Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer

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Abstract. We tested for fine-scale spatial heterogeneity in habitat quality in a roe deer (*Capreolus capreolus*) population in the Chizé reserve located in western France by measuring spatial variation in the availability and plant nitrogen content of principal and preferred plant species. There were significant differences in habitat quality within the reserve: the principal food plants in spring and summer occurred more frequently in the oak woodland in the north than in the beech woodland in the south of the reserve. Within species, plants in the north had higher nitrogen contents than in the south. There was a positive spatial covariation between habitat quality, local density and fawn body weight: animal densities and fawn body weights were highest in the north, the best habitat (i.e. the habitat with more abundant food of higher quality). These results differ from those recently obtained on red deer (*Cervus elaphus*). We suggest that spatial organization and foraging behaviour must be accounted for when considering the effect of habitat quality on individual fitness of ungulates.

Introduction

The dynamics of mammalian populations commonly show spatial as well as temporal variations (Gilpin and Hanski *1991*; Tuljapurkar and Caswell *1996*). The effect of spatial heterogeneity on population dynamics, however, has been studied principally at a large scale, i.e. the metapopulation level (Gilpin and Hanski *1991*; Lebreton *1996*), while local spatial effects (i.e. within populations) have often been neglected. At a coarse spatial scale, differences in habitat quality have been predicted to have only a minor effect on life history parameters, because high animal densities in the best habitats prevent any substantial advantage of high habitat quality (Klein and Strandgaard *1972*). Likewise, at a finer scale, spatial heterogeneity is also considered to have little impact on population dynamics: when habitat quality varies within the population range, individuals are expected to be distributed in an ideal free manner, so that differences in local densities match the differences in habitat quality, leading to balanced resource partitioning among individuals (Fretwell and Lucas *1970*). This has led some authors to suggest that density, rather than habitat quality, shapes life history patterns in populations of relatively sedentary mammals such as roe deer *Capreolus capreolus* (Klein and Strandgaard *1972*; Wahlström and Kjellander *1995*). For this species, the suggestion has even been made that the few animals living in poor habitats could display the highest phenotypic quality (Klein and Strandgaard *1972*).

Recent studies on red deer have also reported that hinds had higher lifetime reproductive success at low density on poor habitats than at high density on the best habitats (Coulson et al. *1997*; Conradt et al. *1999*), supporting the view that local density is of great importance to phenotypic quality. However, red deer differ markedly from roe deer in both their foraging behaviour and social system. The red deer is a non-territorial species in which females live in a matrilineal system and generally aggregate when foraging (Clutton-Brock et al. *1982*). Conversely, male roe deer are territorial and females live with their offspring in small groups, and occupy small home ranges (approximately 30 ha; Hewison et al. *1998*). In contrast to red deer, which are non-selective grazers (Clutton-Brock et al. *1982*), roe deer are generalist browsers and their diet in a given place or season is usually composed of a small number (one to three) of preferred species (Duncan et al. *1998*). Finally, due to their small body size, roe deer may be more dependent on the quality than the quantity of resources compared to larger herbivores (Demment and Van Soest *1985*).

This study was carried out in the 2,614-ha fenced reserve of Chizé in which a roe deer population has been studied intensively since 1978. We aimed (1) to assess the level of spatial heterogeneity in terms of habitat quality in the Chizé forest, where there are two distinct soil types (clayey versus calcareous) and (2) to assess relationships between habitat quality, population density and phenotypic quality of roe deer. Based on previous results, we expected to find (2a) lower body weight during years with high population density than during years with low population density, irrespective of habitat type (Vincent et al. *1995*; Gaillard et al. *1996*), (2b) the highest local density in the best habitat (Klein and Strandgaard *1972*; Coulson et al. *1997*; Conradt et al. *1999*) and (2c) the best phenotypic quality in the poorest habitat (Klein and Strandgaard *1972*).

