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POPULATION SUBSTRUCTURE, LOCAL DENSITY, AND CALF WINTER SURVIVAL IN RED DEER (*CERVUS ELAPHUS*)

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Abstract. Population substructure and the effects of scale have recently received much theoretical attention, but few studies have examined these factors in free-living populations of vertebrates. We used > 200 000 sightings of recognized females recorded over a continuous 20-yr period to explore population substructure and spatial heterogeneity in red deer on the Isle of Rum, Scotland. We used hierarchical cluster analysis to group individuals together by their proximities in space, and we explored the influence of scale, considering scales ranging between the whole population and groups of one or two individuals. Intermediate scales were isolated as being the best at describing calf winter survival, the key factor in determining future population density. The most statistically explanatory scale isolated a population substructure related to vegetation, with higher local densities occurring around herb-rich *Festuca-Agrostis* grassland. Calves at high local density were most likely to die. Patterns of local population density varied between seasons in relation to food availability. High-resolution scales were the best descriptors of calf winter survival in summer; coarser scales were better in winter. In both summer and winter, local population density was more important than total population density in influencing calf winter survival. The effects on calf survival of local population density during the summer interacted significantly with calf sex and the mother's reproductive status. In this study, the technique of grouping animals by their proximity in space was more realistic and informative than discrete spatial divisions of the study area.

Key words: calf winter survival; *Cervus elaphus*; hierarchical cluster analysis; Isle of Rum, Scotland; local population density; red deer; scale; seasonality; total population density.

INTRODUCTION

Biological populations consist of individuals whose movement is limited in space. Consequently, the dynamics of such systems are heterogeneous over a large range of spatial and temporal scales, whether one considers single-species systems (DeJong 1979), competing-species systems (Atkinson and Shorrocks 1981, DeJong 1981, Hanski 1983), predator-prey or host-parasite systems (Crawley 1981, Reeve 1990, Rothman and Darling 1991, Comins et al. 1992), or plant-herbivore systems (Crawley 1983, Strong et al. 1984). Although it has long been recognized that population dynamics should be studied at an appropriate scale (Taylor 1961, O'Neill 1989, Sugihara et al. 1990), and that, in order to discover this scale, data need to be sampled in a hierarchical manner, only in the last few years has finding an optimum scale at which to analyze population dynamics received both empirical (Stirling et al. 1991, Hails and Crawley 1992) and theoretical attention (Rand and Wilson 1995). For example, Hails and Crawley (1992) analyzed mortality of *Andricus quercuscalicis* (a gall-forming wasp) at spatial scales

between individual male turkey oak (*Quercus cerris*) inflorescences and adult trees. For sessile individuals, such as galls, that are distributed in a habitat that is easy to divide discretely (tree, branch, twig, shoot, bud, inflorescence), the choice of scales to explore is straightforward. When considering a population of mobile individuals, it is harder to define obvious scales. Rand and Wilson (1995) approached this problem by defining a system consisting of a lattice of discrete sites, and analyzed scale by superimposing windows of various sizes onto the system. Binary distributions (present or absent) defined whether a square contained a resource, a prey, or a predator; each square could contain only one of each. In a natural system, it is not obvious how to divide space in this way: how is one resource defined?

The exploration of spatial scale requires information concerning the positions of individuals. Can mean positions be used? Red deer (*Cervus elaphus*) are mobile and have overlapping home ranges (Clutton-Brock et al. 1982a). A measure of mean spatial position could place together individuals that never, or rarely, associate. For example, two or more groups of animals could utilize similar areas but avoid each other. In such a case, their mean geographic locations would be similar even though the animals exist as distinct separate

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groups. However, competition between two such groups could be important. To explore the effects of scale in a species with such a social system requires a more dynamic measure of scale than geographic subdivisions of an area. As the scale being considered is altered, such a measure should be capable of both grouping and distinguishing animals that utilize similar areas, but rarely associate. We use hierarchical cluster analysis to group individuals by their proximity to one another. Scale is varied by altering the conditions under which individuals are considered to be grouped (Gordon 1981).

The red deer population on the Isle of Rum, Scotland, consists of loose matrilineal groups with overlapping home ranges (Clutton-Brock et al. 1982a, Albon et al. 1992) aggregated about preferred grazing sites (herb-rich *Agrostis-Festuca* grassland). As population size has trebled during the course of the study, fecundity and juvenile survival have declined (Clutton-Brock et al. 1985a, 1987a, Clutton-Brock and Albon 1989). This density dependence occurs when the entire study population is investigated, but such an approach does not consider whether density dependence is concordant across spatial scales in relation to biotic factors. Earlier research has shown significant differences in calf survival among four spatially distinct regions loosely based on the biotic environment (Guinness et al. 1978), as well as a significant negative relationship between fitness of progeny and the number of relatives in a female's matriline (Clutton-Brock and Albon 1985, Clutton-Brock et al. 1988). In particular, there is evidence that competition, specifically between related, rather than unrelated, females using a particular area, is important at locally high population densities (Clutton-Brock et al. 1982b). The aim of this study is to isolate scales that best define the population substructure at which to analyze calf winter mortality, the key factor regulating the red deer population (Clutton-Brock et al. 1985a). Although the choice of scale is known to be important for interpreting population dynamics, this has not been explored in a population of recognized, mobile individuals, with a social system consisting of distinct parties sharing resources patchily distributed in space. The best scales should tell us what biotic factors are important influences on population dynamics, and how the population is structured. Both of these questions are crucial to understanding ecological systems.

METHODS

Study area and animals

All data were collected in the North Block, Isle of Rum, Scotland (57°01' N, 06°17' W, NM-402996) between 1974 and 1994. Usually, the population has been considered as one unit, although there is evidence that fitness varies spatially across vegetation communities, largely associated with topographical and biotic factors

(Guinness et al. 1978, Iason et al. 1986). Guinness et al. (1978) defined four discrete areas: Upper Kilmory Glen, Lower Kilmory Glen, Intermediate (the Kilmory/Shamhnan Insir watershed), and Shamhnan Insir.

