Individual access to preferred habitat affects fitness components in female roe deer Capreolus capreolus

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Summary

1. Many studies have reported variation in life-history traits and reproductive success within populations. One potential source for the reported variation is fine-scale spatial variation in habitat quality.
2. In this study the effects of differences in home-range quality on individual fitness were investigated in a roe deer population in an agricultural–woodland mosaic landscape in central Norway.
3. Compositional analysis revealed that woodland was the most preferred habitat: its availability was therefore used as an index of home-range quality.
4. It was found that the quality of the does’ winter home-range affected fawn production in the subsequent spring, as females with greatest availability of preferred habitat during winter produced the larger litters the subsequent spring.
5. Furthermore, the winter weights of the fawns seemed to be affected by home-range quality in a complex way. First, home-range quality in the prenatal winter seems to influence the birthdate and in turn the weight of the fawns in August. Also there was an immediate effect of the quality of the home-range that the fawns occupied during the postnatal winter.
6. These results are not consistent with the ideal free distribution theory, suggesting that the mechanisms for roe deer spacing behaviour should be re-examined.

Key-words: fawn winter weight, habitat quality, ideal free distribution, litter size, ungulates.

Introduction

Many long-term studies of marked individuals have revealed the asymmetrical nature of reproductive success within natural populations. For both the study of population dynamics and the evolution of life history, the identification of the sources of this variation is of great importance. One potential source of variation is unequal access to resources, as food is often regarded as a limiting resource in female reproduction (Clutton-Brock, Guinness & Albon 1982). Consequently, spatial variation in life-history parameters induced by environmental heterogeneity have been documented for many species, at different ecological scales (e.g. latitudinal gradient: Sand, Cederlund & Dannell 1995; subpopulation: Pettorelli et al. 2001). However, although environments are heterogeneous at a hierarchy of scales, the majority of the studies examining this subject have looked at large spatial scales, whereas the local spatial scale has often been neglected. Accordingly, the relationship between habitat attributes and fitness at the individual level is poorly understood, at least among non-territorial species. In such species individuals do not defend resources; consequently better habitats are not directly monopolized through aggression. Thus, when the habitat quality varies within the population range, the ideal free distribution theory (sensu Fretwell & Lucas 1970) predicts that the individuals should be distributed proportionally to the resources in such a way that fitness is equalized between the individuals. Although the assumptions of the theory are often violated in the wild, it has been suggested that the theory fits well with observed patterns in cervids (roe deer Capreolus capreolus L. Wahlström & Kjellander 1995; red deer Cervus elaphus L. Conradt, Clutton-Brock & Guinness 1999). However, other studies examining individual variation in fitness of herbivores have demonstrated the importance of fine-scale spatial heterogeneity, and spatial variation in fitness components based on differences in individual’s home-range attributes.
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have been documented for different species (moose Alces alces L. Sæther & Heim 1993; red-necked wallaby Macroporus rufogriseus banksianus (Desmarest): Higginbottom 2000).

Here we investigate the relationship between habitat quality and some life-history traits of individually monitored animals in a medium-sized temperate ungulate, the roe deer. Roe deer does are not territorial in the common sense, although they are quite sedentary, using the same home-ranges for years (Andersen, Linnell & Aanes 1995). Although some recent studies have revealed that spatial heterogeneity in habitat quality can induce spatial variation in phenotypic condition between subpopulations (Focardi et al. 2001; Pettorelli et al. 2001, 2002), the relationship remains unstudied at the individual level. We focus on two central life-history traits; litter size and winter weights of the fawns (influencing early survival, Gaillard et al. 1997, and age at maturity, Gaillard et al. 1992).

Based on the recent findings of Pettorelli et al. (2001, 2002) and Focardi et al. (2001) we expected that spatial heterogeneity in resource distribution will induce spatial variation in life-history traits also at the individual level. Owing to the income breeder tactic of the roe deer (Andersen et al. 2000), our first expectation is that (1) does with the best home-range quality during winter will have larger litter sizes the subsequent spring, as implantation failure is affected by winter conditions (Hewison & Gaillard 2001). Furthermore, we expect (2) that the winter weights of the fawns will be positively influenced by home-range quality through three different paths, potentially influencing winter weights. First (2a) we expect that postnatal investment will be influenced by the summer home-range quality of the does. Postnatal growth will potentially influence the August weight, which is a good determinant for the winter weight (Hewison et al. 2002). Furthermore (2b) we expect that time of birth will be affected by the home-range quality of the doe in the prenatal winter, potentially affecting the weight gained in August by increasing the number of potential growing days during summer. Finally, we expect that (2c) the home-range quality of the fawns in their postnatal winter will have an immediate effect on their winter weights.

