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Fuzzy structure and spatial dynamics of a declining woodland caribou population

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Abstract Examining both spatial and temporal variation can provide insights into population limiting factors. We investigated the relative spatial and temporal changes in range use and mortality within the Red Wine Mountains caribou herd, a population that declined by approximately 75% from the 1980s to the 1990s. To extract the spatial structure of the population, we applied fuzzy cluster analysis, a method which assigns graded group membership, to space use of radio-tracked adult females, and compared these results to a hard classification based on

sums-of-squares agglomerative clustering. Both approaches revealed four subpopulations. Based on the subpopulation assignments, we apportioned the number of animals, radio-days, calving events and mortalities across subpopulations before and after the decline. The results indicated that, as the herd declined, subpopulations were disproportionately affected. In general, subpopulations with the greatest range overlap with migratory caribou from the George River herd experienced comparative reductions in activity and increased mortality. The subpopulation with the least overlap exhibited the converse pattern. The infra-population imbalances were more pronounced when hard clustering was employed. Our results reiterate that refugia from other ungulates may be important in the persistence of taiga-dwelling caribou. We propose that changes across time and space are valuable assays of localised demographic change, especially where individuals exhibit spatial hyperdispersion and site fidelity.

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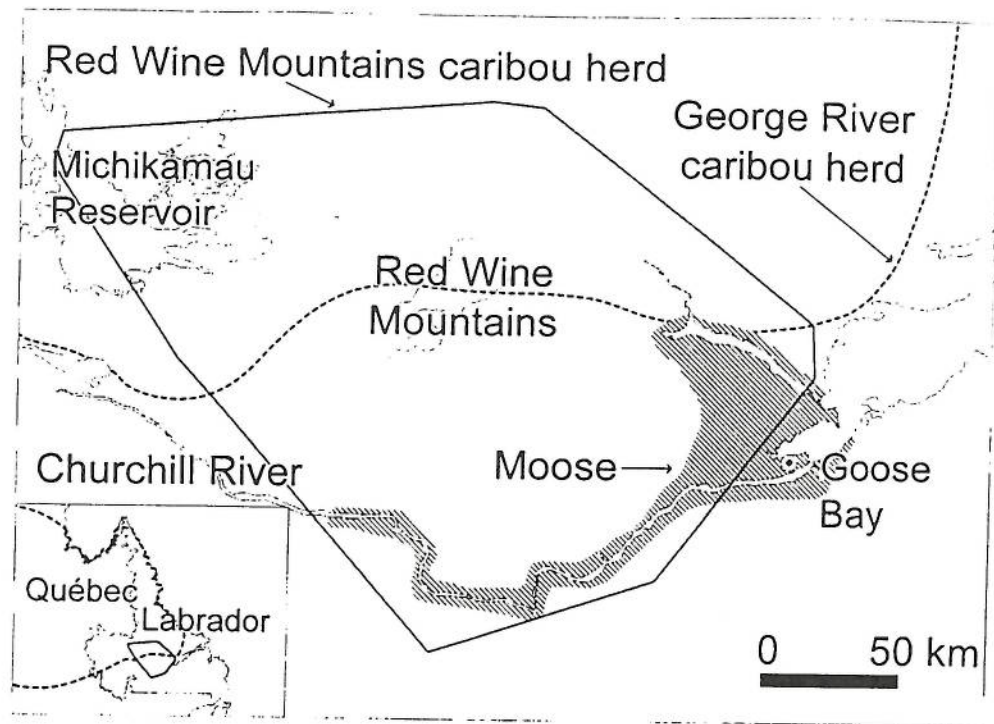
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Introduction

Simultaneous consideration of both spatial and temporal variation is increasing in population ecology (e.g. Underwood 1996; Ranta et al. 1997; Coulson et al. 1999). Demographic studies are, nevertheless, dependent on the identification of discrete groups of organisms. One criterion for distinguishing populations is spatial contiguity (Allen and Hoekstra 1992; Wells and Richmond 1995). For example, by applying cluster analysis to the locations of satellite-tracked polar bears (*Ursus maritimus*), Bethke et al. (1996) defined natural groups for management and study. Especially for such mobile species, including caribou (*Rangifer tarandus*), populations might often be envisaged as semi-permeable entities with somewhat fluid membership. This implies that graded, rather than "hard", partitions may be appropriate for de-

Fig. 1 Study area for the Red Wine Mountains caribou herd, Labrador, Canada, 1982–1997. Areas of high moose density (shaded region) and the approximate range limits of the George River caribou herd (dashed lines) are illustrated



noting the group affiliations of individuals. Such uncertainty can be handled with fuzzy clustering, a method that assigns objects to classes with partial, rather than absolute, membership (Marsili-Libelli 1989; Equihua 1990; Kaufman and Rousseeuw 1990; Podani 1994).