The study area consists of areas of high-quality, herb-rich *Agrostis-Festuca* grassland and poorer quality *Calluna*, *Trichoforum*, *Molina* heath, and *Molinia* grasslands. The darkest areas in Fig. 1a show areas of *Agrostis-Festuca* grassland. The high density of deer has led to little, if any, succession in the plant community (Clutton-Brock et al. 1982a), and the vegetation survey of Ball (1974) is still accurate (T. Coulson, *personal observation*).

The deer year ran from 15 May to 14 May because the calving season began in late May. This study used data on calves and females ≥ 1 -yr old. Stags were not included in the study because their ranging behavior differs from that of females and calves (Clutton-Brock et al. 1985a, 1987c). Clutton-Brock et al. (1987c) showed that segregation between the sexes was very pronounced on short grasslands, and that it increased with density. This difference fits the hypothesis that stags are less tolerant of low plant biomass than are hinds. Because previous work by Clutton-Brock et al. (1982a) has shown large behavioral and ecological differences between the two sexes, we have concentrated on adult female and calf distribution only.

The census data consisted of grid references on an ordnance survey map, making positions accurate to 100 m for each animal seen on each census day. There was a mean of 47 ± 2.6 censuses/yr (mean ± 1 SD), with a total of 207 715 deer sightings and 30 ± 3.9 sightings per animal per year. Age, sex, and reproductive status in the previous year were known for all animals included in the study. Reproductive status was treated as a factor with five levels of females: first breeder (had not bred previously); true yield (did not breed in the previous year); summer yield (bred but the calf died in summer); winter yield (bred but the calf died in winter); milk hind (successfully reared a calf to one year).

Hierarchical cluster analysis (HCA)

The population substructure was analyzed using hierarchical cluster analysis (Gordon 1981), a technique in which animals are grouped together by their proximity in space. For an individual to be included in the analysis, we set a criterion that it must have been sighted on five or more census days per year. A two-dimensional dissimilarity matrix was constructed for each year. These matrices contained the mean distance between all pairs of individuals that were seen at least once on the same day. Thus, a cell ij in a dissimilarity matrix contained:

$$\frac{\sum_{s=1}^n \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}}{n},$$

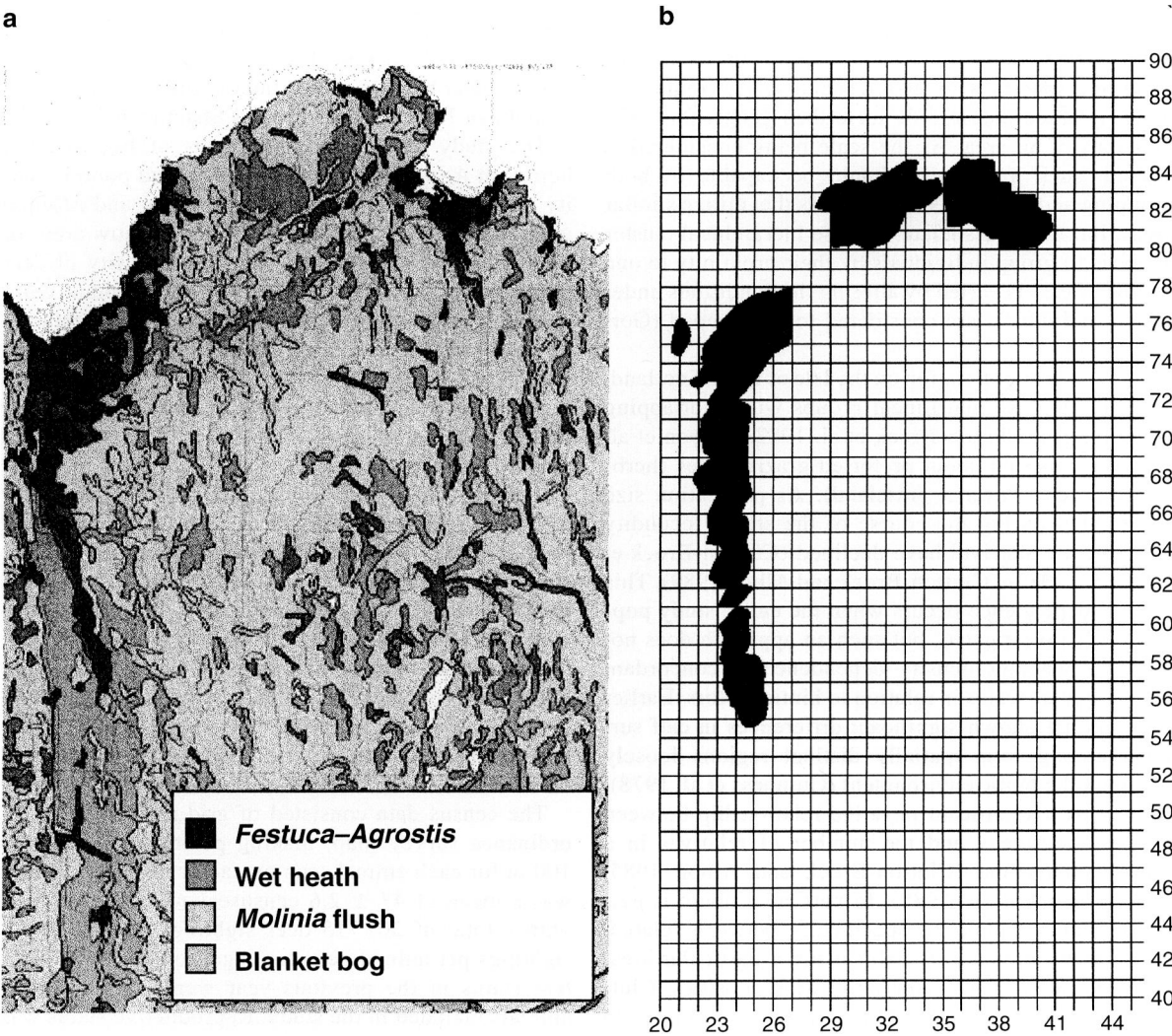


FIG. 1. (a) The distribution of herb-rich *Agrostis-Festuca* grassland through the Isle of Rum study area (darkest shading). (b) Black grid squares contain 95% of all red deer sightings for census data from 1971 to 1993. Grid squares are 100 × 100 m.

where n was the number of census days when individuals i and j were both seen, and x and y are census coordinates.