Methods

STUDY AREA

The study area (7.8 km²) was located on Storfosna (10.8 km²), a small island 2 km off the coast of western central Norway (63°4’N, 09°3’E). The island is made up of a fine-scaled mosaic of heather-dominated moorland (33%), abandoned meadows (18%), cultivated pasture (35%) and mixed coniferous deciduous woodland (12%). The climate is cold oceanic, with about 160–180 growing days each year. The mean precipitation is 1048 mm year⁻¹, and snow rarely settles for more than 1 week at a time. The island provides good foraging conditions for the roe deer population (Tufto, Andersen & Linnell 1996), with spring flush being coincidental with the birth season (Linnell & Andersen 1998). During the study period, from 1991 to 1994, the population density increased from 10.1 deer km⁻² in spring 1991 to 19.3, 30.5 and 34.5 deer km⁻² in spring 1992, 1993 and 1994, respectively (Andersen & Linnell 2000).

DATA COLLECTION

During winter 1991–94 roe deer were caught, radio-collared and radio-tracked as described in Tufto et al. (1996). The radio-tracking was scheduled to equally represent the hours of the day, by shifting the schedule one hour each day. Summer home-ranges were calculated for 5, 20, 31 and 35 adult does in 1991–94, respectively, and winter home-ranges were calculated for 6, 20, 24 and 26 adult and yearling females in 1991–94, respectively. Furthermore, winter home-ranges were calculated for 1, 13, 7 and 12 fawns in 1991–94, respectively.

The fawns were captured and collared as described in Andersen & Linnell (1998). Litter size was estimated at birth (LSBIRTH), 5 days after birth (LS5DAYS) and 35 days after birth (LS35DAYS). Only collared females with known litter size were included in the analysis (4, 16, 19 and 22 in 1991–94, respectively).

The fawns were weighed as described by Andersen & Linnell (1997). Postnatal investment during the first 30 days was estimated as the sum of the individual fawns’ average growth rates (i.e. total growth for the litter), as early growth is linear during this period (Andersen & Linnell 1997). The sexes were pooled, as an earlier study revealed no sex differences in early growth (Andersen & Linnell 1997). A total of 3, 12, 17 and 18 family groups from 1991 to 1994, respectively, were included in the analysis. Fawns captured during their first winter, by the age of 8–11 months, were also weighed. A total of 1, 13, 7 and 12 fawns from 1991 to 1994, respectively, were included in this analysis.

Birth dates were determined by either direct observation of birth, monitoring radio-collared adult doe behaviour and udder development, the visual appearance of umbilical cord and wear on hoof cartilage at first capture of the fawn, or by back calculating along an individual’s growth rate to the mean birth weight (see Linnell & Andersen 1998). All litters were pooled in the analysis, as Linnell & Andersen’s (1998) study revealed no effect of dam age, fawn sex or litter size on date of birth. Birth date for a total of 5, 16, 18 and 18 litters from 1991 to 1994, respectively, were included in the analysis.

The weights of the fawns on 1 August were estimated based on the number of growing days (days between the date of birth and 1 August) multiplied by the individual growth rate, assuming linear growth (Andersen & Linnell 1997). In the analysis we used the mean of the siblings’ weights, owing to the non-independence between siblings in early growth (Gaillard et al. 1998). Consequently, each doe is only represented with one
HOME-RANGE ESTIMATION

We used a robust non-parametric home-range estimator, the 95% fixed kernel, with the smoothing parameter, $h$, selected using least-squares cross-validation, as recommended by Worton (1989) and Seaman et al. (1999).

In the present study, winter home-ranges were calculated based on locations sampled between 1 January and 30 April, and summer home-ranges between 1 May and 31 July. The rut excursions performed by the females in late July (Liberg et al. 1998) were excluded from the home-range estimates, as including them would have greatly overestimated the size of the home-ranges. Thirty fixes/home-range was set as a minimum to be included, as recommended by Seaman et al. (1999), although the mean number ($\pm$ SD) of fixes/home-range used in the analyses were 80 ($\pm$ 27) for summer and 50 ($\pm$ 11) for winter. For the fawn winter home-ranges the mean was 56 ($\pm$ 17). We found no evidence for a further increase in home-range size after 30 fixes/home-range (summer: $r = 0.160, P = 0.130$; winter: $r = 0.160, P = 0.171$); thus we did not adjust for the number of fixes in the analysis.

