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We tracked 12 mule deer (*Odocoileus hemionus hemionus*) between February 1999 and April 2003 by using global positioning system (GPS) radiotelemetry in southeastern British Columbia to provide detailed information on migration and habitat use to local managers. We tested winter resource selection at the home-range and within-home-range scale to test a hypothesis that ungulate resource selection is scale-dependent. All sampled mule deer in this population migrated from low-elevation winter ranges to high-elevation summer ranges, supporting a hypothesis that migration is obligatory in mountainous, heavy-snow areas. We found little consistent selection at the within-home-range scale, but considerable selection at the home-range scale, supporting a scale-dependent hypothesis. Potential mule deer winter range could be predicted from 2 biophysical attributes, elevation and solar duration. Currently suitable winter habitat can then be further delineated on the basis of amount of mature coniferous forest within this zone. Use of GPS radiotelemetry increased sample intensity of individual deer, and thereby accuracy of individual parameter estimates. However, because of high equipment costs and failure rates, increased sample intensity occurred at the expense of sample size, and therefore illustrates a trade-off consideration for future work.

Key words: British Columbia, global positioning system radiotelemetry, landscape pattern indices, mule deer, *Odocoileus hemionus*, resource selection, solar radiation

Mule deer (*Odocoileus hemionus hemionus*) in the interior mountainous regions of North America often are associated with use of low-elevation mature forests in winter followed by movement to higher elevations and more open habitat in summer (Garrott et al. 1987; Thomas and Irby 1990). The proximal cause of this migratory strategy is usually attributed to deep snow accumulations at high elevations during winter and ultimately to seasonal changes in the quality and quantity of available forage within the annual home range of the animal (Garrott et al. 1987). Winter habitat use of mule deer has been reported in the published literature for 2 populations in the interior of British Columbia (Armleder et al. 1994; D'Eon 2001), the northern limit of continuous high-density mule deer. However, previous research has contributed surprisingly little to predicting distribution and habitat use of unstudied deer populations (Pauley et al. 1993). This is especially true of interior winter ranges over the northern one-third of their range,

where mule deer experience deep snow accumulations even at low elevations and little is known about habitat selection in these areas (Armleder et al. 1994). Information on these populations is required and extremely important for providing the amount of detail required by local managers, who have the onus of providing fine-resolution forest management plans that must include provisions for deer winter habitat (e.g., Armleder and Dawson 1992). As well, published accounts of habitat selection for mule deer primarily address preference or avoidance of habitat type classifications and biophysical attributes in winter only, and do not usually consider landscape features or multiscale habitat selection.

We tracked seasonal movements and summer and winter home-range use of mule deer from an unstudied population in a mountainous, forested landscape in southeastern British Columbia by using global positioning system (GPS) radiotelemetry. To our knowledge, this is one of the 1st mule deer GPS radiotelemetry studies. We collected this information to provide detailed habitat use and distribution information to local forest managers in support of ungulate winter range management. As well, we tested winter resource selection from a suite of habitat and biophysical attributes including landscape features such as logging roads, forest edges, and streams. We were interested in

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these landscape features because they have provided mixed results in previous studies, or remain unstudied, and are therefore either unclear or unknown (D'Eon 2002a). This is especially true of mule deer, which have been less studied than other deer species. This has occurred despite an obvious relationship between many landscape elements implicated as factors in a current forest fragmentation problem (D'Eon 2002b; D'Eon and Glenn, in press; Saunders et al. 1991), and traditional deer habitat management that tends toward small patch sizes and high edge densities (Thomas 1979). Because total habitat amount may be more important than spatial configuration of landscape elements (Fahrig 1997), we concurrently tested selection of amounts of mature forest and early seral vegetation and investigated their relative influence.

Finally, because resource selection is predicted to occur at a hierarchy of scales (Johnson 1980; Senft et al. 1987) and is sensitive to the scale of habitat availability (McClean et al. 1998), we focused our tests on comparisons between habitat use and availability at the home-range (2nd-order selection from Johnson [1980]) and within-home-range scales (3rd-order selection from Johnson [1980]) to test a hypothesis that selection of habitat in this study was scale-dependent.

Materials and Methods

Study Area

We captured, radiocollared, and monitored mule deer within the Lemon Creek drainage (49°42′N, 117°25′W), a 21,924-ha mountainous, managed, forested landscape within the Selkirk Mountains, 23 km northwest of Nelson, southeastern British Columbia (described in detail by D'Eon et al. [2002]). Briefly, terrain was generally steep and broken with slope gradients commonly >45°, elevations ranged from 548 to 2,405 m, with aspects of 1–360°. The landscape could be characterized as a coniferous forest matrix interspersed with logging roads and harvest blocks. Midwinter snow depths varied from <10 cm at low elevations, to >2 m at higher elevations (D'Eon 2004; www.forrex.org/jem/2004/vol3/no2/art5.pdf). Average daily summer high and low temperatures were 26.9°C and 9.4°C, respectively; average daily winter highs and lows were 2.2°C and −4.9°C, respectively. Snow is usually persistent on the ground at low elevations from late November until mid March. Forest types are described in detail by D'Eon et al. (2002).