Materials and methods

Study site

The study was carried out in the Chizé reserve, an enclosed forest situated in western France (46°05′ N, 0°25′ W). The climate is oceanic with Mediterranean influences, and is characterized by mild winters and hot, dry summers. Forest productivity is low, probably because summer droughts are common (Gaillard et al. *1996*). According to a geological map based on whole soils measurements (Lambertin

1992) and woodland type, there are two strongly contrasting habitats in the forest (Fig. 1). In the northern part of the reserve (1,397 ha), soils are clayey and dominant trees are essentially oak (*Quercus pubescens*, *Q. robur* and *Q. petraea*). Conversely, in the southern part of the reserve (1,143 ha) where chalky and limestone soils are associated with marl, the dominant tree is beech (*Fagus sylvatica*). To assess the habitat quality of both parts of the reserve, we focused on forage abundance and forage quality. Cover, which is sometimes a significant element of habitat quality (Mysterud et al. *1999*), may be less important here, as Chizé has no predators and a mild climate.
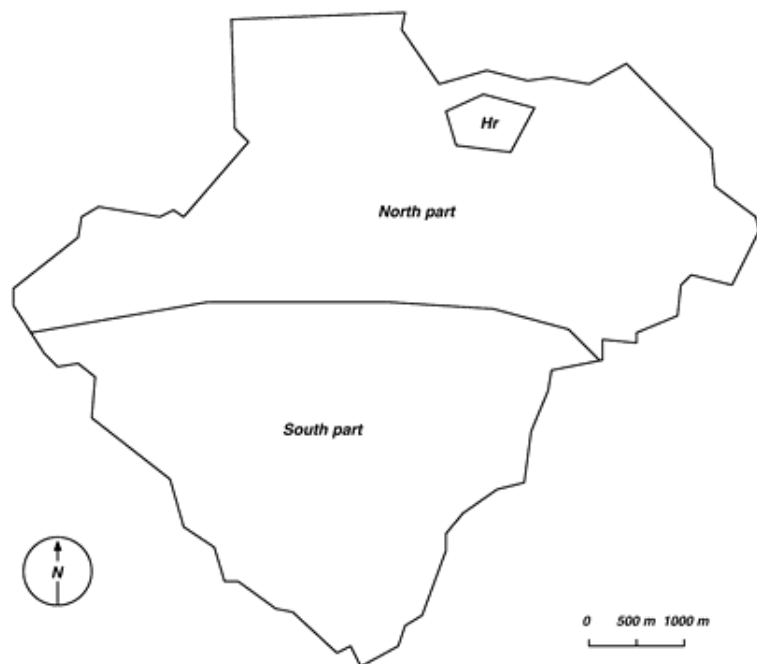

Fig.1. Spatial representation of the Chizé reserve (2,614 ha). In the rich north part of the reserve (1,397 ha), soils have a high clay content and the dominant trees are oaks. In the poor southern part of the reserve (1,143 ha), beech trees dominate and limestone and chalky soils are associated with marl. One main road delimits both parts of the reserve, as it constitutes natural frontiers for roe deer home range delimitation (Hewison et al. *1998*). A typical roe deer home range (*Hr* approximately 30 ha) is also represented

Data collection

Distribution of food resources

To assess the composition of plant communities in both parts of the reserve, we used a plant survey including 145 sampling plots (74 in the north and 71 in the south) performed in 1993 by G.V.L. A 400-m grid was established on a map of the reserve, each intersection of the grid representing a sampling point. Data were collected at the end of winter (February), just before plant growth, to obtain a reliable estimate of plant cover using a modified Aldous method (Morellet *1998*). We focused on 18 consumed woody genera, which include the principal and preferred species for roe deer (Maizeret et al. *1991*; Tixier et al. *1997*). In addition, the cover of one species which is not eaten (Tixier et al. *1997*),

butcher's broom (*Ruscus aculeatus*), was also estimated, as it is an indicator of poor soils (Rameau et al. *1989*). The cover of each species was estimated in a radius of 3.57 m around the sample point and divided into seven classes: absent (class 1), <1% (class 2), 1-5% (class 3), 6-20% (class 4), 21-50% (class 5), 51-75% (class 6), >75% (class 7). Only vegetation accessible to roe deer (<1.20 m) was considered.

Forage quality

Samples for chemical analyses were collected in early May 1999 from three plants (madder *Rubia peregrina*, ivy *Hedera helix* and bramble *Rubus* sp.) at 24 sites of the 145 sampling plots. These plants were selected because they were both abundant (they are among the most widespread species in the reserve: madder was present on 116 of the 145 stations sampled in 1993, brambles on 96 and ivy on 123) and are eaten by roe deer at Chizé (Maizeret et al. *1991*; Tixier et al. *1997*). Madder is consumed in winter at Chizé (G. Van Laere, personal observations), while brambles and ivy are consumed throughout the year (in winter, both plants represent 60% of roe deer diet, in summer,>30%; Maizeret et al. *1991*). Plant sampling was carried out in May because any change in resource quality during this period (when fawns are born) could have important effects on fawn survival and thus on recruitment (Gaillard et al. *1993b*). Trees were chosen at random and samples were collected from different plants (two or more when possible) at each site. Leaves were collected without peduncles and at <1.2 m in height (i.e. accessible to roe deer). Nitrogen content was used as an indicator of plant quality using the Kjeldahl method (Association of Official Analytical Chemists *1980*) with all the material pooled for each species at each site.