Home-ranges were calculated using the RANGES V program (Robert Kenward, CEH, UK). The habitat analyses were conducted using ArcGIS Ver. 8·1 (ESRI 2000) program package. When the home-ranges included small areas of ocean, these parts were excluded from further analysis.

COMPOSITIONAL ANALYSIS OF HABITAT SELECTION

In order to determine which habitat types were preferred, habitat selection within the home-range (third order selection, sensu Johnson 1980) was analysed using the compositional analysis technique (Aebischer, Robertson & Kenward 1993). Missing values in habitat use were replaced by 0·01% (Aebischer et al. 1993), and missing values on habitat availability were replaced by the mean of all non-missing values for that log-ratio (the third, and recommended, option in appendix 2 in Aebischer et al. 1993). When the habitat use of the same doe was measured over more than 1 year the average values for all years pooled were used for each individual in the compositional analysis, to decrease the sampling bias. Results in the habitat ranking matrixes are given as means ($\pm$ SE).

EFFECTS OF HOME-RANGE QUALITY

To test the covariation between fitness components and home-range attributes, the absolute area of preferred habitat (identified from the compositional analysis) within the home-range was used as an indication of home-range quality. The area was log$_{10}$ transformed to approach normality, and because an asymptotic relationship was expected (Sokal & Rohlf 1995). As data on the same doe from different years were included in the analyses, the observations were weighted in such a way that the total weight of each individual was 1 (Tufto et al. 1996). To see how density affected the importance of home-range quality, the period was divided into years with low deer density (1991 and 1992) and years with high deer density (1993 and 1994), following Gaillard et al. (1998). The age groups (2-year-olds, and older does) were pooled in the analysis, as earlier studies revealed no general differences in litter size (Andersen & Linnell 2000), postnatal investment (Andersen et al. 2000) or timing of birth (Linnell & Andersen 1998) due to parity or age in the Storfosna population. To normalize the body weights of the fawns in their first winter (as the time of capture was dispersed throughout the season), the deviation in body weight of each individual from the multiple regression between sex and month was used, as proposed by Tufto et al. (1996).

When analysing our two hypotheses about the effects of the home-range quality, we generally applied a method where we kept other factors known to influence our dependent variable constant in linear modelling (i.e. investigating the partial regression), as our objective was mainly to test our hypothesis, rather than exploring all possible factors influencing our dependent variables. To test our first expectation, about the relationship between home-range quality and litter size the subsequent spring, we fitted a log-normal Poisson regression (Sokal & Rohlf 1995). Otherwise, we used linear least-squares regressions, as the dependent variables were Gaussian distributed.

The statistical analyses were carried out using S-PLUS 2000 (MathSoft Inc. 2000) and SPSS (SPSS Inc. 1999) software. As a large proportion of the population (>$30\%$) was individually marked, we did not use the conservative 5% significance level as an absolute cut-off point for the statistical tests, but rather sought to identify the main patterns in our results.

Results

COMPOSITIONAL ANALYSIS OF HABITAT SELECTION

The compositional analysis of habitat utilization within the winter home-range showed a significant non-random use of habitat (Wilk's lambda $\Lambda = 0.559, F_{5,25} = 6.570, P = 0.002$). Ranking the habitat types according to relative use (Table 1a) gave the following habitat ranking (habitat types not significantly different are in bold type):

Woodland > Moorland > Meadow $\geq$ Pasture
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The habitat use during summer within the home-range was not significantly non-random when all years were combined (Wilk’s lambda $\Lambda = 0.844$, $F_{5,15} = 2.469$, $P = 0.076$). However, by analysing low-density and high-density years separately, a contrasting pattern was found in the two periods. In low-density years a significant non-random habitat selection was evident (Wilk’s lambda $\Lambda = 0.490$, $F_{5,19} = 6.585$, $P = 0.003$).

Establishing a ranking matrix (Table 1b) gave the following habitat ranking (habitat types not significantly different are in bold):

Woodland > Meadow ≥ Moorland > Pasture

In high-density years no significant habitat selection was detected (Wilk’s lambda $\Lambda = 0.900$, $F_{5,17} = 1.371$, $P = 0.267$), although woodland still had the highest ranking.

There was a large variance in the area of woodland within the home-ranges of the different females, with a range of $0–19$ ha in winter and $0–17$ ha during summer.

Table 1. Compositional analysis of habitat use at the within home-range level during (a) winter and (b) summer at low deer density. A negative value in the matrix indicates that the habitat type on the upper line is used more than expected by chance compared with the habitat type in the left column.