Deer Capture and Collaring

We captured 20 adult mule deer (12 males and 8 females) between 18 February 1999 and 29 January 2002. We increased capture efficiency by using a variety of capture techniques. As a result, 15 deer were captured with Clover traps baited with alfalfa (Clover 1954); 3 with a drop-net (D'Eon et al. 2003); 1 by helicopter net-gunning; and 1 was shot with a chemical immobilization dart. Stratified by date, we captured 6 deer (3 males and 3 females) in February 1999; 6 deer (5 males and 1 female) in March 2000; 3 deer (1 male and 2 females) in March 2001; 1 deer (male) in October 2001; and 4 deer (2 males and 2 females) in January 2002. All captured deer were considered to belong to the same local population inhabiting Lemon Creek drainage.

We fitted deer with GPS radiocollars (Advanced Telemetry Systems, Isanti, Minnesota) that contained Garmin GPS 25LP receivers (Wildlink 1990) and remote-release mechanisms. Radiocollar battery life was limited to approximately 1 year. Therefore, we removed and retrieved radiocollars when batteries failed, replaced batteries, and subsequently redeployed them on different deer. Collars

were set to attempt GPS fixes every 4–6 h. We determined fix success rates by calculating the proportion of possible fixes obtained for the time span of a deployed collar. Collars that malfunctioned before 1 year of use were retrieved at the time of malfunctioning.

Animal capture and handling were consistent with the policies and guidelines provided by the Province of British Columbia (1998) and the Animal Care and Use Committee (1998).

Data Management and Analyses

We downloaded data from retrieved collars and deleted obvious anomalies and impossible data (D'Eon et al. 2002). Data from malfunctioning collars were inspected and rejected if suspect. We did not use real-time or postprocessing differential correction because location accuracy of uncorrected data was sufficient (±31 m 95% of the time—D'Eon et al. 2002). Data were not corrected for fix rate bias because a known fix rate bias derived from stationary collars within this study area was demonstrated to have no effect on conclusions about habitat selection (D'Eon 2003).

We considered individual deer as the experimental unit and based selection conclusions on comparisons between values for individual deer and corresponding random values associated with each deer (design 3 from Thomas and Taylor [1990]), rather than pooling all locations among all deer because we had many locations on few individuals, as suggested by White and Garrott (1990) and Aebischer et al. (1993). Doing so avoided pseudoreplication and inflated sample size problems (Hurlbert 1984).

Seasonal movements to and from winter and summer ranges were determined from visual inspection of mapped locations plotted sequentially by date. We stratified locations of individual deer into summer, autumn migration, winter, and spring migration, by inspecting the spatial and temporal distribution of locations. Specifically, we identified winter and summer locations based on congregations of locations on traditional winter and summer ranges. Although offering descriptions of winter and summer ranges, we limited analyses of resource selection to winter because of its importance to deer population dynamics (Unsworth et al. 1999) and because of a management focus on winter habitat in British Columbia and elsewhere (Armleder and Dawson 1992; D'Eon 2001). We calculated descriptive summer and winter range characteristics by determining the mean and 90th percentile range (i.e., upper and lower 5th percentile of values deleted from each parameter for each deer) for 12 habitat parameters based on point data. We determined the sample (n = number of deer) mean and 90th percentile range for each parameter by 1st calculating the mean and lower and upper limits from 90th percentile ranges for individual deer from all individual locations. We then calculated the mean of individual means and lower and upper limits to provide a sample mean and lower and upper limit for each parameter. We used the 90th percentile as a measure of general use to avoid extraneous outliers and provide a more meaningful measure of the range of habitat use.

Data analyses were performed with SYSTAT 8.0 statistical software (SPSS 1998), with the exception of modeling with Akaike's information criterion (AIC), which was performed with the aid of a spreadsheet.

Home-range scale analyses.—To test winter resource selection at the home-range scale (2nd-order selection from Johnson [1980]), we compared attributes of winter home ranges of individual deer to an equal number of random polygons of similar size, as suggested by Potvin et al. (2001). Random polygons represented habitat availability at the home-range scale. For winter ranges, we created 100% minimum convex polygon winter home ranges for each deer (White and Garrott 1990). For random polygons, we randomly selected point locations within the study area and created circular polygons around these

locations equal in size to the average deer winter home range. We then calculated 16 landscape pattern indices for each deer winter home range and random polygon by using ArcView Spatial Analyst software (ESRI 1996). The landscape pattern indices we calculated were mean elevation, mean solar duration, mean slope, ruggedness, mean % fir–pine, mean % cedar–hemlock, mean % spruce–balsam, mean % aspen–birch, mean forest age, % mature coniferous forest, % early seral, % logged, mean crown closure, stream density, edge density, and logging road density. Forest cover and biophysical data were derived from British Columbia provincial forest cover and terrain resource information maps in digital format at 1:20,000 scale. Mean values were calculated by determining the mean value of all 30×30-m pixels in each deer home range and random polygon. Solar duration was calculated as the total amount of solar duration (hours) on each pixel during the late winter period, by using computer-generated digital terrain modeling (Kumar et al. 1997). We used solar duration as a surrogate for aspect because of its correlation ($r = 0.63$; Fig. 1) with aspect class, where $136–240° =$ hot (southwest aspect); $241–285° =$ warm (west aspect), $60–135° =$ cool (east aspect), and $286–59° =$ cold (north aspect), and because it is a useful continuous variable for multivariate statistical applications. More importantly, solar duration incorporates terrain influences such as shading and sun angle, and is therefore a better measure of the effects of solar radiation than aspect alone (Kumar et al. 1997). Ruggedness was calculated as an expression of terrain contour density (Beasom 1983). Mature forest was defined as coniferous forest >80 years; early seral was defined as forest <40 years; logged forest was defined as logged sites <40 years. Edge was defined as the interface between mature and early seral forest. The forest composition variable % fir–pine was the combined amount (as percentage) of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) within each pixel; % cedar–hemlock was the combined amount of western redcedar (*Thuja plicata*) and western hemlock (*Tsuga hetrophylla*); % spruce–hemlock was the combined amount of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*); % aspen–birch was the combined amount of trembling aspen (*Populus tremuloides*), black cottonwood (*P. balsamifera*), and paper birch (*Betula papyrifera*).