Fuzzy clustering may be especially suitable for defining the population structure of forest-dwelling caribou, the sedentary ecotype of *Rangifer* (Bergerud 1988, 1996). We expected that the defining features of this ecotype – the site tenacity of adult females (Brown and Theberge 1985; Schaefer et al., in press) and their spatial overdispersion at calving and post-calving time (Brown et al. 1986; Cumming and Beange 1987; Bergerud et al. 1990) – would impart noticeable population spatial structure. On the other hand, the tendency for sedentary caribou to form a near-continuum across a region of favourable calving sites (Bergerud 1996) implies continuous spatial variation and graded group identity. Both attributes are amenable to fuzzy classification. The method generalises traditional cluster analysis by assigning partial, rather than absolute, coefficients of group membership to each case. Although vagueness may abound in natural populations, fuzzy classification has rarely been applied to reveal their spatial structure (Hall 1997).

Here, we tie together demography and geography to examine the dynamics of a declining population of woodland caribou (*R. t. caribou*), the Red Wine Mountains herd of central Labrador (Fig. 1). The herd declined from some 610–751 animals during the 1980s to an estimated 151 animals in 1997, a decrease associated with lower rates of recruitment and survival of adult females, and emigration to the migratory George River caribou herd (Schaefer et al. 1999). The decline was consistent

with the hypothesis that more alternative ungulate prey, like moose (*Alces alces*), might lead to heightened incidental predation by wolves (*Canis lupus*; Bergerud and Elliot 1986; Seip 1992; Bergerud 1996; Rettie and Messier 1998). Indeed, Red Wine Mountains caribou experienced increases in abundance of both moose and migratory caribou from the George River herd (Schaefer et al. 1999). Because these ungulates occupied distinct portions of the study area (Fig. 1), we surmised that the decline of Red Wine Mountains caribou might be localised, with groups unequally affected by the decline.

In this study, a complement to our whole-population approach (Schaefer et al. 1999), we incorporated space in an attempt “to get a step closer to ecological causality” (Caughley et al. 1988). We began by delineating subpopulations, i.e. subsets of a spatially structured population (Thomas and Kunin 1999), based on the spatial affiliations among individuals (Wells and Richmond 1995). We applied fuzzy clustering to radio-locations of adult females, then used the resultant fuzzy group designations to apportion animals, radio-days, calving events, and mortalities amongst subpopulations. The result allowed us to analyse the relative changes among subpopulations during the periods of comparative stability (1980s) and decline (1990s), which we label as “early” and “late” periods, respectively. To gauge the suitability of the fuzzy approach, we compared these results to those from traditional hard clustering, Ward’s method, a commonly used procedure in ecological classification (Ludwig and Reynolds 1988).

Materials and methods

Study area

The Red Wine Mountains caribou population occupied approximately 25,000 km² of central Labrador (Fig. 1). A prominent feature of the area was the Red Wine Mountains, mostly tundra, which were surrounded by taiga dominated by spruce (*Picea mariana*, *P. glauca*) and mixed with aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) in river valleys. The herd shared parts of its range with two other ungulate populations, moose and migratory caribou from the George River herd (Fig. 1). During the study, moose densities were increasing and highest (approximately 0.2 animals km⁻²) in the eastern and southern portions of the study area, near Goose Bay and the Churchill River (Chubbs and Schaefer 1997). The George River herd, at 600,000–800,000 animals, was the largest caribou population in the world (Couturier et al. 1996). Commencing in 1984, incursions of large but undetermined numbers of George River caribou were frequent in the northern segments of the study area from mid-autumn to spring (Fig. 1).