Cluster analyses on raw distance data can lead to spurious results. Variation in small observed distances between individuals can have a disproportionately strong effect on the results in relation to variation in larger distances. Nostril fly (*Cephenemyia auribablis*) activity is one example of how variation between small dyads can arise in the deer population. During the summer, individual deer are often seen to suddenly move 50–100 m in response to biting flies. Consequently, we transformed the dissimilarity matrix to a relative similarity matrix where

$$\text{similarity} = 1 - \left(\frac{\text{dissimilarity}}{\text{maximum dissimilarity}} \right)^2.$$

Hierarchical cluster analysis is best considered in

geometrical terms, with the q individuals represented by points in space. Initially, each individual is considered as one cluster. The first step combines the two closest individuals together, forming a larger cluster. A series of similar steps repeatedly fuses the two closest clusters. The final step leads to the population being represented by one cluster. The formation of clusters is dependent on how “closest” is defined in various algorithms. We used average link clustering, which uses the mean distance between all members of one cluster with all members of another. This method was chosen because it is unlikely to produce inversions (incorrect combining of clusters that can occur if linking is dependent on cluster centroids; Morgan and Ray 1995). One other danger that can occur with hierarchical cluster analysis is nonuniqueness (Morgan and Ray 1995). This occurs when the distances between two or more pairs of clusters are equal. In such a case,

it is not obvious which two clusters should be linked first. Because we used data from many censuses and because individuals had to be seen at least five times to be included in the analysis, nonuniqueness was never likely to be a problem in this data set. Of 1000 randomly selected clusters, all dissimilarities with closest clusters were unique, suggesting that nonuniqueness was not a problem.

Results of cluster analysis can be displayed in a dendrogram, with a scalar representing the range of distances needed to fuse all clusters together. A dendrogram, in itself, does not provide a classification of scale; however, the dendrogram can be cut at an arbitrary level of scale. Any division of the dendrogram can be described by the value of the linear scalar. The value of this scalar is set at 100 for individual animals, and decreases as clusters are fused together. Values close to 100 define a fine scale, whereas lower numbers describe a coarse scale. The scalar value, in itself, is of no biological importance other than as a pointer to the number of individuals within each cluster, or to the number of clusters into which the population is subdivided at different scales. The scalar value can be transformed back into distances, using both the maximum observed dissimilarity in any one year and the algorithm used to calculate similarities. In this paper, we refer to scalar values and describe summary statistics of the population structure at that scale (e.g., the mean number of clusters and standard deviation, and the mean number of individuals per cluster and standard deviation). Previous research from the study has defined "groups" and "parties" (Clutton-Brock et al. 1982a). To avoid confusion, we use the term "local density" to describe the number of individuals in each cluster as the population is subdivided. Although we do not give values of individuals per square meter, local density is an appropriate term, because HCA forms clusters using the proximity of individuals to one another. The term "group identity" refers to an arbitrary identity given to a group in any one year. One potential problem of using dissimilarities to compare scale across years is that the maximum dissimilarity could vary between years. This would lead to the same scalar value representing different scales over time. We analyzed maximum dissimilarities between years to check that this effect was not occurring.

Albon et al. (1992) showed that, in the early part of the study (1974–1983), spacing behavior of female red deer changed as density increased. As spacing behavior varied through the course of the study, we divided the data in three different ways: (1) lumping all years together; (2) dividing the data into two segments, 1974–1983 and 1984–1993; and (3) dividing the data into summer and winter associations (April and October excluded). Summer was defined as May to September, winter as November to March. By exploring these different combinations, we examined how our results were

affected by density-dependent changes in spacing behavior.

Scale and winter calf survival

Of 1129 calves entering their first winter between 1974 and 1993, 69% survived. Winter calf survival was described as a binary response variable, with 0 representing animals that died between 1 October of the birth year and 15 May of the following year, and 1 describing those that survived. We used a logistic regression model to test for density dependence (Cox and Snell 1989). We specifically considered whether or not the proportion of calves surviving was a function of local density and other variables, using scales that ranged from groups of one or two individuals to the entire population. The inclusion of terms (cluster size, population density, sex, mother's age, mother's reproductive status) within these models was based on tests of reduction in the residual deviance, where the reduction in deviance is distributed approximately as χ^2 , with degrees of freedom equal to the additional number of parameters fitted (McCullagh and Nelder 1983). Deviance is a measure of goodness-of-fit of a model and is the logarithm of the ratio of two likelihoods. The proportion of calves that died per combination of terms included in the model was linearized by the logit function, a logarithmic transformation of the odds ratio $\ln(p/(1-p))$, and the maximum likelihood estimates obtained for the density-dependent parameters (Crawley 1993). The deviances explained by the inclusion of local density at different scales were then compared. The scale at which the most deviance was explained was regarded as the best scale.

Changes in deviance only show how models compare to one another, not whether a particular model is suitable for the data. We examined nonlinearity, the effect of outliers, and a nonrandom distribution of residuals to ensure that data did not need to be transformed. The model was considered suitable if 95% of standardized residuals were between 1.96 and -1.96 and the plot of standardized residuals against fitted values showed no pattern. To compare two models when one was a subset of another, we tested for a significant difference between deviance explained by the two models, with degrees of freedom equal to the difference in the number of degrees of freedom. Because the explained deviance approximately follows a χ^2 distribution, we quote the χ^2 statistic. If there was no significant difference between the two models, the model with the least number of parameters was considered better. If both models had equal degrees of freedom, the model that explained the most deviance was selected. Because the female population size of the entire study area was known to affect winter calf survival (Clutton-Brock and Albon 1989), it was included in analyses. Spacing behavior varied between summer and winter (Clutton-Brock et al. 1982a), so we also explored the effects of season. Sex of the calf and reproductive status of the mother,