To test resource selection we compared mean landscape pattern indices between deer home ranges and random polygons by using Student's *t*-tests (Zar 1984). To investigate multivariate relationships in the data we used logistic regression analyses and evaluated model fit by using Akaike's information criterion adjusted for small sample (AIC$_c$) size because $n/K < 40$ (where K is number of model parameters—Burnham and Anderson 1998; reporting follows Anderson et al. [2001]). Models were chosen a priori based on expectations from past work in the study area.

Within-home-range scale analyses.—To test winter resource selection at the within-home-range scale (3rd-order selection from Johnson [1980]), we compared mean values from individual deer locations to mean values of an equal number of random locations from within the winter home range of the associated deer. Random locations were assumed to represent habitat availability at the within-home-range scale. We calculated the following parameters for each set of deer use locations and associated random locations: mean crown closure, mean forest age, mean elevation, mean slope, mean distance to edge, mean distance to stream, mean distance to logging road, mean patch size, mean solar duration, mean % fir–pine, mean % cedar–hemlock, and mean % aspen–birch. We selected variables for their similarity with variables tested at the home-range scale so that comparisons could be performed between the 2 scales. To test resource selection at the within-home-range scale we performed *t*-tests between individual sets of deer use and random locations (i.e., $n =$ number of
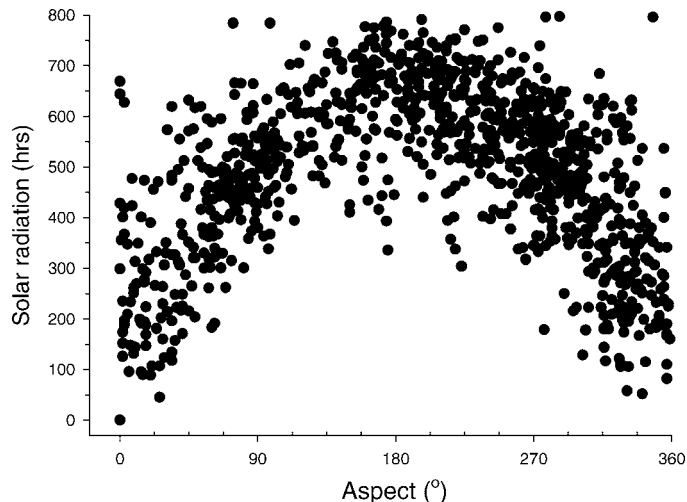

FIG. 1.—The relationship between aspect and solar radiation duration (total hours over late winter period) for 1,000 random locations in Lemon Creek drainage, southeastern British Columbia.

locations for 1 deer), then evaluated selection based on the results from all deer (i.e., $n =$ number of deer). We tested deer use of logged sites by comparing the number of individual deer locations and random locations within logged sites for each deer by using a chi-square test (Zar 1984). We then evaluated selection for logged sites based on the results from all deer, similar to all other variables at this scale.

RESULTS

Radiotelemetry

Of the 20 radiocollars deployed, 8 malfunctioned or provided unusable data. The remaining 12 collars for 7 males and 5 females had overall fix success rates (i.e., proportion of radiocollar fix attempts that successfully resulted in obtaining a GPS location) ranging from 27% to 67% ($\bar{X} = 48\% \pm 3.3$ *SE*). The proportion of fixes by collar that were 3-dimensional ranged from 48% to 63% ($\bar{X} = 54\% \pm 1.5$ *SE*). The total number of recorded locations (all seasons combined) per collar ranged from 181 to 1,199 locations ($\bar{X} = 799$ locations ± 86.8 *SE*); numbers of summer locations per collar ranged from 50 to 573 locations ($\bar{X} = 282 \pm 54.2$ *SE*); numbers of winter locations per collar ranged from 75 to 409 locations ($\bar{X} = 217 \pm 34.9$ *SE*). We detected no seasonal bias in fix rate success (Fig. 2).