Data collection

We collected observations from May 1982 to October 1988 (the "early" period), and March 1993 to August 1997 (the "late" period). We deployed radio-collars as spatially evenly as possible by searching for animals throughout the study area. Nonetheless, some differences in spatial deployment of collars occurred. In particular, during the late period, no collars were deployed in the extreme western portion of the study area, west of the Red Wine Mountains. A systematic aerial survey in January 1997, however, indicated no caribou or their sign in this area (J.A. Schaefer, unpublished work), suggesting that this change in live-capture distribution was a consequence, not a cause, of observed changes in space use by the herd.

For the live capture of caribou, we administered chemical immobilising agents, by firing darts from a helicopter, to adult (≥ 1 -year-old) females, haphazardly selected within groups. We used both VHF transmitters (Telonics, Mesa, Ariz., USA or Lotek Engineering, Newmarket, Ontario, Canada) with mortality sensors and satellite-tracked (Service Argos, Landover, Md., USA) platform terminal transmitters (PTTs; Telonics, Mesa, Ariz., USA) with 1-h and 24-h activity sensors. We carried out VHF aerial reconnaissance at approximately 1-month intervals during the early period, and approximately weekly during the late period. PTTs during the early period operated on a 1-day transmission cycle for 8 months; PTTs during the late period operated on a 4-day transmission cycle for 2 years. We replaced radio-collars prior to battery exhaustion and attempted to maintain at least 12 active collars. We amassed 4,204 locations and 37,431 radio-days from 48 females during the early period, and 3,715 locations and 18,125 radio-days from 36 females during the late period. Each animal was tracked for a minimum of 90 days.

We determined parturition in early to mid-June in 9 years (i.e. 1982–1984, 1987, 1988, and 1994–1997) by helicopter. We assumed that a calf, if present, was visible at heel of its dam. We collected totals of 63 calving locations from 38 females during the early period, and 29 locations from 20 females during the late period, including up to three observations of parturition per female.

We investigated mortalities based on a lack of activity and movement conveyed in collar transmissions (Schaefer et al. 1999). Date of death was inferred from the cessation of activity and movement, and condition of the carcass in the field. We inferred predation as cause of death where the carcass was disarticulated and large bones crushed, or, where only the radio-collar was found, where blood or tooth marks were present. We documented 22 deaths during the early period, and 17 deaths during the late period.

Data analyses

For the copious satellite telemetry data, we selected the animal location during each day of data transmission based on the best quali-

ty class (NQ) as provided by Service Argos, and discarded locations with $NQ < 1$ due to their inherent imprecision (Keating et al. 1991). We applied fuzzy *c*-means clustering (Bezdek et al. 1984; Odeh et al. 1992) to identify subpopulations, following the general approach for population delineation of Bethke et al. (1996). First, we mapped radio-telemetry locations in a flat projection and converted the points to Universal Transverse Mercator (UTM) coordinates in MapInfo (MapInfo Corp., Troy, N.Y., USA). Second, we computed the median easting and northing for each animal. As noted by Bethke et al. (1996), the median is a measure of central tendency that is less influenced by outliers. Third, we computed group membership coefficients for each animal (Minasny and McBratney 1999, <http://www.usyd.edu.au/su/agric/acpa>) based on Euclidean distances among the median locations of individuals.

For fuzzy classification, one must specify the weighting exponent (*m*), which governs the fuzziness of the membership assignments (Bezdek et al. 1984). At $m=1$, the algorithm is identical to a "hard" classification; as *m* increases, the delineations between clusters become more blurred. We set $m=2.0$ to produce a moderately fuzzy classification (Bezdek et al. 1984). We used the fuzziness performance index, *F'*, and the normalised classification entropy, *H'* (Odeh et al. 1992), to indicate an appropriate number of groups from the classification. Minimum values of *F'* and *H'*, plotted against the number of clusters, signify the number of clusters where the information about data substructure is maximised (Odeh et al. 1992). Repeating the analysis at other values of *m* provided qualitatively consistent results (i.e., 4 clusters) for $1.5 \leq m \leq 2.5$.