Phenotypic quality

We used fawn body weight in January-February as a proxy for individual phenotypic quality. This choice is based on Hanks' (*1981*) review which indicates that juvenile body weight is a suitable measurement of population condition because juveniles are sensitive to variations in environmental conditions. For roe deer, fawn body weight has a marked effect on individual fitness, as fawn body weight in January-February is closely related to subsequent adult body weight (Gaillard *1994*), winter survival (Gaillard et al. *1993a*) and age at maturity (Gaillard et al. *1992*). We used data from 1,131 fawns, which were caught and weighed in January and February 1978-1999 using an electronic balance; the site of capture (the fawns' birth sites, because 8-month fawns have not yet dispersed; Hewison et al. *1998*) and the sex were noted.

Population density

More than 70% of roe deer in Chizé were individually marked in most years, so a reliable estimation of population size was available, based on the generalized Cormack-Jolly-Seber model (Gaillard et al. *1993a*). Since 1978, 10 days of capture in January and February have allowed 250-350 roe deer to be caught each year. Each day of capture involved >250 people who drove animals into 2-5 km of nets. Density estimates for individuals aged >1 year varied between 6-22 individuals per 100 ha (Fig. 2). The population density varied strongly because of management. It increased until 1985 because few animals were removed. Thereafter, large numbers were removed to reduce the animals' impact on the woodland, until 1990.
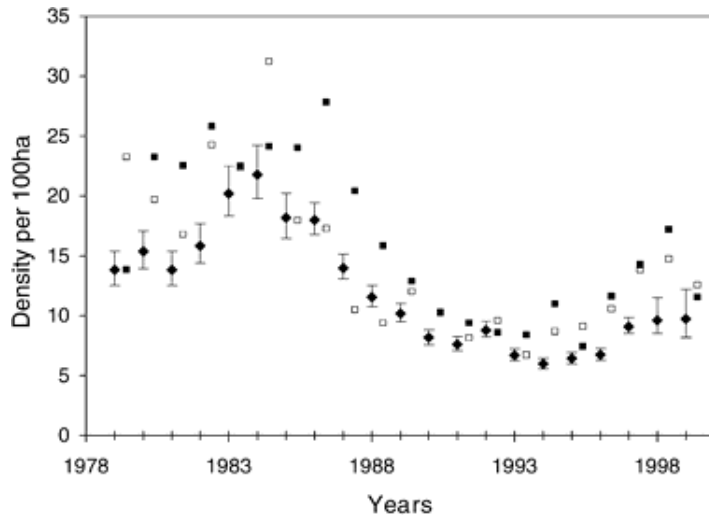
Fig.2. Yearly estimates of population density in March (individuals >1 year per 100 ha) in the Chizé reserve (France), estimated by the Cormack-Jolly-Seber model (*diamonds* with 95% confidence intervals) *Squares* represent yearly variations of an index of local density (number of individuals captured divided by the area sampled): *black squares* north, *open squares* south

An index of local density obtained for both habitats was calculated from 1979 to 1999 as the number of individuals captured divided by the area sampled by the drives. Removals were distributed equally between the habitats, and the densities varied synchronously (Fig. 2). We assume that roe deer are equally catchable in both habitats despite differences in cover in favour of the richest habitat.

Statistical procedures

To test for differences between the habitats in the probability of occurrence of the plant species, we used the Wilcoxon matched-pairs signed-ranks test. Butcher's broom was not included in this analysis, because it is not consumed at all by roe deer.

Nitrogen concentrations were arcsine square root-transformed (Sokal and Rohlf *1995*) before performing a two-way ANOVA (with plant species and habitat as factors) using Statview 4.2 (Roth et al. *1992*) to test whether the nitrogen content of each species differed significantly between the habitats.