<table>
<thead>
<tr>
<th>(a) Winter</th>
<th>Woodland</th>
<th>Moorland</th>
<th>Meadow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moorland</td>
<td>$-0.36$ ($0.15$)*</td>
<td>$-0.27$ ($0.10$)*</td>
<td>$-0.05$ ($0.10$)</td>
</tr>
<tr>
<td>Meadow</td>
<td>$-0.62$ ($0.17$)**</td>
<td>$-0.32$ ($0.10$)**</td>
<td></td>
</tr>
<tr>
<td>Pasture</td>
<td>$-0.86$ ($0.25$)**</td>
<td>$-0.32$ ($0.14$)*</td>
<td>$-0.17$ ($0.17$)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(b) Summer</th>
<th>Woodland</th>
<th>Meadow</th>
<th>Moorland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meadow</td>
<td>$-0.46$ ($0.18$)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moorland</td>
<td>$-0.58$ ($0.20$)**</td>
<td>$-0.15$ ($0.17$)</td>
<td></td>
</tr>
<tr>
<td>Pasture</td>
<td>$-0.75$ ($0.16$)**</td>
<td>$-0.32$ ($0.14$)*</td>
<td>$-0.17$ ($0.17$)</td>
</tr>
</tbody>
</table>

*$P < 0.05$, **$P < 0.005$, ***$P < 0.001$ (two-tailed).

EFFECTS OF HOME-RANGE QUALITY ON LITTER SIZE

As there was no difference in litter size between high-density and low-density years in any stage (all $P > 0.20$, $t$-tests), both periods were pooled in the analyses. There was a positive main effect of the home-range quality index during winter on litter size at all the age stages ($LS_{BIRTH}$: $F = 4.167$, d.f. = 59, $P = 0.046$; $LS_{5\text{DAYS}}$: $F = 4.123$, d.f. = 59, $P = 0.047$; $LS_{35\text{DAYS}}$: $F = 3.689$, d.f. = 59, $P = 0.059$, Poisson regression). The positive values of the regression coefficients ($LS_{BIRTH}$: $\beta = 0.355$, $LS_{5\text{DAYS}}$: $\beta = 0.391$, $LS_{35\text{DAYS}}$: $\beta = 0.400$) show that the does with the highest home-range quality index during winter produced the larger litters, and also had the largest litters when most mortality was finished 35 days after birth (Fig. 1). We could not find any differences in the regression slopes between high- and low-density years ($LS_{BIRTH}$: $F = 1.102$, d.f. = 57, $P = 0.298$; $LS_{35\text{DAYS}}$: $F = 0.432$, d.f. = 57, $P = 0.514$; $LS_{35\text{DAYS}}$: $F = 0.377$, d.f. = 57, $P = 0.542$, Poisson regression), that is, the relationship was the same regardless of density within the range of densities at this study.

EFFECTS OF HABITAT QUALITY ON FAWN WINTER WEIGHTS

No differences between the high-density and low-density years were evident in postnatal investment ($P = 0.98$, $t$-test, after adjusting for litter size), thus the periods were pooled. There was, however, an effect of litter size on postnatal investment ($P < 0.001$, ANOVA). When including the litter size into the model, there was no evidence for a linear effect of the habitat quality index of summer home-range on postnatal investment ($t = -0.707$, d.f. = 51, $P = 0.483$). This result seemed to be unaffected by density, as there was no interaction between the regression slopes in high-density and low-density years ($t = -0.230$, d.f. = 50, $P = 0.819$).
Investigating the second path of our hypothesis about winter weights of the fawns, we found a slight tendency for the females with high home-range quality indices during winter to give birth earlier in the subsequent spring ($\beta = -5.03$, $t = -1.543$, d.f. = 53, $P = 0.129$). However, much variance remained unexplained, as the model (home-range quality) only accounted for 5% of the total variance (Fig. 2a). To see if this effect of the winter home-range could be expected to have any persistent effects, the winter home-range quality index was tested against the estimated weights (in kg) of the fawns on 1 August. Again, a slight tendency occurred for the females with higher home-range quality index to have fawns with the highest estimated weights, when holding the litter size constant ($\beta = 0.85$, $t = 1.077$, d.f. = 45, $P = 0.287$). However, excluding one statistically defined outlier with a high Coock’s distance (female no. 259 in 1994) made the relationship more clear ($\beta = 1.48$, $t = 2.044$, d.f. = 44, $P = 0.047$). Nevertheless, the model (litter size and home-range quality) explained only 14% of the total variance in the estimated weights at 1 August (Fig. 2b).