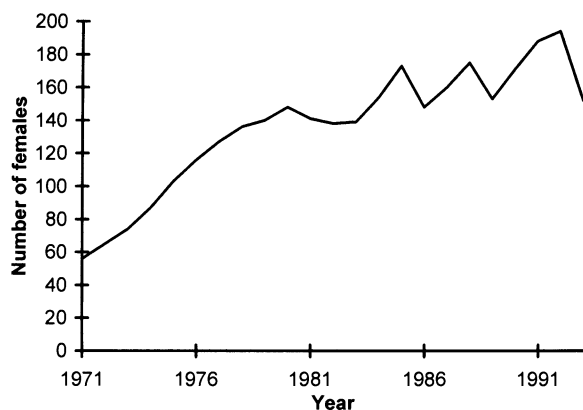


FIG. 2. Number of females (≥ 1 -yr old) over time. From 1974 to 1983, the population increased, and it has since been fluctuating around 167 ± 16 animals (mean ± 1 SD).

factors known to influence calf winter survival, were also incorporated in the analysis. Some females appeared in the data over several years, which would lead to problems of nonindependence if the mother's identity had a significant effect on calf survival. We checked for nonindependence within the data by fitting the identity of the mother as a factor.

Comparing discrete and continuous space

The spatial dynamics of the population previously had been considered by splitting the study area into four discrete geographical areas (Guinness et al. 1978). To show that these divisions were, in effect, arbitrary, we ran Monte Carlo simulations by randomly dividing the study area into four regions. This was done by randomly generating three straight lines that transected the study area. Because the mean positions of animals within the study area occurred in a rough arc (Fig. 1b), lines were not allowed to cross within this arc. Individuals were assigned to areas by their mean x - y position, and area was fitted as a factor to models of calf winter survival. This was repeated 1000 times.

RESULTS

Effects of total population density

Population density, measured as the total number of females ≥ 1 yr old (Fig. 2), significantly affected calf winter survival (all years: $\chi^2 = 79$, $df = 1$, $P < 0.001$; early years: $\chi^2 = 23$, $df = 1$, $P < 0.01$; late years: $\chi^2 = 102$, $df = 1$, $P < 0.001$). These χ^2 values equate to 5.7%, 2.1%, and 13.3% of the total deviance explained, respectively. Thus, density dependence was stronger in late years than in early years.

Dividing the population discretely

The historical division of the study area resulted in significant differences in calf winter survival among the four areas ($\chi^2 = 84$, $df = 3$, $P < 0.01$). However, because matriline fission has occurred, the boundaries

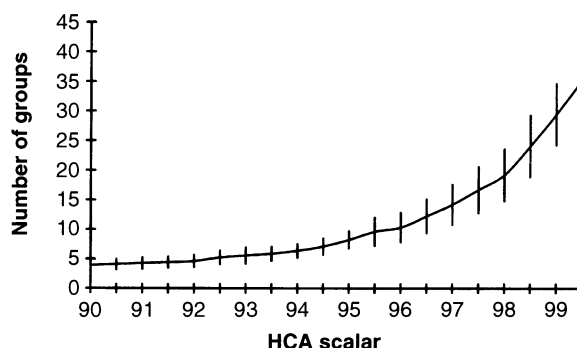


FIG. 3. The mean number of cluster (deer groups) at different hierarchical cluster analysis (HCA) scalars. Means are across all 20 years, and the error bars represent standard deviations.

between these areas have become blurred (Albon et al. 1992). This was shown by the fact that 25% of 1000 random divisions of the study area into four discrete regions explained more of the total deviance than did the historical division.

HCA isolated discrete groups of individuals, with more groups being formed at finer scales (Fig. 3). Group ranges can overlap, so it is not possible to assign groups to discrete space. Therefore, not surprisingly, fitting group identity as a factor had no significant effect on calf winter survival, regardless of scale (at the most descriptive scale for group identity, $\chi^2 = 1.5$, $df = 1$, $P > 0.05$). However, a regression of a group's mean y position against the number of individuals within it was highly significant ($t = 40.90$, $df = 1$), with larger groups more likely to be found in the north of the study area. Residuals did not appear to be random in this regression: all large groups were found in the north of the study area and smaller groups occurred throughout the study area.

Vegetation community

Between 1984 and 1993, 72% of all red deer sightings occurred on *Agrostis-Festuca* grassland (Fig. 1). Seasonal differences showed that sightings on *Agrostis-Festuca* grassland were more likely in summer (78%) than in winter (65%). This result is similar to that of Clutton-Brock et al. (1982a, 1987c) showing that *Agrostis-Festuca* grassland was selected more than other vegetation types for grazing, and that there were seasonal differences, *Agrostis-Festuca* grassland being used more heavily in summer than winter.

Local density: the number of individuals associating together

Variation in maximum dissimilarities between years was negligible, $\approx 3\%$ of the mean maximum dissimilarity over all years. This indicates that identical scalar values between years represent the same scale. Some scales were significantly better at describing calf winter survival than was total population density. Population