To compare these fuzzy classes to a crisp classification, we subjected the same matrix of Euclidean distances to sums-of-squares agglomerative clustering (Ward's method), based on the minimisation of within-cluster, versus between-cluster, variance (Ludwig and Reynolds 1988). Hard clustering was performed with STATISTICA (StatSoft, Tulsa, Okla., USA). We recognised an appropriate number of clusters by a sudden rise in the linkage distance when clusters were joined.

To examine the spatiotemporal dynamics among subpopulations, we used the fuzzy membership coefficients for each animal, which sum to 1 over all groups (Equihua 1990; Kaufman and Rousseeuw 1990; Podani 1994), to apportion the number of animals, radio-days, calving events, and mortalities amongst the subpopulations. We computed a relative mortality rate for each subpopulation as the number of mortalities per 1000 radio-days. We treated cases of lost VHF signals by ending the radio-day tally and not including such observations as mortality. We repeated this accounting procedure based on the all-or-nothing memberships from the hard classification.

To visualise the resultant subpopulations in space, we assigned each animal to the group where its fuzzy membership coefficient was highest. We used the program Range Manager (Data Solutions, St. John's, Newfoundland, Canada) to construct individual 60% harmonic mean home ranges (White and Garrott 1990) for each individual to project the areas of intense range use of each subpopulation.

We examined variation in home range size between periods. Because of the different numbers of locations for each animal, we computed unweighted Jennrich-Turner 95% ellipses, a method insensitive to the number of locations per individual (White and Garrott 1990). For the analysis, we retained only those animals having at least 30 locations for at least 1 year, which provided sample sizes of 14 and 11 animals in the early and late periods, respectively. We transformed the data into UTM coordinates and applied the algorithm in SAS (SAS Institute, Cary, N.C., USA) from White and Garrott (1990).

Results

Clustering revealed that the Red Wine Mountains herd could be decomposed into four subpopulations. For the fuzzy classification, *F'* and *H'* both attained minima at the four clusters (Fig. 2) indicating the most efficient

classification at that number of groups. Similarly, the linkage distance from the hard classification, using Ward's method, indicated an appreciable rise at the four-cluster level, although there was some evidence for re-recognising two or three clusters (Fig. 2).

The differences among animals in the frequency and extent of radio-telemetry observations potentially affected our subpopulation designations. To probe for potential biases, we conducted tests based on the maximum fuzzy

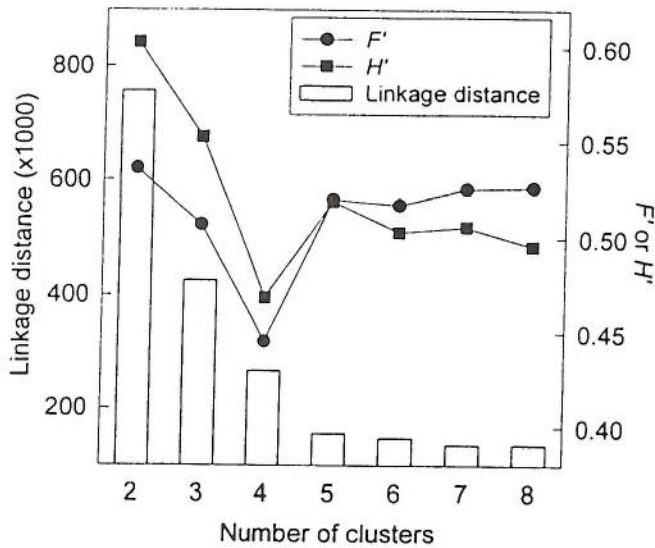
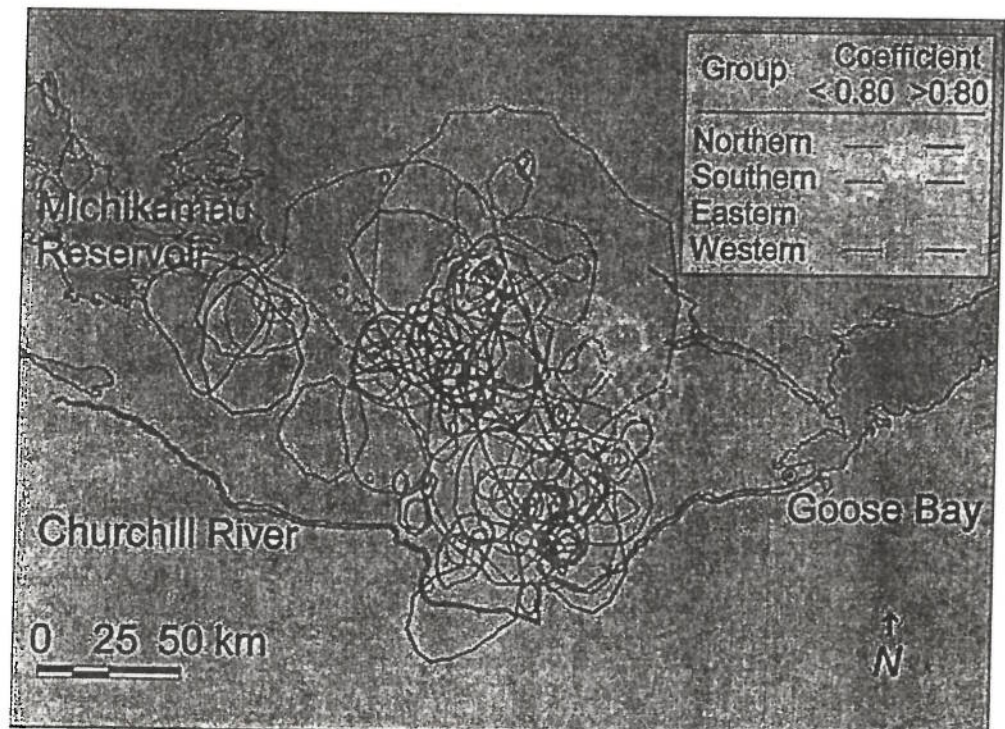