Seasonal Movements and Home-Range Characteristics

Seasonal movement patterns observed in this population can be described as a general congregation in 1 low-elevation winter range area, followed by individual migrations to more dispersed high-elevation summer ranges (Fig. 3). Winter range aggregation was high, with all individual winter ranges overlapping. However, summer ranges were more dispersed, with 2 distinct aggregations (both with 5 deer each) 4.0 km and 13.2 km from the winter range aggregation (distances calculated as the linear distance between combined seasonal home-range centroids). These 2 summer aggregations were separated by 10.7 km. An exception was seen in 1 deer that
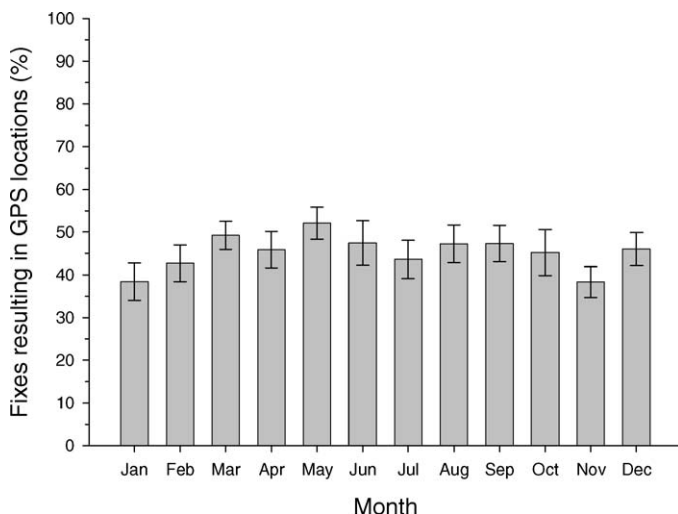
FIG. 2.—Percentage of radiocollar fix attempts that resulted in global positioning system location data for each month, shown as mean ± 1 SE for 12 radiocollared mule deer in southeastern British Columbia between February 1999 and April 2003.

TABLE 1.—Mean winter and summer values and 90th percentile ranges for forest and biophysical attributes used by 12 wintering mule deer in Lemon Creek, British Columbia, from January 1999 to April 2003.

Habitat attribute[a]	Winter			Summer		
	$\bar{X}$[b]	SE	90th percentile range[c]	$\bar{X}$[b]	SE	90th percentile range[c]
Elevation (m)*	983	24.9	808−1,171	1730	30.2	1,493−1,973
Solar duration (h)	572	12.7	469−650	593	14.2	458−692
Slope (%)*	54	1.2	29−82	47	2.5	21−77
Stand age (years)*	118	6.8	66−169	79	9.3	3−176
Crown closure (%)*	46	4.5	20−69	22	1.8	1−54
% fir−pine*	84	1.9	48−100	8	1.8	0−38
% cedar−hemlock	1	0.2	0−6	2	1.5	0−13
% spruce−balsam*	0	0	0−0	40	8.5	2−85
% aspen−birch	0	0	0−0	0	0	0−0
Distance to edge (m)*	263	27.1	20−622	127	18.1	9−391
Distance to logging road (m)*	386	34.0	87−639	852	228.6	188−1,559
Distance to stream (m)*	583	72.9	234−902	187	13.7	21−448

[a] Derived from average values for 30 × 30-m pixels within digital resource inventories. Significant differences (t-test, $P < 0.05$) between winter and summer means are indicated with asterisks.

[b] Mean values calculated as mean ($n = 12$) of means from individual deer locations.

[c] Upper and lower limits of 90th percentile ranges were calculated as mean ($n = 12$) upper and lower limits of 90th percentile ranges from individual deer.

used a distinct summer home range that was 10.8 km from the winter range aggregation and 12.5 km and 13.5 km from the other 2 summer range aggregations. Average migration distance between summer and winter home ranges was 8.3 km ± 1.4 SE (range = 3.2–13.2 km; $n = 11$), calculated as the linear distance between individual summer and winter home-range polygon centroids. Annual home-range size averaged 4,441 ha ± 940 SE (range = 869–8,700 ha; $n = 11$); summer home-range size averaged 1,068 ± 425 ha (range = 41–4,937 ha; $n = 11$); winter home-range size averaged 301 ± 55 ha (range = 46–756 ha; $n = 12$). Although migration distance and home-range sizes tended to be slightly larger for males than females, no statistical difference occurred between home-range size between sexes (t-test, all $P > 0.05$).

Median date of arrival on winter home ranges was 1 February (range = 17 December–9 April; $n = 9$; only cases where a true migration date could be determined were used). Median date of departure from winter ranges was 10 May (range = 3 April–30 May; $n = 11$); median date of arrival on summer home ranges was 29 June (range = 28 May–9 September; $n = 11$); median date of departure from summer home ranges was 30 October (range = 6 October–21 December; $n = 11$).

When compared to summer ranges, deer used significantly lower elevations in winter, slightly steeper slopes, older forests, and higher crown closures (Table 1). Solar duration and use of aspect classes and was similar (Table 1; Fig. 4; $G_{adj} = 6.966$, $P = 0.073$), with most locations occurring on south (41% of locations in both seasons) and west (34 % in summer and 28% in winter) aspects, followed by north (16% in summer and 25% in winter) and east (10% in summer and 6% in winter) aspects. In winter deer used fir–pine almost exclusively, compared to summer, when spruce–balsam was the most heavily used forest type (Table 1). Cedar–hemlock and aspen–birch forest types were virtually unused in both seasons. In winter, deer were farther from edges and streams than in summer, but closer to roads (Table 1).
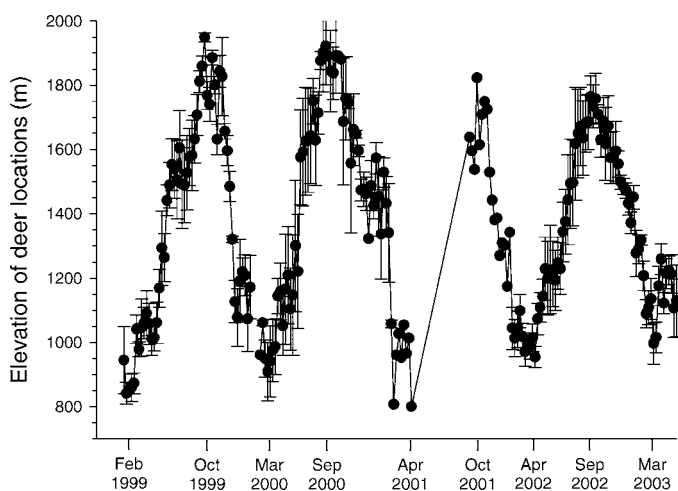