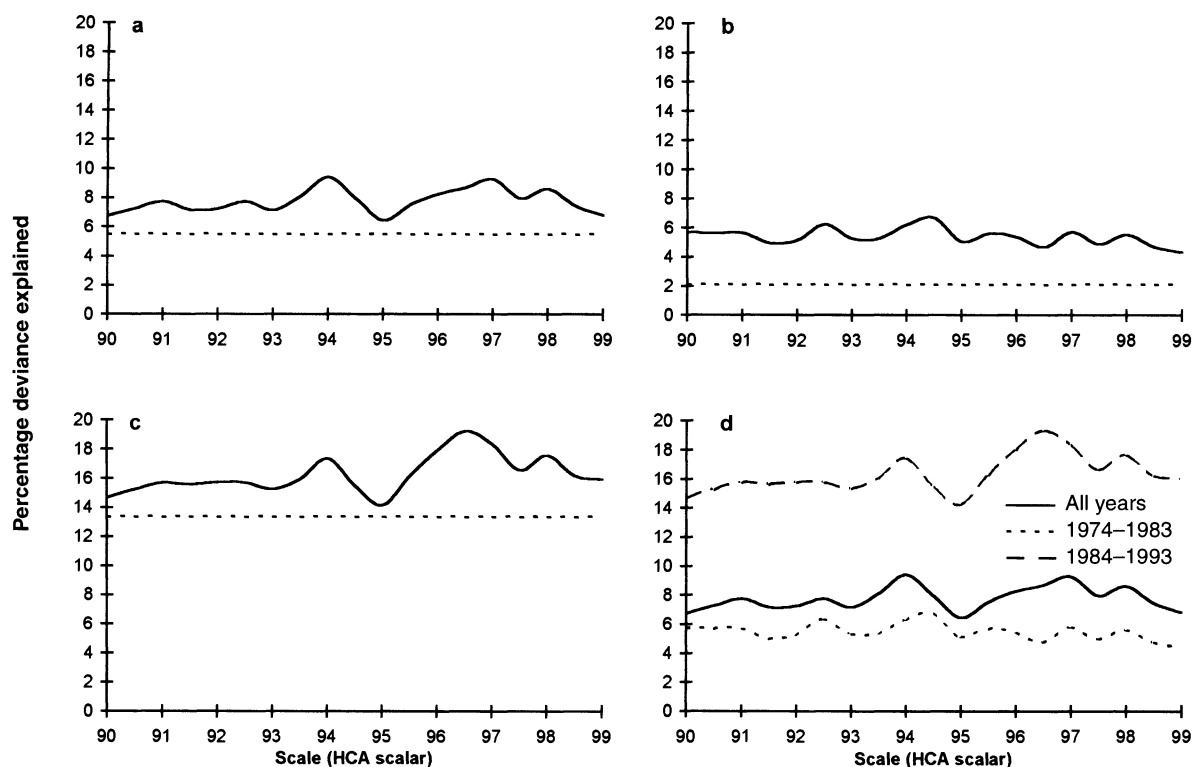


FIG. 4. Percentage deviance explained at different scales if the number of individuals within a group is considered for (a) all years combined, (b) 1974–1983, and (c) 1984–1993. In (a), (b), and (c), the dotted lines represent the percentage deviance explained if the study area population is fitted alone; (d) is a combination of (a), (b), and (c).

density explained 5.7% of the total deviance. Inclusion of local population density at the best scale (HCA scalar value 94) explained 10%, whereas population density and local population density at the worst scale (HCA scalar value 95) explained only 7.7% of the total deviance. If the data are divided between early and late years, the most descriptive scale differs (HCA scalar values 94 and 96.5, respectively). Fig. 4a–d shows the explanatory power of a range of scales in explaining

calf winter survival for all divisions of the data. In the early years, no scale explained significantly more deviance than any other (maximum change in $\chi^2 = 1.7$, $df = 1$). Consequently, we now concentrate on later years when the population was fluctuating close to its presumed carrying capacity.

In additive models in which total population density was fitted first, followed by local population density, some scales were significantly better at describing calf winter survival than others. The worst scale was little better than total population density alone ($\chi^2 = 4.8$, $df = 1$, $P < 0.05$), whereas the best scale was significantly better ($\chi^2 = 46$, $df = 1$, $P < 0.001$). The maximum percentage deviance explained by local population density was at HCA scalar value 96.5. Figure 5 shows the relationship between HCA scalar and distance at which the population was considered divided. A scalar value of 96.5 corresponds to a distance of 964 m (interannual variation 834–1071 m). Across the ten years, this divided the population into 10–12 clusters (10.9 ± 0.7 clusters, mean ± 1 SD). Figure 6 shows the frequency distribution of sizes of these groups. At this scale, calves in large groups were significantly more likely to die during the winter than were those in smaller ones ($\chi^2 = 67$, $df = 1$, $P < 0.001$; Fig. 7a). If a model was fitted to include total population density and local population density, both terms were significant ($\chi^2 = 102$

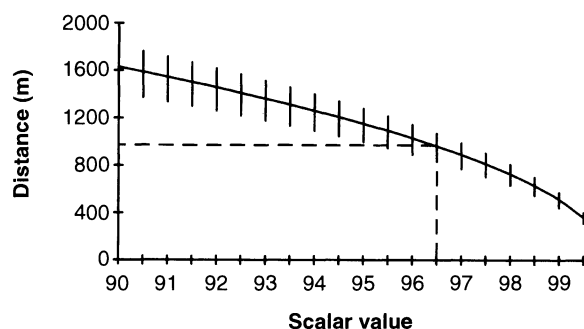


FIG. 5. The relationship between HCA scalar group and the scale in meters at which deer clusters are formed. Clusters fuse at a scalar value, but clusters can overlap in the space they use. The error bars represent the range of distances at which clusters were formed over time. This is due to variation in the maximum dissimilarity between years.

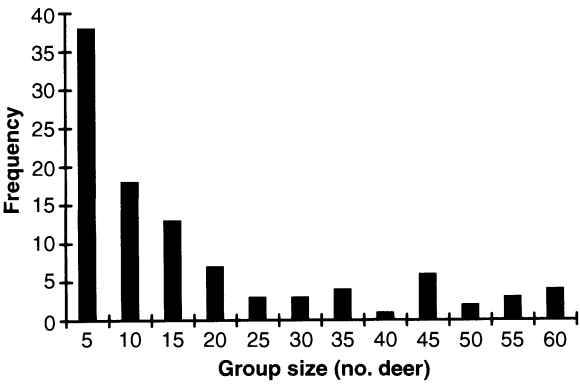


FIG. 6. The frequency distribution of groups of different sizes for scalar 96.5 in deer years 1984–1993.

and $\chi^2 = 31$, respectively, $df = 1$, $P < 0.001$; Fig. 7b). The interaction term between local population density and total population density was not significant ($\chi^2 = 1.2$, $df = 1$, $P > 0.1$).