Fig. 2 Indicators of the appropriate numbers of clusters from Ward's method (i.e. linkage distance) and fuzzy clustering (i.e. fuzziness performance index, F' , and the normalised classification entropy, H')

Fig. 3 Subpopulations of the Red Wine Mountains caribou herd based on fuzzy classification of space use by adult females. Each polygon represents the 60% harmonic mean of home range for an adult female. Animals with high membership coefficients (>0.80) are denoted by solid lines; those with lower membership coefficients (<0.80) are indicated by dashed lines



group designations of individuals. First, because satellite and VHF collars differed greatly in the intervals between successive relocations, we carried out chi-square tests of independence on the frequency matrix of collar type carried by an animal (satellite or VHF) versus its subpopulation designation. There was no significant interaction in either the early ($\chi^2=3.54, df=3, P>0.25$) or late period ($\chi^2=2.90, df=3, P>0.25$). Second, because the duration of radio-tracking varied greatly among animals, we conducted one-way ANOVAs to search for differences among subpopulations in the number of radio-tracking days. The extent of radio-tracking was not significantly different among groups in the early ($F_{3,44}=1.43, P=0.247$) or late period ($F_{3,32}=0.706, P=0.555$). These results suggest no substantial bias due to the frequency or extent of radio-tracking on our conclusions about herd spatial structure.

When individual home ranges were plotted, using both early and late animals, the fuzzy subpopulations occupied partially overlapping areas in the northern, southern, eastern, and western segments of the herd's range (Fig. 3). Uncertainty existed at the group boundaries, especially amongst the northern, southern, and eastern subpopulations where shared use of the Red Wine Mountains was evident. The ambiguity in the data substructures was underscored by the individual fuzzy membership coefficients; maximum values for each animal averaged 0.773 and ranged from 0.394 to 0.997.

We found high concordance between group designations from fuzzy and hard clustering. Based on the maximum fuzzy membership coefficients, most animals were placed in the identical class by the two procedures; entries along the diagonal of the classification matrix made

Table 1 Comparison of fuzzy (fuzzy *c*-means) and hard (Ward's method) clustering of the subpopulation structure of the Red Wine Mountains caribou herd. The subpopulation class for each animal from fuzzy clustering was represented by the group with the largest membership coefficient. Entries represent the numbers of animals. Categories with zero entries are *blank*

Subpopulation class from hard clustering	Subpopulation class from fuzzy clustering			
	Northern	Southern	Eastern	Western
Northern	30	1	1	
Southern		26	2	
Eastern	1		19	
Western				4