FIG. 3.—Elevational locations for 12 radiocollared mule deer from February 1999 to April 2003 in Lemon Creek drainage, southeastern British Columbia. Values are shown as mean ± 1 SE. Dates along x-axis correspond to elevational highs and lows.

Resource Selection

Mean values for all landscape pattern indices were similar between wintering males and females, based on nonsignificant t-tests (all $P > 0.05$). On this basis we assumed similar winter habitat use patterns between sexes and did not differentiate between sex in further analyses.

Home-range scale selection.—Winter home-range size ranged from 46 to 756 ha ± 54.8 SE ($\bar{X} = 301$ ha, $n = 12$). We therefore

created 12 random circular polygons of 301 ha representing habitat availability at the home-range scale. Deer use of elevation, % cedar–hemlock, % spruce–balsam, % early seral, % logged, and stream density were significantly less than random (*t*-test, all *d.f.*=22, *P* < 0.05; Fig. 5); solar duration, % fir–pine, stand age, % mature, and crown closure were greater than random (*t*-test, all *d.f.*=22, *P* < 0.05; Fig. 5); slope, ruggedness, % aspen–birch, edge density, and logging road density were similar to random (*t*-test, all *d.f.*=22, *P* > 0.05; Fig. 5).

Before multivariate analyses, correlated (*r* > 0.7) landscape pattern index variables were deleted so that a final model set of uncorrelated variables remained and included elevation, % mature, solar duration, edge density, ruggedness, % cedar–hemlock (logarithmically transformed), and % aspen–birch (square-root transformed). Logistic regression analyses resulted in several 1- and 2-variable models. More complex models (≥3 variables) failed to converge (Table 2). The best model from all models considered consisted of elevation and solar duration (log likelihood = −2.72, AIC_c = 12.65, ρ^2 = 0.836; Table 2). A model consisting of % mature forest and edge density provided a very close 2nd-best model (evidence ratio = 1.06; Table 2).

Within-home-range selection.—Individual habitat preferences were mixed at the within-home-range scale (Table 3). Most variables showed no consistent preference or avoidance by deer based on number of deer with mean use values greater than, less than, or similar to random values. However, elevation showed some degree of preference, where 6 of 12 deer used locations of lower elevation than random; distance to edge, where 7 of 12 used locations closer to edges than random; and distance to road, where 6 of 12 deer used locations farther from roads than random.

An analysis of use of logged sites demonstrated that 5 of 12 deer made higher use than expected of logged sites (χ^2-test, all *d.f.*=1, *P* < 0.05), 1 deer made lower use than expected (χ^2 = 5.444, *d.f.*=1, *P* = 0.020), and 6 deer made similar use than random of logged sites (χ^2-test, all *d.f.*=1, *P* > 0.05).

DISCUSSION

Movement Patterns

Mule deer in this drainage in British Columbia displayed a consistent migratory pattern from low-elevation winter ranges near the mouth of Lemon Creek to high-elevation summer ranges, similar to mule deer migration patterns described by Garrott et al. (1987) for northwestern Colorado. All deer in our study were migratory, similar to mule deer tracked by Garrott et al. (1987), but in contrast to Brown (1992), who reported up to 48% of mule deer as nonmigratory in southeastern Idaho, and Nicholson et al. (1997), who reported female nonmigrants in southern California. In both studies, nonmigration was attributed to mild winter conditions. Although a variety of factors contribute to the timing of migration (Nicholson et al. 1997), Garrott et al. (1987) suggested that migration is obligatory for mule deer living in northern mountainous areas. We concur with this suggestion and further suggest that this phenomenon may be more critical to deer in our study, where
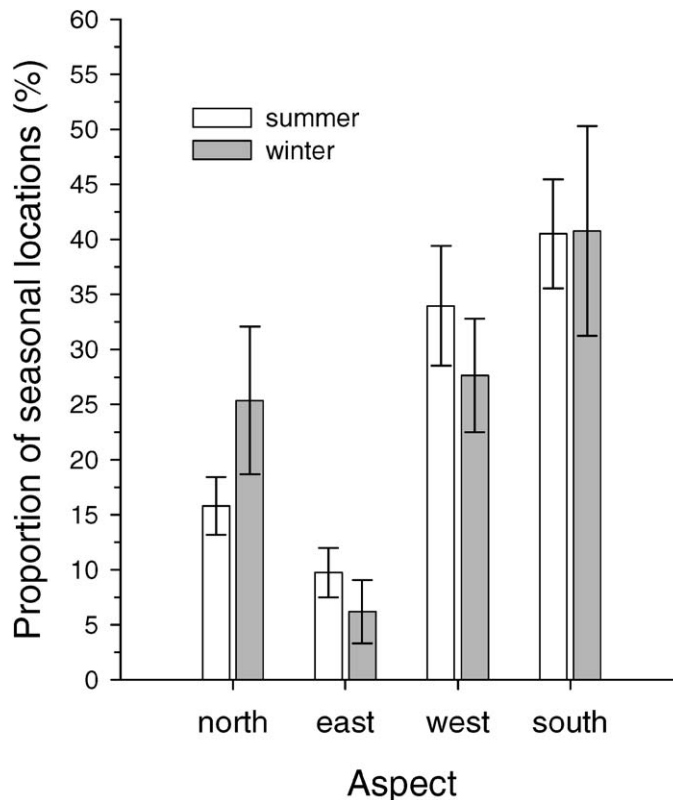