Phenotype, sex, and local density

Models describing calf winter survival as a function of local population density, total population density, mother's age (fitted as a quadratic), calf sex, and reproductive status showed that local population density was more important than sex or phenotypic factors during 1984–1993. If each term was fitted individually, total population density was the most important factor ($\chi^2 = 79$, $df = 1$, $P < 0.001$), followed, in order of significance, by local population density ($\chi^2 = 67$, $df = 1$, $P < 0.001$), reproductive status ($\chi^2 = 28$, $df = 4$, $P < 0.001$), mother's age (fitted as a quadratic: $\chi^2 = 10.7$, $df = 2$, $P < 0.01$), and calf sex ($\chi^2 = 4.3$, $df = 1$, $P < 0.05$). Mother's identity was not significant ($\chi^2 = 114$, $df = 203$, $P > 0.05$), suggesting that the data could be treated as independent. The model explaining the greatest proportion of total deviance (24%) included total population density, local population density, sex, mother's age fitted as a quadratic (age + age²), and the interaction term between local population den-

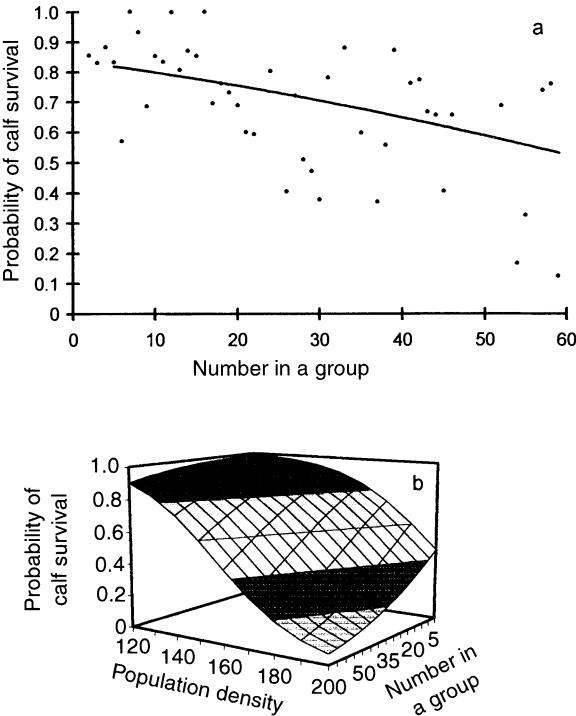


FIG. 7. (a) The relationship between calf winter survival (P_s) and local population density at a scalar value of 96.5. The fitted line is a logistic curve. (b) The relationship with total population density is incorporated into the model.

sity and sex (model A, Table 1). Female calves were less affected than males by group size ($\chi^2 = 7.2$, $df = 1$, $P < 0.05$), with a predicted probability of survival (P_s) declining from 0.90 in a group of 10 adult females to 0.66 in a group of 60 individuals (Fig. 8). Male calves, in comparison, were significantly more likely to die at high local population density ($P_s = 0.46$, 60 individuals per cluster) than at low local density ($P_s = 0.92$, 10 individuals per cluster).

Seasonal differences

The best scale for describing calf winter survival differed markedly between summer and winter (Fig.

TABLE 1. Logistic analysis of winter survival of red deer calves, with seasonal data combined for 1984–1993. Local population density is at HCA scalar value 96.5. Model A is the full model ($df = 6$) and explains 24% of the total deviance. Deviance is distributed approximately as χ^2 . Significance of these terms is shown in the final row.

Model	A	B	C	D	E	F	G	H
Population density	x		x	x	x	x	x	x
Local population density (lpd)	x	x	x	x	x	x	x	
Mother's age	x	x		x		x	x	x
Mother's age ²	x	x	x			x	x	x
Sex	x	x	x	x	x	x		x
Sex \times lpd interaction	x	x	x	x	x			
Regression deviance (χ^2)	176	94	167	163	152	172	168	116
Decrease in df		1	1	1	2	1	2	2
Decrease in regression deviance†		82	9	13	24	4	8	60
P		<0.001	<0.01	<0.001	<0.001	<0.05	<0.05	<0.001

† This is the change in deviance as terms are deleted from the model (blank cells), with the resulting decrease in degrees of freedom.

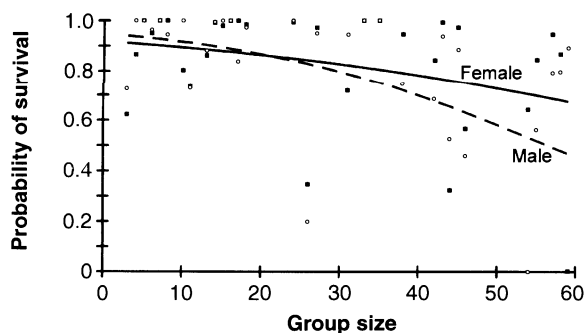


FIG. 8. The difference in the probability of calf winter survival between the sexes in relation to local population density. The fitted lines are predictions from the full model, with the other significant terms held constant. Open circles are females, filled squares are males.

9). In summer months, the maximum amount of deviance explained was with local population density at scalar value 96.5, which divided the population into a mean of 10.9 clusters. This is the same scale as described when the data were not divided by season. However, during the winter months, the best scale was at HCA scalar value 90. This corresponds to a distance of 1630 m (interannual variation 1410–1810 m), with the population being subdivided into 4.9 ± 0.3 groups (mean ± 1 SD, range 3 to 5 groups). In both summer and winter, local population density explained more of the deviance than did total population density (summer: total population density $\chi^2 = 43$, $df = 1$, $P < 0.01$, and local population density, (HCA scalar value 96.5) $\chi^2 = 47$, $df = 1$, $P < 0.01$; winter: total population density $\chi^2 = 54$, $df = 1$, $P < 0.01$, and local population density (HCA scalar value 90.0) $\chi^2 = 62$, $df = 1$, $P < 0.01$). The interaction between population density and local population density was not significant in either season.