There was a difference between low-density and high-density years in fawn winter weights ($t = 2.738$, $n = 33$, $P = 0.011$, $t$-test); thus this factor was included into the model as a dummy variable. The partial regression coefficient between the home-range quality index the postnatal winter and adjusted winter weights of the fawns, represented by the residual weight after variation caused by density has been removed. Note that the $x$-axis is log$_{10}$-scaled.

Discussion

A striking feature of our results was that variation in individual fitness parameters could be linked to individual home-range attributes within a population. The fact that the habitat selection was significantly non-random (with the exception of high-density summer conditions) is in full agreement with other studies (e.g. Tufto et al. 1996). Also the preference for woodland was no surprise, as many studies have addressed the importance of cover in habitat selection and use for small ungulates (see Mysterud & Østbye 1999 for a review).

In support of our first expectation, females having best access to woodland during winter produced the largest litters the subsequent spring. We believe that this is due to reduced implantation failure, as Hewison & Gaillard (2001) found that implantation failure was associated with winter conditions. This is also plausible, as the roe deer is characterized as an income breeder (Andersen et al. 2000), indicating that winter/spring conditions should be of great importance for the litter size the subsequent spring. The fact that the does with the best home-range quality during winter also had the highest litter sizes 35 days after birth shows that this effect is persistent, despite the slightly higher mortality rate among triplets, reported by Andersen & Linnell (1998). As almost 95% of all fawn deaths occurred during the first month (Andersen & Linnell...
1998), the litter size by then should be close to the number of fawn raised that year. The importance of implantation failure, rather than fertilization success, in determining litter size in roe deer (Hewison & Gaillard 2001) can also help explain the fact that Wahlström & Kjellander (1995) failed to find any habitat-specific differences in their study which was based on corpora lutea counts.

Our second expectation, that the winter weights of the fawns were affected by the home range quality, was only partly supported. However, the paths are a bit complex, as suggested in Fig. 4. Firstly, we found no effect of the home-range quality during summer on postnatal investment. This might seem a bit surprising, because of the income breeder nature of the roe deer (Andersen et al. 2000). However, on Storfosna the spring flush coincides with the birth period (Linnell & Andersen 1998). During this period, high-quality forage is available (possibly superabundant) over much of the island, in diverse habitats. However, females with a high home-range quality index during winter tended to give birth at an earlier stage, although much variance was left unexplained. As birth date is independent of copulation date in roe deer because of delayed implantation (Linnell & Andersen 1998), it might be plausible to believe that females with good winter home-ranges are better capable of meeting the high energy requirements during late gestation (Sempèrè, Mauget & Mauget 1998), and thus give birth at an early stage. As 80% of all reported births on Storfosna happened within a window of 26 days, and the distribution of dates was normal, i.e. without the long tail typical for ungulates (Linnell & Andersen 1998), the time of birth seems to be constrained from both sides. Our results suggest that giving birth early within this window of 1 month is favourable. The weight of the fawns at the onset of the winter is a central determinant of winter weights (Hewison et al. 2002). However, the significance of birth date remains to be further investigated, as both the mechanisms and effects remain unclear. Furthermore, the winter weights of the fawns were affected by the instantaneous effect of their home-range during their postnatal winter. Whether this effect induced by differences in habitat quality in the postweaning period is caused by increased weight gain or reduced weight loss remains unclear. Although Hewison et al. (2002) reported growth in the postweaning period for roe deer fawns, substantial differences in the body mass development of adults during winter between Scandinavian and French populations have been reported (Hewison et al. 1996; Holand et al. 1998).

To our knowledge, this is the first time fine-scale effects of habitat quality have been documented at the individual level in roe deer or indeed for any other cervid, although similar results exists from the subpopulation scale (Focardi et al. 2001; Pettorelli et al. 2001, 2002). Our results contradict the predictions of the ideal free distribution hypotheses. Wahlström & Kjellander (1995), in contrast, found no spatial differences in fitness components, and suggested that roe deer are distributed in an ideal free manner. However, when testing the hypothesis that no difference exists, there is always a danger of accepting the hypothesis even if it is wrong. With the rising evidences for fine-scale spatial variance in fitness components induced by environmental heterogeneity, we therefore strongly suggest that the mechanisms for roe deer spacing behaviour should be re-examined. The fact that roe deer only partially adjust their home-range size in accordance with forage availability (Tufto et al. 1996) further strengthens this view. Future studies should focus on the role of dispersal in the spacing behaviour of roe deer, and how density and phenotypic quality influence the dispersal, in order to understand the mechanisms behind this spatial variation in reproduction and growth.

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