

# Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland

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## Abstract

Data on 22 radio-collared adult female roe deer *Capreolus capreolus* in the Chizé forest were used to test whether their home-range size was influenced by resource availability and reproductive status. As roe deer females are income breeders and invest heavily in each reproductive attempt, they should be limited by energetic constraints. Thus it was expected that: (1) heavier females should have larger home ranges; (2) that home-range size should decrease with increasing vegetation biomass; (3) home-range size should increase with increasing reproductive effort (i.e. females with two fawns at heel should have larger home ranges than those with one fawn, which should have larger home range than females without fawns). To test these predictions, variation in spring–summer home-range size was studied in 2001 and 2002, using 95% kernel home-range estimation. Results showed that females do not adjust their home-range size in response to body mass or age. Home-range size increased with increasing reproductive success, but the magnitude of the change varied over the period of maternal care. Finally, although their home-range size decreased with increasing plant biomass (slope =  $-0.11$ , SE =  $0.065$ ), female roe deer at Chizé did not fully compensate for declines in food availability by increasing home-range size.

**Key words:** biomass, *Capreolus capreolus*, habitat quality, habitat use, home range, roe deer, ungulates

## INTRODUCTION

Variations in the size of home ranges in mammals have been attributed to many different factors including body size and mass (e.g. Swihart, Slade & Bergstrom, 1988), sex and age (Cederlund & Sand, 1994; Relyea, Lawrence & Demarais, 2000), reproductive status (Bertrand *et al.*, 1996), season (Nicholson, Bowyer & Kie, 1997), availability of forage (Tufto, Andersen & Linnell, 1996; Powell, Zimmerman & Seaman, 1997; Relyea *et al.*, 2000), availability of water (Hervert & Krausman, 1986; Bowers, Welch & Carr, 1990), fragmentation of landscape (Kie *et al.*, 2002), trophic level (Harestad & Bunnell, 1979), subspecies (Kie *et al.*, 2002), and intra- (Riley & Dood, 1984) and interspecific competition (Loft, Kie & Menke, 1993). Interspecific variation in home ranges has been studied in some depth (Gittleman & Harvey, 1982; Lindstedt, Miller & Burskirk, 1986), but there has been little work on the causes of intraspecific variation in home-range sizes.

According to the concept of the ideal free distribution (IFD; Fretwell & Lucas, 1970), the size of the home range of an animal within a population should be related to the abundance of its nutritive resources to optimize fitness. According to this theory, animals should occupy the smallest area which contains the resources they require (Harestad & Bunnell, 1979). As the nutritive value of plants changes considerably during the spring and summer (Deinum, 1984), the home-range size of individuals should vary during this period. These predictions were tested on roe deer *Capreolus capreolus*, a selective feeder experiencing large fluctuations in the distribution and abundance of selected plants (Andersen, Duncan & Linnell, 1998). During summer the home-range size of roe deer of both sexes is strongly influenced by the food supply (Bobek, 1977) and female habitat use may be even more directly influenced by resource availability because of reproductive constraints (Tufto *et al.*, 1996). Indeed, female roe deer allocate high levels of resources to reproduction compared to most other ungulates (Andersen *et al.*, 1998) and the survival of fawns is strongly affected by environmental variation, probably through effects on maternal nutrition (Gaillard, Liberg *et al.*, 1998).

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In a detailed study of home ranges of roe deer living in a heterogeneous habitat including woodland, heath and grassland, Tufto *et al.* (1996) found, as expected from the IFD concept, that food abundance influenced home-range size, which increased in areas where resources were relatively sparse, but the compensation was only partial. This result suggests that there were costs involved in expanding the home range to compensate fully for decreased resources. Female reproductive status (breeding *vs* non-breeding) also had an effect on home-range size. As expected from their higher energy requirements, breeding females had larger home ranges than non-breeding females. However, the number of fawns did not influence home-range size. Deer habitat in most deciduous forests in temperate areas of Europe only includes woodland and is therefore expected to be less heterogeneous at the population scale than that studied by Tufto *et al.* (1996). On the other hand, at the scale of roe deer home ranges, food resources in temperate forests are expected to be more diversified compared to northern countries. In support of this view, Pettorelli and Colleagues (Pettorelli, Gaillard, Duncan *et al.*, 2001; Pettorelli, Gaillard, Van Laere *et al.*, 2002; Pettorelli, Dray, Gaillard *et al.*, 2003) in France and Focardi *et al.* (2002) in Italy reported marked spatial variation in life-history traits of roe deer at a small scale. In this study we assess whether the ecological factors found to influence home-range size in the northern habitat of Norway shape the size of female home range in deciduous forests, the typical roe deer habitat. More precisely the following predictions were tested (p1–p3):