FIG. 4.—Proportion of seasonal locations by aspect among 12 mule deer in Lemon Creek, British Columbia, from February 1999 to April 2003, shown as mean ± 1 *SE*.

they are near the northern limits of mule deer range, where midwinter snow depths >40 cm are common even at the lowest elevations, and exceed 2 m on summer ranges (D'Eon 2001). Snow depths of this nature virtually eliminate mule deer food availability on summer ranges during winter and make migration obligatory. Indeed, even in an extremely mild winter (January–March 2000; 40% of average snowfall), all radio-collared deer in our study migrated to low-elevation winter ranges, thus supporting this hypothesis.

Inspection of movement patterns illustrated that deer used areas north of Lemon Creek (which flows east to west) almost exclusively throughout the year, indicating a reluctance, in all seasons, to use the primarily north- and east-facing slopes on the other side of the valley dominated by cedar–hemlock forests at lower elevations, and spruce–balsam forests at higher elevations. As a result, the pattern of aspect use was similar between summer and winter. Although the use of south and west aspects in winter is consistent with other work and attributed to higher solar radiation leading to lower snow depths (D'Eon 2001), primary use of south and west aspects in summer has not been reported to our knowledge. We suggest this may be related to higher primary production on these sites leading to higher food abundance and quality. This is particularly important in light of the weather–forage regulation hypothesis (i.e., that severe weather and forage availability regulate mule deer populations) proposed by Peek et al. (2002), and Parker (1988) who concluded that summer forage intake rates had one of the greatest
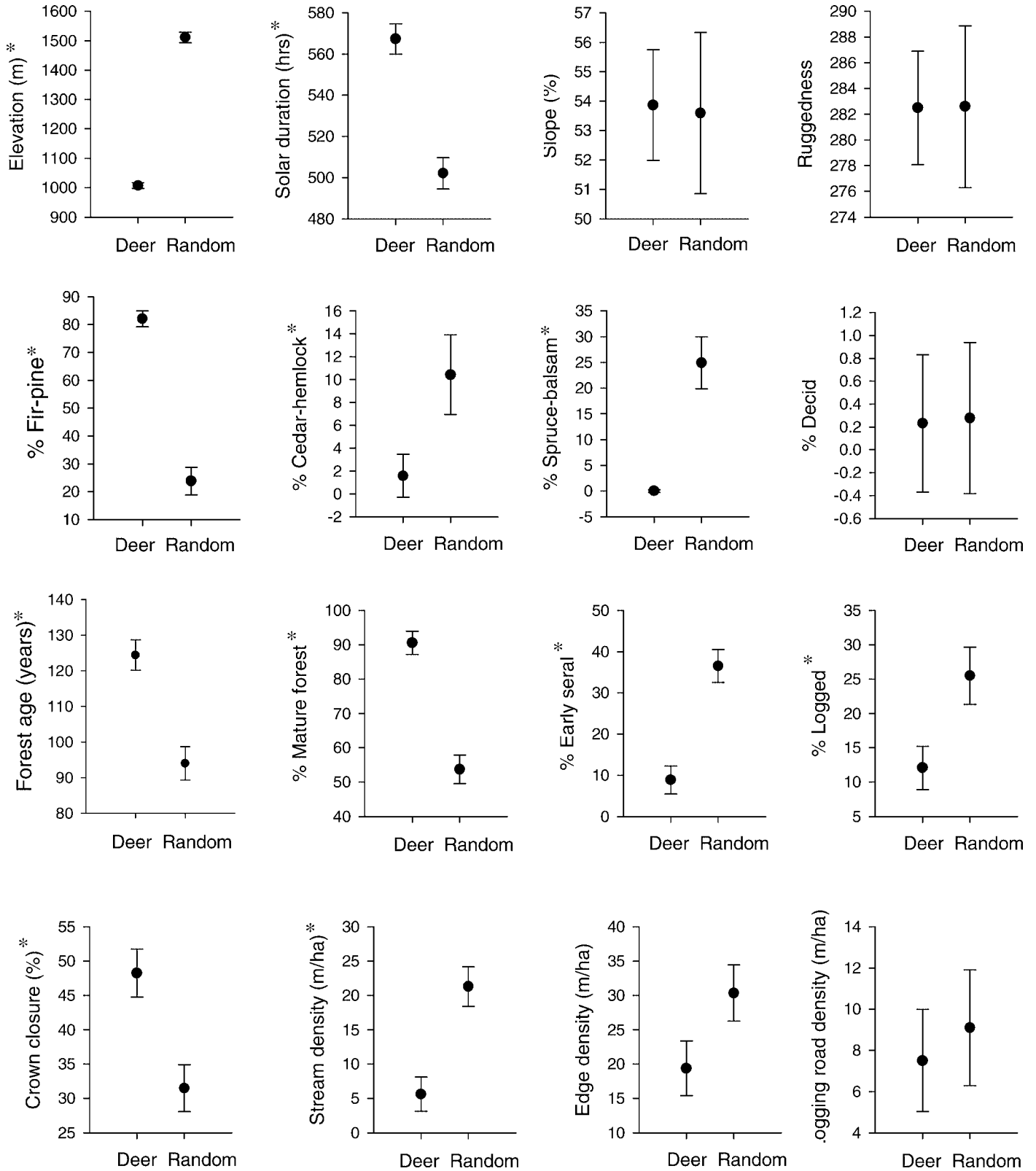
Fig. 5.—Comparisons of values between deer winter range polygons ($n = 12$) and random polygons ($n = 12$) for biophysical, forest, and landscape attributes at the home-range selection scale for 12 mule deer in Lemon Creek drainage, southeastern British Columbia, shown as mean $\pm$ 1 *SE*. Significant differences (*t*-test, *d.f.* = 22, $P < 0.05$) are indicated with asterisks.