Because roe deer at Chizé show slight sexual dimorphism in size (Gaillard et al. *1996*), we included sex as a factor when analysing covariation between spatial variation in habitat quality, local density and fawn body weight. To avoid excessive statistical power generated by the very large sample (>1,000 individuals), we performed the analysis on sex- and habitat-specific yearly means of body weight. The effects of roe deer density, sex and habitat (i.e. rich vs poor) on logarithm of mean fawn weight (Sokal and Rohlf *1995*) were tested using a three-way ANCOVA (with density per 100 ha as a covariable) using GLIM software (Francis et al. *1993*).

Finally, we tested the null hypothesis of equal densities in the rich and the poor habitat by performing the Wilcoxon matched-pairs signed-ranks test, each point representing 1 of the 21 years sampled (1979-1999).

Results

Of the 18 plants considered, 14 occurred more frequently in the north than in the south (Table 1; z=-2.24, P=0.025), in particular *Acer campestre*, *Crataegus* sp., *Cornus sanguinea* and *C. mas*, *Carpinus betulus*, *H. helix* and *Quercus* sp., which together represent >60% of the summer diet of roe deer (Maizeret et al. *1991*). *R. aculeatus*, an indicator of poor soils, occurred mostly in the south (Table 1).

Table 1. Spatial heterogeneity in the abundance of plant species in the Chizé reserve, measured as the probability of occurrence (*N* number of stations in which a given species was present, *pN* probability of occurrence of each species in the northern part, SD_N standard deviation of pN, *pS* probability of occurrence of each species in the southern part, SD_S standard deviation of pS)

Species	N	pN	SD_N	pS	SD_S
Acer campestre	42	0.36486	0.00651	0.21127	0.00575
Acer monspessulanum	53	0.39189	0.0066	0.33803	0.00666
Carpinus betulus	59	0.48649	0.00675	0.32394	0.00659
Cornus mas	53	0.45946	0.00673	0.26761	0.00624
Cornus sanguinea	38	0.33784	0.00639	0.1831	0.00545
Corylus avellana	3	0	0	0.04225	0.00283
Crataegus sp.	110	0.89189	0.0042	0.61972	0.00684
Evonymus europaeus	12	0.10811	0.0042	0.05634	0.00325
Fagus sylvatica	27	0.01351	0.00156	0.3662	0.00679
Hedera helix	123	0.89189	0.0042	0.80282	0.0056
Ligustrum vulgare	82	0.58108	0.00667	0.5493	0.00701
Lonicera periclymenum	4	0.05405	0.00306	0	0
Prunus spinosa	34	0.22973	0.00568	0.23944	0.00601
Quercus sp.	40	0.31081	0.00625	0.23944	0.00601
Rosa sp.	37	0.2973	0.00618	0.21127	0.00575
Rubia peregrina	116	0.74324	0.0059	0.85915	0.0049
Rubus sp.	96	0.66216	0.00639	0.66197	0.00666
Ruscus aculeatus	71	0.27027	0.006	0.71831	0.00634
Sorbus torminalis	20	0.21622	0.00556	0.05634	0.00325

There were no significant interactions between the effects of habitat and species for the nitrogen concentrations ($F_{2,66}$=0.664, P=0.518). These varied markedly among habitats and species (habitat: $F_{1,66}$=14.17, P<0.0001; species: $F_{2,66}$=31.07, P<0.0001), with mean nitrogen content being consistently higher in samples from the north than from the south (17.44 vs 13.94% for madder; 11.88 vs 10.31% for

ivy; 17.56 vs 15.56% for brambles). The analyses of habitat quality thus confirm that the north is a "richer" habitat for roe deer compared to the south, because plant species important in roe deer diets occurred more frequently in the north than in the south, and they were of better nutritional quality in the north.