*P1.* Assuming that home-range size of female roe deer is determined mainly by resource availability (Tufto *et al.*, 1996) and reproductive constraints (Linnell, 1994), and considering the strong spatial heterogeneity of food resources at the scale of roe deer home range, marked differences were expected in home-range sizes among months and among females. Thus for a given home-range quality, larger individuals should have larger ranges owing to their higher absolute energy requirements (P1.1), and home-range size should decrease from April to May–June and then increase in response to changes both in vegetation biomass and quality (Bobek, 1977; Harestad & Bunnell, 1979; Cederlund, 1983; Tufto *et al.*, 1996) and reproductive constraints (in April, with no offspring, the sizes of the home ranges should be larger than in May–June, when newborn offspring with little mobility should lead to a decrease in the size of the home ranges of the mothers, while increased mobility of offspring in July–August should lead females to increase their home-range size) (P1.2).

*P2.* Because roe deer females: (1) do not store large body reserves (income breeder tactic, Andersen, Gaillard *et al.*, 2000) and (2) allocate a high level of energy to each reproductive attempt (Mauget, Mauget & Sempéré, 1999), for a given home-range quality, females with two fawns were expected to have larger ranges than females with one fawn, which would have a larger range than unsuccessful mothers.

*P3.* Assuming that the distribution of non-territorial females fits an IFD (as supported by Kjellander & Wahlström, 1995, but see Pettorelli, Gaillard, Duncan *et al.*, 2001), roe deer females were expected to adjust their home-range size to the amount of resources they can get there. Therefore, a negative isometric relationship was expected between biomass of preferred plants (a measure of home-range quality) and home-range size.

These predictions were tested for roe deer living in a deciduous oak–beech forest, using data recorded for 2 years on known-age females for which body mass and yearly reproductive success was measured.

## MATERIAL AND METHODS

### Site

The study was carried out in the Chizé reserve, 2614 ha of enclosed forest in western France (46°05'N, 0°25'W). The climate is oceanic with mild winters and hot, dry summers. The dominant trees are deciduous, and detailed information about the Chizé forest is available in Gaillard, Delorme, Boutin *et al.* (1993) and Pettorelli, Gaillard, Van Laere *et al.* (2002). Principal food plants for roe deer in spring and summer are oak *Quercus* sp., hornbeam *Carpinus betulus*, maple *Acer campestre*, hawthorn *Crataegus monogyna*, and dogwood *Cornus* sp. at Chizé (see Duncan *et al.*, 1998).

### Roe deer population

The population at Chizé has been monitored intensively since 1978 using capture–mark–recapture methods. The dynamics of this population is well known (Gaillard, Delorme, Boutin *et al.*, 1993; Gaillard, Boutin *et al.*, 1997; Gaillard, Liberg *et al.*, 1998): it grew from *c.* 200 in 1979 to a peak of 550 in 1983 and then decreased to < 200 in the mid-1990s owing to both density-dependent responses of recruitment and severe summer droughts in the late 1980s. In roe deer, births are highly synchronized and occur mostly in May (with 80% of fawns being born between 5 and 25 May, Gaillard, Delorme, Jullien *et al.*, 1993; Linnell, Wahlström & Gaillard, 1998). The mothers therefore lactate from May to October (Sempéré *et al.*, 1986) with peak requirements in May–June.

### Home-range sizes and their quality

Twenty females were monitored in 2001 and 17 in 2002 (including 15 monitored in 2001 and 2 new females) using Biotrack<sup>®</sup> radio-collars. All radio-collars were removed at the end of the monitoring, during the intensive yearly captures (with about half the population captured each year, Gaillard, Delorme, Boutin *et al.*, 1993). All females were of known-age because they had been caught as fawns. As the key period for fawn survival of roe deer is the summer (Gaillard, Liberg *et al.*, 1998), the study

**Table 1.** Home-range size (ha, estimated from the selected model), reproductive success (number of fawns at heel), and body mass of female roe deer *Capreolus capreolus* monitored during spring–summer (April–August) 2001 and 2002