TABLE 2.—Model selection results for logistic regression models[a] when using winter home-range and random polygon attributes to predict mule deer winter home-range selection in a forested landscape in southeastern British Columbia.

Model variables	K	Log L	AIC_c	ΔAIC	AICω	Evidence ratio
Elevation + solar duration	3	−2.72	12.65	0.000	0.365	1.00
Mature + edge	3	−2.78	12.76	0.110	0.346	1.06
Mature + cedar−hemlock	3	−3.96	15.11	2.466	0.106	3.43
Mature	2	−5.77	16.12	3.469	0.064	5.67
Elevation	2	−6.16	16.89	4.241	0.044	8.34
Elevation + ruggedness	3	−5.56	18.32	5.674	0.021	17.06
Mature + deciduous	3	−5.75	18.70	6.052	0.018	20.61
Mature + ruggedness	3	−5.77	18.73	6.084	0.017	20.95
Mature + solar duration	3	−5.77	18.74	6.096	0.017	21.07
Solar duration	2	−13.02	30.62	17.969	0.000	7,980.16
Cedar−hemlock	2	−13.47	31.51	18.863	0.000	12,477.90
Edge density	2	−15.28	35.12	22.477	0.000	76,017.15
Deciduous	2	−16.62	37.81	25.163	0.000	291,185.06
Ruggedness	2	−16.64	37.84	25.195	0.000	295,881.49

[a] $n = 24$ (12 mule deer winter home ranges, 12 random polygons); K = number of model parameters; Log L = log likelihood; ΔAIC = change in Akaike's information criterion (AIC) value from the best model; AICω = AIC weights; best-model $\rho^2 = 0.836$.

TABLE 3.—Winter resource selection by individual deer ($n = 12$) by using biophysical, habitat, and landscape attributes at the within-home-range scale in a mule deer global positioning system radiotelemetry study in southeastern British Columbia. "Number of deer" reflects the number of individual deer (total $n = 12$) with mean use values greater than (+), less than (−), or equal to (0) an associated set of random locations, based on significant t-tests ($P < 0.05$) between use and random locations.

Variable	Preference (number of deer)		
	+	−	0
Elevation	3	6	3
Slope	2	2	8
Solar radiation	4	4	4
Forest age	2	3	7
Crown closure	5	5	2
% Fir−pine	3	3	6
% Cedar−hemlock	2	2	8
% Aspen−birch	1	0	11
Distance to edge	2	7	3
Distance to road	6	2	4
Distance to stream	5	3	4

effects on black-tailed deer (*Odocoileus hemionus columbianus*) condition. However, these and other summer range considerations in this population require further examination.

Resource Selection

Resource selection by wintering mule deer in this study was scale-dependent. Few consistent trends occurred for selection of biophysical, habitat, or landscape attributes at the within-home-range scale. Combined results of individual selection were mixed for most attributes at this scale. However, exceptions included lower elevations preferred by 6 of 12 deer, smaller distances from edges used by 7 of 12 deer, and larger distances from roads used by 6 of 12 deer. In contrast, significant selection occurred at the home-range scale. At this scale, wintering deer preferred winter home ranges that had lower elevations, higher solar duration, and higher amounts of mature forests with high fir–pine content, older stand ages, and higher crown closures; and they avoided areas of cedar–hemlock and early seral stands including logged sites. Several cross-scale relationships are therefore apparent. Although deer chose winter home ranges on the basis of several biophysical and habitat attributes at the home-range scale, once localized on winter ranges deer tended to use the same features in a mixed or random fashion. The reverse situation also occurred for some attributes. No evidence was found that logging roads and edges were selected or avoided at the home-range scale. However, once on winter ranges, deer tended to avoid roads and use edges more. Interestingly, logged sites and streams were avoided at the landscape scale, but then used randomly within winter home ranges.