Sex, phenotype, seasonality, and local density

1. *Summer months.*—When each explanatory variable was fitted alone, local population density was the most important factor in explaining calf winter survival ($\chi^2 = 94$, $df = 1$, $P < 0.001$), followed by total population density ($\chi^2 = 84$, $df = 1$, $P < 0.001$), reproductive status ($\chi^2 = 19.4$, $df = 4$, $P < 0.001$), mother's age, fitted as a quadratic ($\chi^2 = 11.5$, $df = 1$, $P < 0.001$), and sex ($\chi^2 = 6.2$, $df = 1$, $P < 0.05$), respectively. The model explaining the largest amount of total deviance included local population density, population density, reproductive status, sex, mother's age, and the interaction terms between reproductive status and local population density and between sex and local population density (Table 2, Fig. 8). The interaction term shows that males are more likely than females to die in larger groups.

2. *Winter months.*—Fitted alone, local population density ($\chi^2 = 80$, $df = 1$, $P < 0.001$), total population density ($\chi^2 = 73$, $df = 1$, $P < 0.001$), reproductive

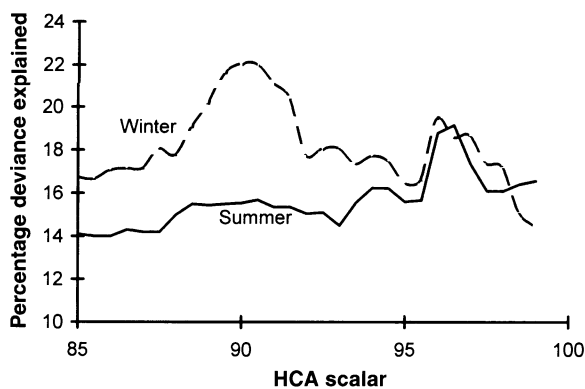


FIG. 9. The difference in the percentage deviance explained when the data are divided into winter and summer seasons. During the winter (dotted line), the maximum is at a scalar value of 90. This corresponds to the population being divided into, on average, five groups. During the summer, the maximum is at scalar value 96.5, which is the same maximum when the whole population is considered.

status ($\chi^2 = 20.7$, $df = 4$, $P < 0.001$), and sex ($\chi^2 = 8.3$, $df = 1$, $P < 0.01$) all significantly affected calf winter survival; mother's age (quadratic: $\chi^2 = 3.7$, $df = 2$, $P > 0.05$) had no significant effect. The model explaining the greatest amount of total deviance (23%) contained total population density, local population density, mother's age fitted as a quadratic (age + age²), and reproductive status (Table 3). In contrast to summer, there were no significant interaction terms in winter.

DISCUSSION

The spatial distribution of individuals is often heterogeneous, which leads to variation in local dynamics within populations. An understanding of these local dynamics is crucial in explaining the dynamics of a whole population (Taylor 1961, O'Neill 1989, Sugihara et al. 1990). The choice of scale at which to explore these dynamics is often not apparent in populations of mobile individuals. Here, we used a novel technique to explore local dynamics over a wide range of scales. We showed, for a population of red deer on Rum, Scotland, that the most descriptive scales were intermediate between the individual and the population. The most descriptive scale differed between summer and winter, and the dynamics at these within-season scales explained calf winter survival better than did total population density.

The technique we used in this paper, hierarchical cluster analysis (HCA), is normally used in ecology to explore social organization in populations (Morgan et al. 1976, Penzhorn 1984, Cairns and Schwager 1987). We used HCA to explore population substructure over a range of scales from groups of one or two individuals to the entire population. HCA offers a powerful tool for exploring the importance of spatial scale in popu-

TABLE 2. Logistic analysis of calf winter survival, with the data restricted to local population density during the summer months of 1984–1993. Models A–H do not consider interaction terms; models I–R do. Model I is the full model (df = 8) and explains 27% of total deviance.

Model	A	B	C	D	E	F	G	H
Population density	x		x	x	x	x	x	x
Local population density (lpd)	x	x		x	x	x	x	x
Mother's age	x	x	x		x		x	x
Mother's age ²	x	x	x	x			x	x
Sex	x	x	x	x	x	x		x
Reproductive status (rps)	x	x	x	x	x	x	x	
Sex × lpd interaction								
Rps × lpd interaction								
Regression deviance	161	133	116	157	153	138	160	149
Decrease in df†		1	1	1	1	2	1	4
Decrease in regression deviance†		28	45	4	8	23	1	12
P		<0.001	<0.001	<0.05	<0.01	<0.001	NS	<0.05

† The decrease in regression deviance (equivalent to χ^2 values) and in df values are for terms not included (blank cells).

lations in which the choice of a suitable discrete scale is nontrivial.

Calf winter survival, the most important factor affecting the population size of red deer on Rum (Clutton-Brock et al. 1985a, 1987a, b, Albon et al. 1987), declines with increasing deer density and varies in discrete space (Guinness et al. 1978). Although treating space discretely yields significant results, it is a slightly unrealistic way of grouping individuals that are mobile and have overlapping home ranges. Consequently, defining boundaries between discrete areas can separate individuals that associate together. Hierarchical cluster analysis is a more realistic method of exploring population substructure; the technique considers the proximity of individuals to one another, but does not assign them to a specific area. The spacing behavior of red deer changes with population density; as numbers increase, deer become closer together. Consequently, analysis of population substructure over a wide range of population densities (early years) with HCA is confounded because the mean proximity of individuals decreases. This means that the analysis of scale with HCA is only suitable for populations at, or close to, equilibrium (later years). Clusters of animals are not temporally constant in size or composition, making group identity a poor factor in describing calf winter mortality.

Later years

As scale varied in our study, the amount of deviance explained in models of calf winter survival changed. Surprisingly, the scales that explained most deviance were not at the level of the individual, but were at intermediate scales, showing substructuring of the population. At these scales, local density tended to be higher in the north of the study area, where the majority of the best grazing occurred (Clutton-Brock et al. 1982a, Iason et al. 1986, Clutton-Brock et al. 1988). This suggests that the best scale at which to analyze calf winter survival is related to the distribution of vegetation communities.