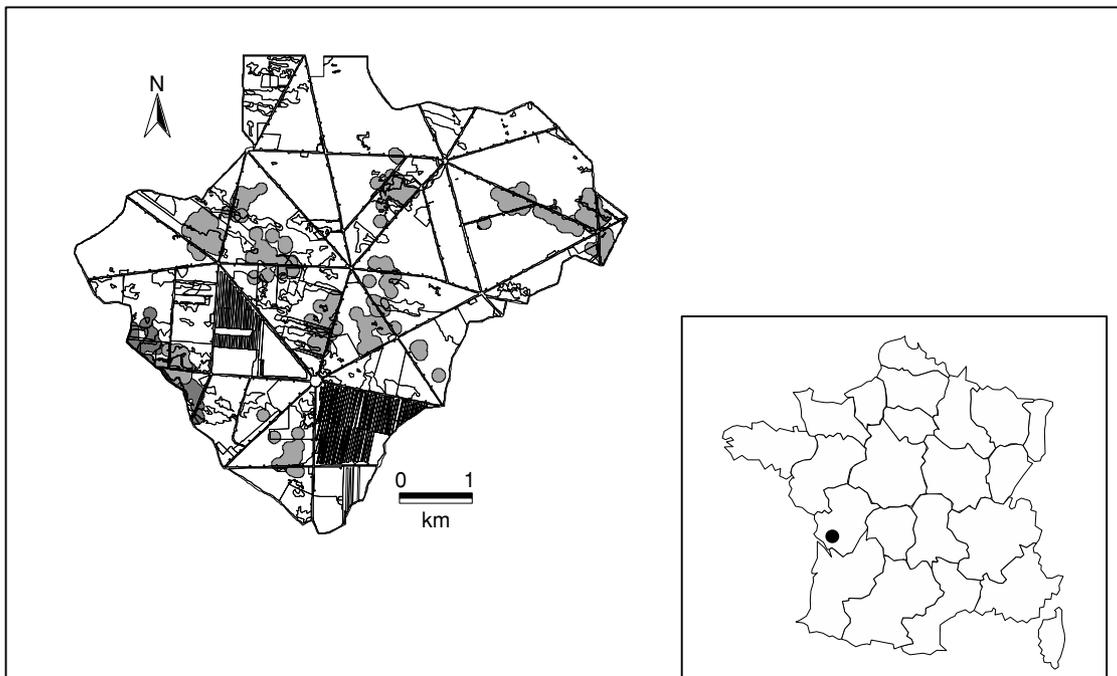
Female identity	Home-range size	Reproductive success		Mean body mass
		2001	2002	
1	21.20	2	0	23.7
2	23.56	0	2	24.7
3	20.86	2		25.1
4	23.14	0	2	24.4
5	26.70	1	1	22.1
6	24.10	2	2	25.4
7	25.78	2	1	22.98
8	25.04	1		25
9	29.30	1		18.1
10	24.16	2	1	25.5
11	27.81	2		23.35
12	22.75	1	1	24.7
13	23.92	2	2	23.23
14	24.58	1		23.75
15	24.41		2	22.9
16	22.15		1	24.9
17	24.93		0	25.2
18	23.00		2	24.9
19	32.04		1	24.35
20	30.11		2	23.35
21	26.20		2	22.45
22	20.92		2	25.25

was focused on the spring–summer period, so the females were located on an average of 17 occasions per month (between 16 and 18) from April to August (Table 1). The minimum interval of time between 2 locations varied

from 6 to 8 h. This study therefore encompassed the key-periods of late gestation (April), birth (May) and the strict lactation period (*sensu* Pontier *et al.*, 1989) in June. Equal numbers of observations were made each month around dawn, midday, evening and at night (6 h blocks): dawn: 6 to 9 h in April and 05:00–8:00 in May, June and July; midday: 09:00–19:00 in April and 08:00–20:00 in May, June and July; evening: 19:00–22:00 in April and 20:00–23:00 in May, June and July; night: 22:00–06:00 in April and 23:00–05:00 in May, June and July; with a minimum of 1 location made per week and per 6 h block.

Radio-tracking data were analysed using the GIS application Arcview 3.2 (Environmental Systems Research Institute Inc., Redlands, U.S.A.) and the Animal Movement extension (<http://www.absc.usgs.gov/glba/gistools/index.htm>) (Hooge & Eichenlaub, 1997). Home-range sizes were estimated for each period, using fixed kernel estimator (Silverman, 1986; Worton, 1989; Fig. 1).

To assess whether home-range size varied among months (prediction P1.2), the data from each month were analysed separately, and the analysis for the 95% kernel (Worton, 1989) conducted. The analyses were also conducted at the 50% level, which led to the same results, so only the results for the most common estimate of home-range size, the 95% kernel, is reported here. Although some authors have previously warned against the use of kernel estimates when < 30 locations are available (e.g. Seaman *et al.*, 1999), it was found that 17 locations provided reliable monthly estimates of home-range size in roe deer at Chizé. Indeed, similar size and position of home ranges were found when comparing our estimates with a GPS monitoring involving 180 locations/month (M. Pellerin, S. Saïd, P. Duncan & J. M. Gaillard, pers. obs.).