Our second hypothesis (2a), that total density would have a negative effect on fawn weight, was supported. No significant interactions were observed among habitats (rich vs poor), density and sex effects (all $P>0.46$, $n=84$). On the other hand, the main effects of habitat ($F_{1,80}=6.25$, $P=0.014$), sex ($F_{1,80}=10.42$, $P=0.0018$) and density ($F_{1,80}=38.75$, $P<0.0001$) markedly affected winter body weights of fawns (Fig. 3). When other effects were accounted for, fawn body weight decreased on average by 0.15 kg for an increase of one roe deer per 100 ha, males being on average 0.77 kg heavier than females.
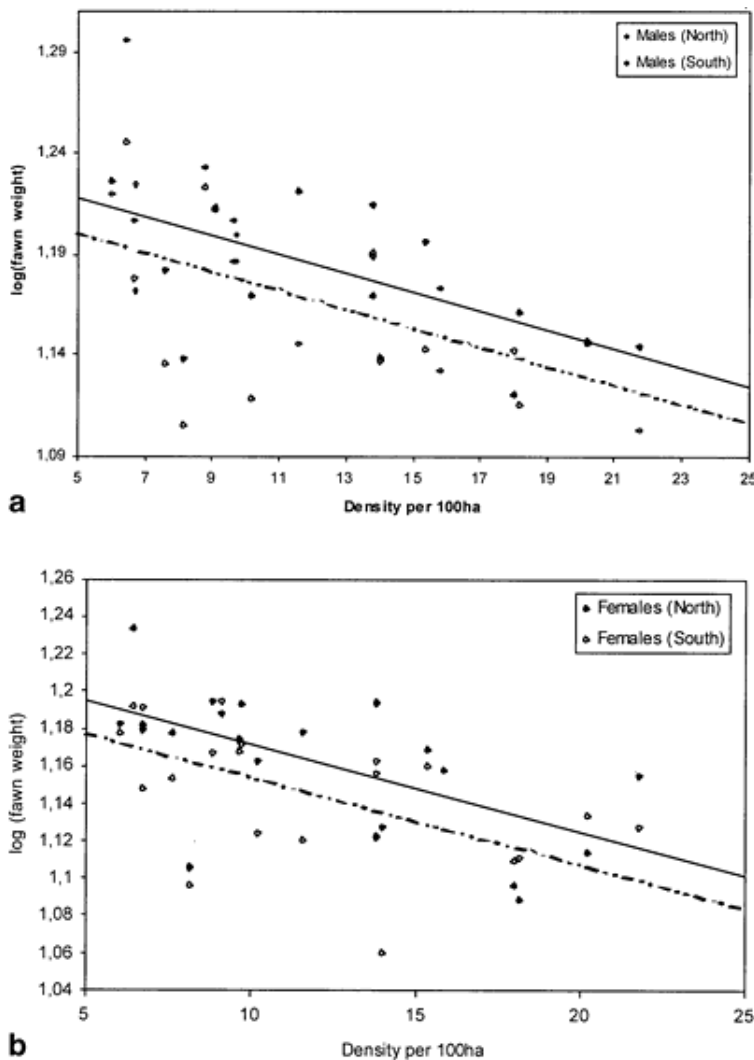

Fig.3. Relationship between the mean body weights (after log transformation) of male (**a**) and female (**b**) roe deer fawns at the onset of winter and the population density (number of individuals per 100 ha). Density estimates were obtained by the Cormack-Jolly-Seber model. Each *point* represents the average weight of males or females living in the north or south at a given density (i.e. yearly means between 1979 and 1999). For both sexes, the adjusted model for the north (*continuous line*) and south (*dashed*

line) is shown

As expected from our second prediction (2b), the local density of roe deer tended to be higher in the richer north than in the poorer south (z=1.93, P=0.054). Finally, contrary to expectation 2c, the selected model (i.e. additive effects of total density, sex and habitat) showed that fawn weights were on average 0.6 kg higher in the rich habitat than in the poor one, although roe deer density was higher in the rich north than in the poor south.

Discussion

A limitation of this study is that different time scales were used for measuring the variables we analysed. Fawn weights were collected over 21 years, the composition of the plant communities in a single winter (1993) and plant nitrogen content in a single spring (1999). However, the main factors which affect roe deer population dynamics in Chizé are climate and population density (Gaillard et al. *1998a*), and both 1993 and 1999 were average years for these variables. For the analysis of the plant communities, additional surveys were available for 1995 and 1997. Although these were performed by different observers and may be less reliable (Morellet *1998*), they gave very similar results, showing a marked contrast between the frequency of occurrence of the principal and preferred food plants of roe deer between the rich north and the poor south. Although we cannot assess the generality of our results for plant quality, we are confident that the different time scales used in this study did not affect its main conclusions.

Habitat quality is markedly heterogeneous at Chizé, and is much higher in the north than in the south. First, the principal plant species in the spring and summer diets of roe deer, such as hornbeam, dogwood, maple and hawthorn, occurred more frequently in the northern oak woodland than in the southern beech woodland. Second, ivy, madder and brambles all had higher nutritional quality in spring in the rich north than in the poor south as measured by nitrogen content. The spatial distribution during spring of both floristic composition and plant quality may affect roe deer population dynamics strongly. The early development of fawns is the critical stage in roe deer population dynamics (Gaillard et al. *1998a*), and any change in available resources for roe deer fawns or for their mothers during spring may affect fawn survival and thereby recruitment to the population.