Table 2 Relative spatial and temporal changes in the subpopulation dynamics of Red Wine Mountains caribou during early (1982–1988) and late (1993–1997) periods, based on fuzzy (fuzzy *c*-means) and hard (Ward's method) clustering. Proportions are expressed as the fraction of events or animals amongst subpopulations for each period. Mortality rate is the ratio of deaths to 1,000 radio-days

Demographic variable and clustering method	Subpopulation and period							
	Northern		Southern		Eastern		Western	
	Early	Late	Early	Late	Early	Late	Early	Late
Proportion of animals in each subpopulation								
Fuzzy <i>c</i> -means	0.43	0.19	0.22	0.45	0.24	0.32	0.11	0.04
Ward's method	0.54	0.17	0.19	0.53	0.21	0.28	0.06	0.03
Proportion of calving events in each subpopulation								
Fuzzy <i>c</i> -means	0.42	0.21	0.23	0.48	0.24	0.29	0.11	0.02
Ward's method	0.54	0.21	0.21	0.55	0.19	0.24	0.06	0.00
Mortality rate in each subpopulation								
Fuzzy <i>c</i> -means	0.76	1.09	0.72	0.51	0.38	1.49	0.34	2.15
Ward's method	0.85	1.29	0.60	0.46	0.31	1.87	0.00	8.07
Proportion of radio-days in each subpopulation								
Fuzzy <i>c</i> -means	0.38	0.23	0.20	0.49	0.29	0.26	0.13	0.03
Ward's method	0.47	0.21	0.18	0.60	0.26	0.18	0.09	0.01

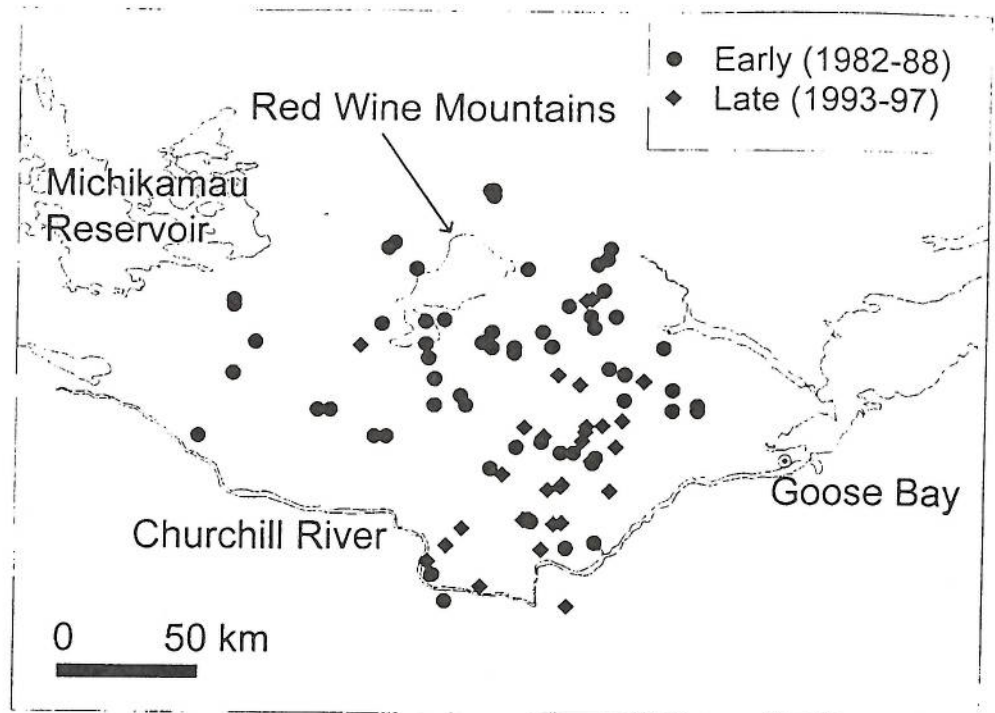
up 94% of cases (Table 1). We found that, in the five instances of discrepancy between the approaches, the animals tended to reside near the interstices of the northern, eastern, or southern fuzzy groups (Fig. 3). The average maximum membership coefficients of these discordant cases ($=0.489$) was much lower than that for the animals classified similarly by the hard and fuzzy approaches ($=0.791$), emphasising the vagueness of subpopulation identities.