Calves at high local density are more likely to die than are those at lower densities, possibly due to competition for food or a greater chance of being parasitized or contracting disease. In some species, high density increases competition for resources (Crawley 1983), and can increase the incidence of attack by parasites (Crawley 1992) and pathogens (Wandeler et al. 1974). Juveniles are less able to compete than adults, and may be more vulnerable to disease than adults. In some species, individuals at high density are more likely to avoid predation through increased vigilance than are those at lower densities (Hamilton 1971, Alexander 1974, Sherman 1977, Pulliam and Caraco 1984). A decreased risk of predation may be why red deer form associations (Clutton-Brock et al. 1982a). However, because the deer on Rum have no natural predators, this is no longer an advantage. We propose that high local density of deer occurs on herb-rich *Agrostis-Festuca* grassland. Calves born here are more likely to die due to high levels of competition for food than in other areas of poorer grazing and low local density. Over time in a population at equilibrium, the opposite effects of high food quality and decreased calf survival with high local density might be expected to counterbalance one another, with this effect being stronger in males than females. The cost to an adult hind of decreased calf winter survival could be a trade-off associated with an increased probability of her survival or future reproductive success.

Seasonal difference

Phenotypic traits of a mother (reproductive status, age) significantly affect the probability of a calf surviving; however, if the data are not divided by season, they do not interact with local population density. Ranging behavior of deer varies with season, with female home ranges being larger in summer than in winter (Graf 1956, Clutton-Brock et al. 1982a). There are two reasons for this: (1) there is more good grazing in summer, and (2) during the colder, winter months, animals remain on sheltered, lower ground. Spacing be-

TABLE 2. Continued.

I	J	K	L	M	N	O	P	Q	R
x		x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x	x	
x	x		x		x	x	x	x	x
x	x	x			x	x	x	x	x
x	x	x	x	x	x	x		x	x
x	x	x	x	x	x	x	x		x
x	x	x	x	x		x		x	
x	x	x	x	x	x		x		
183	150	179	175	160	178	165	176	153	117
	1	1	1	2	1	4	2	8	3
	33	4	8	23	5	18	7	30	66
	<0.001	<0.05	<0.01	<0.001	<0.05	<0.01	<0.05	<0.001	<0.001

havior of animals also varies with season; on average, animals tend to be at higher local density in summer than in winter. High-quality (nutritious) food is also more aggregated in summer than in winter. During both seasons, competition for food is an important factor influencing population dynamics (Clutton-Brock et al. 1982a). Herb-rich *Agrostis-Festuca* grassland is fast-growing and nutritionally rich, making it the preferred vegetation community for an individual to graze upon. The difference between good and poor grazing is greater in summer than in winter: most vegetation growth occurs in the hotter months, with young shoots being richer in energy and easier to digest than older plants. High-resolution scales are good descriptors of population substructure during summer, when good grazing is distributed heterogeneously: the population is best considered as many small groups. In winter, there is less high-quality grazing because there is no vegetation growth (Ball 1974), leading to a homogeneous distribution of grazing: thus, individuals are less aggregated. The difference between the scales may be due to contest competition for high-quality food distributed heterogeneously during the summer, with scramble competition being more important during the winter.

Sex, reproductive success, and local population density

Males are more likely to die than females because they grow faster (Clutton-Brock et al. 1982b). Thus, they require more food and could suffer more from competition. The interaction between sex, local population density, and calf winter survival is significant during the summer months but not in winter. The main factor influencing whether or not an individual will survive the winter is its condition at the end of summer. During the summer, calves need to rapidly gain body mass if they are to survive the winter (Clutton-Brock et al. 1982a). Competition for food increases with local density, with the faster growing males being more vulnerable than females to food shortage (Clutton-Brock et al. 1985b). With scramble competition for poor-quality food during winter, males and females do not differ significantly in probability of survival, if local population densities in winter months are considered alone. Like sex, reproductive success interacts significantly with local population density during summer but not winter. The body condition of a mother is dependent on her previous reproductive history (Clutton-Brock et al. 1982a). A mother is likely to be in better condition

TABLE 3. Logistic analysis of calf winter survival, with data restricted to local population density at HCA scalar value 90.0 during the winter months of 1984–1993. Model A is the full model (df = 8) and explains 23% of the total deviance.

Model	A	B	C	D	E	F	G
Population density	x		x	x	x	x	x
Local population density (lpd)	x	x		x	x	x	x
Mother's age	x	x	x		x		x
Mother's age ²	x	x	x	x			x
Reproductive status	x	x	x	x	x	x	
Regression deviance (χ^2)	159	110	102	157	156	150	149
Decrease in df†		1	1	1	1	2	4
Decrease in regression deviance‡		49	57	2	3	9	10
P		<0.001	<0.001	NS	NS	<0.05	<0.05

† This represents the number of degrees of freedom associated with each missing term.
‡ This shows the values attributable to missing terms.

if she has not bred in the previous year and/or has not had to compete heavily for food. True yields and summer yields are least affected by local density; first breeders, winter yields, and milk hinds are more affected. Generally, true yields and summer yields are in better body condition than other animals because they either did not breed in the previous year, or lost a calf soon after birth. These individuals do not have the costs of lactation, and thus gain mass faster through the summer. In contrast, milk hinds and winter yields are typically in worse condition, having lactated for ≥ 4 mo. The absence of an interaction between local population density and reproductive success in winter presumably reflects the dependence of a calf's condition at the start of winter on its nutritional status during the summer. As we have argued, competition for food may be more acute in summer; by the winter, the effects of sex and mother's reproductive status have already manifested themselves and do not play as important a role.

We have demonstrated the importance of local population density for calf winter survival, the most critical factor influencing future population size, and also the importance of the scale at which to explore local dynamics. This corroborates the empirical results of Hails and Crawley (1992) and the model of Rand and Wilson (1995) that, as scale is varied, the analysis of dynamics can lead to different results. The spacing behavior of individuals of many species varies temporally for a variety of reasons, including mating systems, food availability, or weather factors (Galante and Cassini 1994, Koehn et al. 1994, Perezbarbaria and Nores 1994). We show here that local dynamics vary between summer and winter, and that the best scale at which to analyze dynamics may not be constant over time.

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