114	0·24	0·623
Cost of movement	0·001	1·45	0·229
Predation risk	0·024	6·40	0·011
Caribou B91A: $\chi^2 = 28\cdot05$, d.f. = 7, $P < 0\cdot001$; $n = 366$, $R^2 = 0\cdot13$; Class. accuracy = 85·3% (small-scale = 98·4%, large-scale = 7·6%)			
Lakes/rivers	0·101	6·55	0·011
Alpine–grass	0·088	2·96	0·086
Alpine–little vegetative cover	0·066	1·25	0·264
Mid-elevation coniferous	0·102	0·80	0·371
Cost of movement	0·001	15·83	< 0·001
Predation risk	0·014	0·67	0·414

[1]Positive and negative regression coefficients (β) suggest selection for environmental features during large- and small-scale movements, respectively.

MODEL EFFECTIVENESS AND ECOLOGICAL INFERENCE

Data on movement rates for caribou collected during winter (1 December–31 March) were stratified by their corresponding two-process r_c values (Table 1). Caribou E41A had the highest ratio of small- to large-scale movements at 114·5 (229 : 2), followed by 1D2B at 17·6 (351 : 20), 772B at 6·2 (526 : 85), 042B at 6·2 (505 : 82) and B91A at 5·6 (316 : 56). With only two large-scale movements, we could not use logistic regression to compare the two scales of movement for caribou E41A.

All logistic regressions were statistically significant, but classification accuracy was greater for small-scale movements (Table 2). Greater use of lakes/rivers discriminated large- from small-scale movements of caribou 042B, 772B and B91A. Large-scale movements also were associated with patches of mid-elevation coniferous forest, Krummholz and pine–spruce. Three of the four caribou demonstrated greater energetic costs while making large-scale movements (Table 2). Cover types that significantly increased the risk of predation included pine, spruce and wetland/lakes/rivers. Caribou 1D2B and 772B experienced a lower risk of predation during large-scale compared to small-scale movements. Given that the weighting factor for kill sites may have influenced the results relative to predation risk, we also determined that a non-weighted logistic model had little influence on these conclusions. Small-scale movements occurred in patches of alpine–little vegetative cover and pine terrace.

Discussion

MODEL FIT AND INTERPRETATION

We adapted the Sibly *et al.* (1990) non-linear model to delineate scale-specific movements of woodland caribou because it is based on intuitive mechanistic parameters. Rates and frequencies are observable biological phenomena that are directly related to use of the environment. The non-linear model also provides a mathematically proven (Slater & Lester 1982), objective and easily calculated break-point to define scale. Fractal analyses have shown promise as an alternative to identifying responses of organisms to heterogeneous environments (Johnson *et al.* 1992). Most applications of fractals, however, have been restricted to quantifying the tortuosity of movement paths relative to the allometry of different organisms (e.g. With 1994), and do not identify break-points for scale in accordance with environmental heterogeneity. Fractals are less mechanistic than the approach we advocate, and when applied to animal movements may violate the critical assumption of self-similarity (Turchin 1996).

We predicted that changes in the frequency of movement rates would reflect hierarchically structured within-patch, between-patch and migratory-type behaviours. This interpretation and the workings of the model are consistent with much of the theory concerning the hierarchical relationships of ecological phenomena. Hierarchy theory is premised on the assertion that scale can be identified using the frequencies and rates of activities (Allen & Star 1982). Senft *et al.* (1987) adopted those principles and identified an ecological hierarchy of large foragers using the frequencies of foraging events (i.e. selection of diet, feeding-area, home range).

For most combinations of caribou and season, the three-process model was ineffective at discriminating scales of movement that occur when caribou migrate. Nonsensical r_c values or overfitting of the model to the data indicated that either the technique is insensitive to events with a very low frequency (e.g. migration), or that those events were absent from the data. The negative result does not, however, imply that a three-process model is inappropriate for all situations (Berdoy 1993). We encourage researchers to apply the non-linear model according to their knowledge of the subject species and its behaviour, and if necessary to accommodate greater than three processes. In our study, the two-process model achieved a good fit to all but one combination of data for caribou by season. We interpret all movements less than the r_c threshold as frequent small-scale intrapatch movements, which probably correspond with foraging behaviours, and all movements greater than the respective r_c as less frequent interpatch and migratory movements.