The relative changes in demographic variables differed markedly among the four subpopulations as the herd declined (Table 2). The spatio-temporal variations based on fuzzy clustering were less abrupt than those based on hard partitions. For the northern and western subpopulations, there were disproportionate declines in spatial activity, expressed as the proportions of animals, radio-days, and calving events. The southern subpopulation exhibited the converse. In the early period, the southern group made up less than one-quarter of the herd and its activity, but these proportions more than doubled in the late period. For these three subpopulations, these changes corresponded to differences in mortality rate.

Where activity and numbers declined, mortality rates of adult females generally increased; the converse was true as well (Table 2). In the eastern subpopulation, however, the pattern was less clear. The mortality rate increased and relative number of radio-days declined marginally, but its share of the population and calving activity increased from the early to late period. Differences in small-scale dynamics, although qualitatively consistent, were exaggerated when hard clustering was employed (Table 2).

The demographic imbalance among subpopulations was evident as erosion of the northern and western bounds of the calving range (Fig. 4). During the late period, virtually no parturition occurred in the northwestern half of the original calving range of the herd. The extent of calving, determined by a minimum convex polygon around known calving locations, declined concomitantly with population size, from 16,200 km² to 4,000 km² (excluding one outlier from 1993 near the Red Wine Mountains; Fig. 4). There was little change in population density expressed as a function of the calving range, i.e., from 0.046 animals km⁻² in the early period

Fig. 4 Known calving locations of Red Wine Mountains caribou during early (1982–1988) and late (1994–1997) study periods



to 0.038 animals km^{-2} (excluding the outlier) in the late period. The stark, regionalised disappearance of calving activity, apparent by 1993, suggested that the decline had begun prior to the beginning of the late period.

The spatial retraction of the population was not evident at the individual level. Between study periods, adult females did not show significant alteration in home range sizes. Area estimates from 95% elliptical home ranges in the early period ($\bar{x}=8,026\pm 987 \text{ km}^2$; $\pm\text{SE}$) were not statistically distinguishable from those during the late period ($\bar{x}=10,041\pm 1,039 \text{ km}^2$; $t=1.39$, $P=0.177$), indicating that range retraction of the herd was not a product of diminished home range size.

Discussion

The potential for arbitrary delineations of population boundaries has long been recognised (Caughley 1977) but the research implications of setting these bounds are only emerging (Ray and Hastings 1996; Coulson et al. 1999). Space use is valuable in detecting natural “surfaces” between groups (Allen and Hoekstra 1992; Wells and Richmond 1995). Here, two forms of imprecision exist: the uncertainty of where individuals are located in space and the uncertainty of group membership of those individuals. The uncertainty of animal movements has commonly been addressed by analyses of home range, a family of techniques widely-used in animal radio-tracking (White and Garrott 1990). The second source of ambiguity, group identity, has less often been considered. Whereas larger sample sizes might improve the precision of home range estimates, no amount of data will remedy

the vagueness of borderline group identity (Sorensen 1989; McBratney and Odeh 1997; Regan et al. 2000). Such ambiguity is appropriate for fuzzy classification. The technique readily accommodates open populations by relaxing the strict binary approach of traditional cluster analysis (Marsili-Libelli 1989; Equihua 1990). In lieu of all-or-nothing affinities to clusters, fuzzy membership coefficients range between 0 and 1. Although population spatial organization is a central concern to biologists (Thomas and Kunin 1999), the application of fuzzy clustering has been surprisingly rare (Green 1996; Hall 1997).

For woodland caribou, several investigations have revealed a pattern of extensive overlap of space use by individuals at one scale, with segregation at a larger scale (Edmonds 1988; Ouellet et al. 1996; Rettie and Messier 1998). Population organisation (Fig. 3) appears to arise from the behaviour of adult females. Females of the sedentary ecotype tend to display (1) hyperdispersion, the tendency to “space out” especially during calving and post-calving (Cumming and Beange 1987; Bergerud et al. 1990; Bergerud 1996), and (2) site fidelity, the tendency to return or remain in a particular segment of the population range (Brown and Theberge 1985; Schaefer et al., in press). In this way, forest-dwelling caribou may form natural population units (Thomas and Kunin 1999) at several scales (Rettie and Messier 1998), discernible from their patterns of space use.