These findings support predictions of Johnson (1980) and Senft et al. (1987) that resource selection occurs at a hierarchy of scales. This has important implications. Concluding that mule deer made or did not make habitat-use choices, based on either of the 2 scales, would be misleading in some cases. As Johnson (1980) implied, mule deer in this study may indeed have chosen winter home ranges based on landscape-scale attributes and once localized into winter home ranges used habitat in a random or mixed fashion, thus illustrating the importance of scale considerations in ungulate resource selection analyses (Apps et al. 2001), which is rarely done (Mysterud and Østbye 1999).

Multivariate analyses indicated that the best predictors of winter range at the home-range scale were elevation combined with solar duration. This is consistent with the work of D'Eon (2001), who similarly found elevation and aspect among the best predictors of mule deer habitat. However, unique to this study, slope gradient and ruggedness (related to slope) were not significant variables at either scale. As well, 2 landscape features (amount of mature forest and edge density) provided a very close 2nd-best model, indicating that these landscape-level features are important winter range characteristics in this case. Indeed, because higher amounts of mature forest are inextricably related to other landscape attributes such as lower amounts of early seral forest and logging, lower road and edge densities, and larger forest patches (D'Eon and Glenn, in press; Fahrig 1997), the amount of mature forest provides a generalized landscape-level surrogate for several landscape features.

GPS Radiotelemetry

To our knowledge, this is among the 1st published reports of long-term ungulate GPS radiotelemetry (but see Nelson et al. [2004]). As such, we wish to offer our insight into this relatively new technology. GPS radiotelemetry is becoming increasing popular because of the obvious advantages of automated tracking of animal movements and will no doubt set new standards for wildlife resource use studies (Rodgers et al. 1996). Indeed, we obtained numbers of locations per animal that were

orders of magnitude larger than what would have been possible in traditional very high frequency (VHF) radiotelemetry. This is especially relevant in mountainous areas where severe winter weather precludes aerial monitoring, and thus obtaining VHF locations, much of the time. Although not increasing population sample sizes (i.e., number of deer), increasing the number of locations per animal (i.e., higher sampling intensity) increases the accuracy of individual home-range estimates and other habitat use parameters (Girard et al. 2002; Otis and White 1999). The much-cited autocorrelation issue (i.e., lack of independence among locations) with radiotelemetry data (and especially GPS data) is not a problem if the analysis technique uses individual animals as the source of replication for testing statistical significance (Aebischer et al. 1993; Alldredge and Ratti 1986), as we did. As well, collar malfunction–one of the largest problems in contemporary GPS radiotelemetry (D'Eon et al. 2002)–appears to be diminishing because only 1 of 6 of the recently improved models in our final year malfunctioned (versus ~50% in previous years), suggesting an improving trend in technical performance of GPS radiocollars.

Despite the advantages to GPS, a large concern persists. Although GPS techniques drastically increase individual sampling intensity, GPS radiocollars remain expensive at about 10 times the cost of a comparable VHF radiocollar, and have much shorter battery life (about one-fourth depending on GPS fix schedule). This could lead to reduced sample sizes (number of animals), and thereby statistical power, on projects with budget limitations, and represents a major trade-off decision for researchers: VHF will increase sample size but decrease individual sampling intensity; GPS will increase individual sampling intensity but decrease sample size. This conundrum must be addressed and based on project objectives. In our case, a power analysis (D'Eon 2002a) illustrated adequate power because of remarkably similar habitat use patterns and winter range fidelity among deer. This might not have been the case if individuals had differed more in habitat use patterns.

Management Recommendations

Aspect, or more directly, solar radiation and its affects on snow accumulation, is clearly an important attribute of mule deer winter range in heavy snow zones. We found solar radiation measured as solar duration to be an effective measure of this phenomenon, and therefore recommend its use. Most importantly, because it is a continuous variable it is easily incorporated into parametric and multivariate statistical techniques and modeling, unlike aspect, which is difficult to incorporate because of its circular nature.

In this landscape, managers can safely identify potential mule deer winter habitat at broad scales (sometimes referred to as "habitat capability") on the basis of 2 biophysical attributes: warm aspects (or high solar duration) and low-elevation sites. Suitable wintering habitat (i.e., suitable at the current time, sometimes referred to as "habitat suitability") on these sites can then be further delineated and managed on the basis of mature forest amounts, especially mature forests dominated by Douglas-fir and ponderosa pine in this population. Amounts of

mature forest can be used as a surrogate for other landscape attributes associated with highly suitable mule deer winter range. As well, an almost total avoidance of cedar–hemlock and spruce–balsam forests means managers can safely remove these sites from winter range management zones in this and similar populations. Aspen–birch was neither avoided nor preferred; however, little can be inferred in this population since this forest type made up <1% of forests in the study area.

Although logging roads were not a significant factor at the home-range scale, deer tended to avoid them within winter ranges. This suggests that although other landscape-level attributes such as amount of mature forest are more important, high road densities could negatively affect wintering mule deer and should be minimized within winter ranges. Interestingly, edges were neither selected nor avoided at the home-range scale, again suggesting that other attributes such as amount of mature forest are more important. However, edges tended to be used within winter home ranges, and logged sites were used randomly at this scale, suggesting that logged sites and the associated edge are not detrimental to wintering mule deer provided enough mature forest exists—again underlining the importance of mature forest amount at the home-range scale.

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