We demonstrated a seasonal effect where two-process models in winter fitted better, relative to a one-process linear equation, than summer models. Relatively poor model fit, high r_c values and failure to fit a two-process model for one individual suggest that during the summer woodland caribou may respond to the environment in a non-scalar fashion (Table 1). Forage is relatively abundant during that season and the environment less patchy, resulting in a continuum of movement over the range of scales we measured. In contrast, model fit was best during winter, and r_c values were relatively small and exhibited little variability. This is consistent with a patchy environment, where snow conditions and lichen distribution restrict foraging activity to small discrete patches. During two winters of tracking caribou on the ground (Johnson *et al.* 2001), we observed caribou in both the alpine and forest foraging intensely over relatively small areas and then moving some distance to new patches. Similarly, during the spring and autumn green vegetation is in a state of flush, or sequestration and dormancy, respectively, leading to a patchy environment. Calving and rutting also may lead to scale-dependent movement behaviours. Others have noted a behavioural response by *Rangifer* to variations in environmental patchiness. This includes the tracking of vegetation release following snow melt (Skogland 1984), selection of feeding areas and sites where the snow conditions are favourable for cratering (Brown & Theberge 1990), the use of areas according to forage availability and nutrition (White & Trudell 1980), and the selection of snow patches for behavioural thermoregulation or as relief from insect harassment (Ion & Kershaw 1989).

Although we have discussed a few possible explanations for scale-explicit responses to a patchy environment, we acknowledge that the suite of biotic and abiotic factors that influence the movements of caribou are too numerous to parameterize and understand all possible interactions. Environmental heterogeneity is, however, well documented as a causal agent in the movement and distribution of terrestrial and aquatic animals and can result in scale-dependent behavioural responses (Kotliar & Wiens 1990; Schaefer & Messier 1995; Wallace *et al.* 1995). The non-linear model appears to reflect the response of caribou to environmental heterogeneity, where heterogeneity occurs within spatial and temporal domains. Patches that differ in size, composition and configuration across time and space elicit that response.

Model fit and the interpretation of our results may be confounded by the use of movement rates instead of distances. Caribou may be capable of making fast movements over short intervals (e.g. 20 min), but unable to maintain that rate of movement over longer periods (e.g. 16 h). Similarly, a series of movements measured over short intervals would be more precise and sum to a longer distance than fewer movements measured over longer periods. If these factors biased our data we would expect shorter time intervals to have greater mean movement rates. Indeed, this was the case for movements over periods of 20 min, but not longer intervals. Despite large sample sizes, significant differences were not noted for other interval comparisons.

Furthermore, once 20-min data were removed, strong linear relationships existed between movement rate and distance suggesting that our assumption of rate being related to scalar phenomena based on distance (e.g. intra-, interpatch and migratory movements) was valid. In support of our argument, Reynolds & Laundré (1990) reported a negative exponential relationship for the difference in real distance vs. estimated distance travelled by coyotes (*Canis latrans* Say) and pronghorns (*Antilocapra americana* (Ord)) at successively longer time intervals. In their study, curves for both animals were nearly vertical at the 1-h interval, but the slopes showed appreciable decline after 4 h.

ECOLOGICAL INFERENCE: THE IMPORTANCE OF A MULTI-SCALE APPROACH

Our assertion that the two-process non-linear model is an effective means of differentiating scales of movement is supported by logistic regression analyses. If the logistic regressions had not fitted data on movement we would conclude that either a scaling relationship was not present, the non-linear model was ineffective at discriminating scales or the scale of patchiness that we mapped misrepresented the scale of patchiness to which caribou respond. For the multivariate regression models, R^2 values were relatively low and there was a high misclassification of large-scale movements. When animals move between patches they probably do not avoid cover types associated with small-scale movements. At the level of detail we mapped the landscape, perfect separation of movements based on cover type is highly unlikely and some discrimination error should be expected. Misclassification of cover types and the resulting errors in the map of predation risk (i.e. based on cover type) also could obscure relationships between movements and those independent variables.

