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.

Keywords  Demography · Fuzzy clustering · Population structure · Rangifer tarandus · Scale

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-
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 Messeier 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).