Interactions across space and time can represent effective means of identifying population limiting factors (e.g. Schroeter et al. 1993; Underwood 1996; Coulson et al. 1999; Eeva and Lehikoinen 2000). In our previous whole-population analysis (Schaefer et al. 1999), we

found the decline of Red Wine Mountains caribou to be associated with reduced adult female survival, lower recruitment, and perhaps emigration to the migratory George River caribou herd. Predation by wolves represented the chief limiting factor during both periods of study (Schaefer et al. 1999). The lack of change in the parturition rate (Schaefer et al. 1999) and the substantial increase in body size of adult females (J.A. Schaefer, unpublished work) tended to discredit nutritional limitations. These observations led us to conclude that incidental predation by wolves, as a result of increased ungulate prey, and egress to the migratory herd represented the principal mechanisms of decline. Our present geographic analysis tends to reinforce these conclusions. Indeed, the demographic imbalance amongst subpopulations (Table 2) indicated detrimental effects most highly coincident with areas of ingress by George River caribou (Fig. 1). Taken together, these results imply that the decline of the Red Wine Mountains herd was linked to the increase in this other ungulate population (Schaefer et al. 1999).

Nevertheless, we advocate some caution with respect to interpretation of the spatial patterns, especially when considered in isolation. Caughley et al. (1988) emphasized that care is warranted because of the appreciable chance of misidentifying the geographic trend. Indeed, for subpopulations of the Red Wine Mountains herd, the negative correlation between declining activity and heightened mortality was not universal (Table 2) and our sample size of four subpopulations was small. In addition, the gregariousness of caribou may have contributed to the contrast in activity amongst subpopulations. However, the general increase in relative mortality rates in those subpopulations that declined (Table 2), and the regionalized disappearance of calving activity (Figure 4), at a time when philopatry is pronounced (Schaefer et al., in press), tend to diminish translocation as the mechanism behind these patterns.

Because measures of range activity will be sensitive to the spatial deployment of collars, per capita measures, like mortality, may serve as more robust indicators of demographic change. Here, fuzzy clustering, in comparison to its crisp counterparts, may provide a more conservative approach. If among-group boundaries are vague, individuals are more likely to be affiliated with several fuzzy groups; measures of population well-being will be parcelled out accordingly. Indeed, the contrasts amongst Red Wine Mountains subpopulations were more pronounced when based on a strict binary classification (Table 2). This implies greater likelihood of mistaken implication (type I error) when demographic units are treated as sharply-defined classes.

For species like caribou, the assessment of environmental effects and their usefulness as indicator species has been regarded as problematic because of their vagility (McLaren et al. 1998; Hilty and Merenlender 2000). At the same time, large mobile mammals may be most vulnerable to human-caused habitat changes due to their vast requirements for space (Harestad and Bunnell 1979;

Bergerud 1988). We propose that spatially structured populations might permit the detection of localised detrimental effects, recognisable as imbalances among groups in measures of population well-being. The approach should be applicable to other species exhibiting philopatry and spatial overdispersion.

The abundance and distribution of caribou are linked (Messier et al. 1988; Bergerud 1996). Retraction or expansion of range may herald a change in population size. Our infra-population analysis, indicating a negative relationship between space use and mortality, supports recent evidence (Hobbs and Mooney 1998; Parmesan et al. 1999) that the range expansion or contraction of species will be manifest as the establishment or elimination of populations. There is increasing recognition of space in the conservation of taiga-dwelling caribou, whose persistence seems to depend on refugia from predation, governed by the distance of caribou to other ungulate prey (Bergerud and Page 1987; Scip 1992; Bergerud 1996; Cumming et al. 1996; Stuart-Smith et al. 1997; Rettie and Messier 1998). Our results are consistent with this conclusion.

Populations may be defined on a number of spatial scales (Allen and Hoekstra 1992; Amarasekare 1994; Coulson et al. 1999). Clustering methods combining both hierarchical and fuzzy approaches might be suitable, therefore, to the delineation of demographic units at several scales, for example, populations and metapopulations. We believe that fuzzy classification, with its capacity to handle imprecision and continuous variation, is an avenue toward maturation of the population concept.

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