Caribou movements were related to only one scale of patch heterogeneity that may encompass smaller or be included within larger scales of heterogeneity (Kotliar & Wiens 1990). Our trailing studies revealed finer scales of patchiness (e.g. distribution of terrestrial lichens; Johnson *et al*. 2001). There also may be larger scales of heterogeneity consisting of collections of patches (Stuart-Smith *et al*. 1997). The land-cover map that we used appears to represent one patch scale that is relevant to the foraging decisions of woodland caribou. For example, caribou foraged on patches of terrestrial lichens within larger patches identified as pine terrace and alpine–little vegetative cover. The two-process model identified the small-scale movements within those patches. Similarly, large interpatch movements of caribou in the forest were associated with patch types, such as lakes/rivers, mid-elevation coniferous, Krummholz and pine–spruce; areas not associated with foraging behaviours (Johnson *et al*. 2001).

The energetic costs of movement were greatest at large scales for three of the four caribou tested (Table 2).

As would be expected, caribou making large-scale movements traversed greater distances and topographic variability than animals making small-scale movements. This is consistent with our assumption that rate is correlated with distance. Caribou 772B had a more uniform distribution of movement events and was the exception to this trend.

Decisions such as habitat selection, time dedicated to predator vigilance and animal positioning relative to escape cover may all be modified by the presence of predators or the perceived risk of predation (Roberts 1996; Frid 1997; Kramer & Bonenfant 1997). Risk-adverse behaviours may result in significant time and energy costs and direct consequences for individual fitness (Lima & Dill 1990). Of four caribou we analysed, 1D2B and 772B demonstrated that risk differed between large- and small-scale movements. In those instances, distance to risk was greater, and the risk of predation lower, during large-scale movements. This difference is probably the result of those caribou foraging across high-risk, low-elevation areas and then making large-scale movements across lower-risk mid-elevation forest types to access alpine areas. The variation in risk was not a direct consequence of selection for habitats that offered lower risks during movement, but resulted from occupancy of alpine winter range with advantageous foraging conditions and lower risk of predation (Johnson *et al*. 2001).

We identified two scales of movement that we hypothesize are consistent with a broad group of within-patch behaviours (e.g. foraging, ruminating, social interaction) and movement to other patches. Adopting a single-scale approach for selection analyses (Boyce & McDonald 1999) would result in the intra-patch movements being lumped with the interpatch movements. The overall affect on the conclusions of those analyses would depend on the frequency of interpatch movements. Relative to the four caribou we tested, selection of particular environmental variables may still be apparent, but relocations collected while those animals were engaged in interpatch movements would add 'noise' to the prediction process (Gardner *et al*. 1989). Caribou B91A had the lowest ratio of intra- to interpatch movements and would be most susceptible to the effects of pooling locations. Further, a single-scale approach may result in the loss of infrequent events. For example, we attempted to identify migratory movements with the three-process model, but were unsuccessful. Despite sample-size limitations to modelling habitat selection in our study, identification of large-scale movements may provide insight into the use of corridors and the importance of habitat connectivity (Lord & Norton 1990).

Description of animal movements and habitat selection at large spatial scales is largely concerned with the question of *where*. Biological meaning often is inferred from animal relocations related to maps of vegetation or differences in home-range size. The assumption is made that animal distribution is correlated

to vegetation and that specific vegetation types drive animal movements at all scales. Using a two-process non-linear model, we demonstrated that different variables are important to caribou at different spatial scales. A scalar relationship between movement and predation risk also suggests that the importance of environmental factors to individual animal fitness varies with scale (Rettie & Messier 2000). We argue that to imply explanatory reasoning for *why* animals select or move to certain portions of their range, it is necessary to identify the scales at which animals respond to the environment. By using scale to delimit behaviour, we can begin to infer mechanisms that drive movement and resource selection, and ultimately population processes.

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