For roe deer at Chizé, habitat quality, local density and fawn body weight are positively correlated. Adult body mass also varied spatially, with animals in the rich north weighing about 1 kg more than in the poor south (N. Pettorelli, unpublished data). A previous study (Cibien *1984*) also showed that adults were heavier in thickets (i.e. good-quality habitat) than in mature coppice (i.e. poor habitat), where local density was also found to be lower (Cibien and Sempéré *1989*). However, these results were obtained with very small sample sizes (body weights were available for six males and five females), the study was conducted only in the rich northern habitat and the assessment of habitat quality was limited to a measure of the abundance of brambles.

Spatial covariation between habitat quality, local density and life history parameters has also been reported for other ungulates. Coulson et al. (*1997*) reported higher calf survival in poor habitats with low local density for red deer on Rum, Scotland. Conradt et al. (*1999*) recently supported this conclusion, and showed that lifetime reproductive success of red deer hinds was highest in the poorest area, i.e. with the lowest amount of grassland, but also with the lowest hind density. As with red deer on Rum, roe deer

in Chizé tended to have the highest local density in the best habitat. However, in contrast to the results for red deer, the roe deer fawns were heaviest in the best habitat, despite a negative between-year effect of density on fawn weight (Gaillard et al. *1996*). This means that differences in density between habitats do not match differences in resources available per capita.

These contrasting results may be accounted for by two different hypotheses. First, the principal determinant of phenotypic quality in roe deer is the quality of the habitat (Strandgaard *1972*) and of the mother (family and cohort effects; Gaillard et al. *1998b*). In the highly productive population of Trois Fontaines (France), we have found marked heterogeneity in the reproductive success of females under near-constant population density (Gaillard et al. *1998b*). Therefore, density-dependent effects in roe deer may be dampened by differences in female quality to a greater extent than in red deer. At Chizé, roe deer showed density-dependent responses in several life history traits including fawn body mass (Gaillard et al. *1996*; this study), early survival (Gaillard et al. *1997*) and age at first breeding (Gaillard et al. *1992*). However, even at the peak density, the roe deer population still increased faster than 20% per year (Gaillard *1994*), indicating that this population was still far from the carrying capacity. The small body size of roe deer may mean that they are less sensitive to reductions in the absolute amount of available food, and more sensitive to variations in the quality of the resources (which can be due to variations in the abundance of preferred species and/or their biochemistry). Andersen and Linnell (*2000*) reported only quite weak responses of roe deer to a threefold increase in density in a rich northern habitat, supporting this hypothesis. These results are also consistent with Conradt et al.'s (*1999*) suggestion that the typical spatial organization and foraging behaviour of red deer is responsible for the overwhelming negative effect of local density on individual performance. Roe deer females, in contrast, generally live with their offspring and do not aggregate with other females when feeding in forest habitats (Hewison et al. *1998*). Intraspecific competition for resources is therefore indirect. Even at high local density, females can use all the resources available within their home range, contrary to red deer hinds which compete directly for access to resources (Clutton-Brock et al. *1982*).

An alternative hypothesis is that the between-habitat differences in density in this study were not marked enough to match the between-habitat differences in quality. The difference in local density was less than twofold in our study, and cover differences could have affected the netability of roe deer in both habitats, thereby biasing our index of density. Conradt et al.'s (*1999*) study took place when the density in the best habitat (Kilmory) was about four times higher than in the poorest habitat (Upper Glen). However, Milner-Gulland et al. (*2000*) reported for the same population highest fitness of red deer hinds in the richest habitat when differences in density in favor of the richest habitat were much more limited (less than twofold).

Neither hypothesis, however, explains why individuals in the poorer south do not disperse northwards to improve their condition, as roe deer females do not defend territories (Hewison et al. *1998*). Whatever the reason, our analyses showed that spatial heterogeneity affects life history traits in roe deer populations. We now need (1) to confirm local density differences, e.g. by exploring differences in recapture probabilities, and (2) to understand better the role of dispersal in shaping between-habitat differences in fitness components of roe deer populations. In addition, further comparative studies will be required to assess whether between-species differences in foraging behaviour may lead to differential effects of spatial heterogeneity on fitness components.

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