**Fig. 1.** Chizé reserve (2614 ha of enclosed forest in western France) showing individual home ranges (grey) of 15 roe deer *Capreolus capreolus* females monitored in 2001. Inset, position of the reserve in France.

### Abundance of the food in the home ranges

On the basis of previous work, plants were classified into 3 classes of acceptability (preferred and/or principal *sensu* Duncan *et al.*, 1998, used as available and avoided) in spring (April, May) and summer (June, July, August; Tixier *et al.*, 1997). In the analyses described below, the relationships between home-range size and the abundance of these categories were consistent with the results for total biomass, which is therefore used for simplicity. The abundance of the plants was assessed using a vertical, 3-D 25 × 25 × 120 cm quadrat (Saïd *et al.*, 2005), with 6 replicates at 8 stations randomly placed in each home range. The touches of edible organs (leaves and flowers) were counted at 2 height sections 0–45 cm and 45.1–120 cm (the maximum feeding height; Duncan *et al.*, 1998), and then converted to biomass using prediction equations developed from a sub-set of quadrats where all the edible organs were clipped and dried to constant weight. Only 1 measure of biomass was calculated each year for a given female from samples performed in May–June. This method of assessing plant biomass is similar to the point intercept method commonly used in Northern Europe (see Jonasson, 1988). There were significant differences among plant species in the relationship between biomass and the number of touches, so separate equations were calculated for the 10 commonest trees (average  $r^2 > 0.59$ ), 13 fairly common trees and shrubs were grouped in pairs and a trio of similar species (average  $r^2 = 0.60$ ), and the remainder lumped other food plants, mostly forbs (9 species,  $r^2 = 0.55$ ), graminoids ( $r^2 = 0.65$ ), a group of avoided species (10 species,  $r^2 = 0.38$ ).

### Reproductive success

As in most temperate ungulates, virtually all the summer mortality of roe deer fawns occurs within the first weeks of life (Gaillard, Festa-Bianchet *et al.*, 2000). Observations were therefore made of each female in late summer, after the hiding phase but before weaning, and the number of fawns at heel was counted. The number of fawns was determined by observations of the females from August to September (2001) and November (2002). The female was slowly driven with her young to a road where 2 observers were stationed. Either the person driving the female saw the mother with her fawns directly, or these were seen by the observers. This procedure was repeated at least 3 times when a females had < 2 fawns, to be sure that a fawn had not been missed.

### Statistical analyses

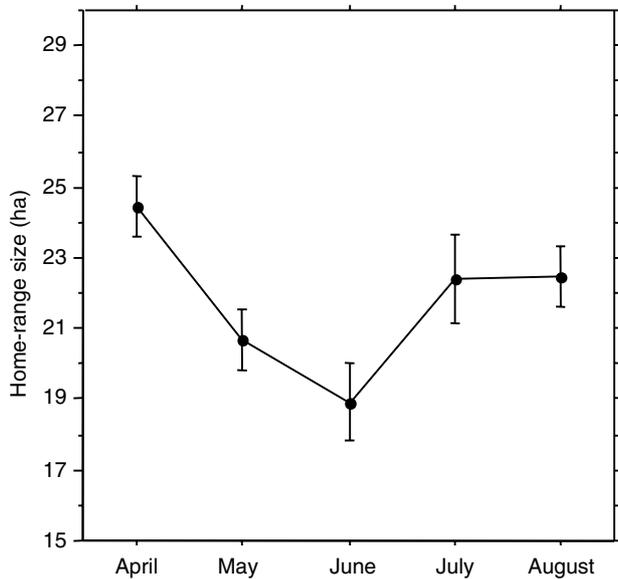
To test our predictions about the sources of variation in home-range size of females, the monitoring of radio-tracked females performed from April to August was used. A linear mixed model was fitted with the 95% kernel as the dependent variable, and the year (2001 or 2002) as a

2-modality fixed factor, the month (April, May, June, July and August) as a 5-modality fixed factor, the reproductive success (0, 1 or 2 fawns at heel) as a 3-modality fixed factor, the female body mass, her age and the biomass of her home range as 3 covariates, and the female identity as a random factor. A REML procedure was used and the significance of the model terms tested for the fixed effects using Wald tests. To select the best model, the Akaike information criterion (AIC) was used as recommended by Burnham & Anderson (1998). The model with the lowest AIC value (i. e. the best compromise between accuracy and precision) was retained. When the difference between 2 models was < 2, the simplest model was retained according to the parsimony rules (Burnham & Anderson, 1998). All the analyses were performed by using the R 1.9.1 statistical package (R Development Core Team, 2004).

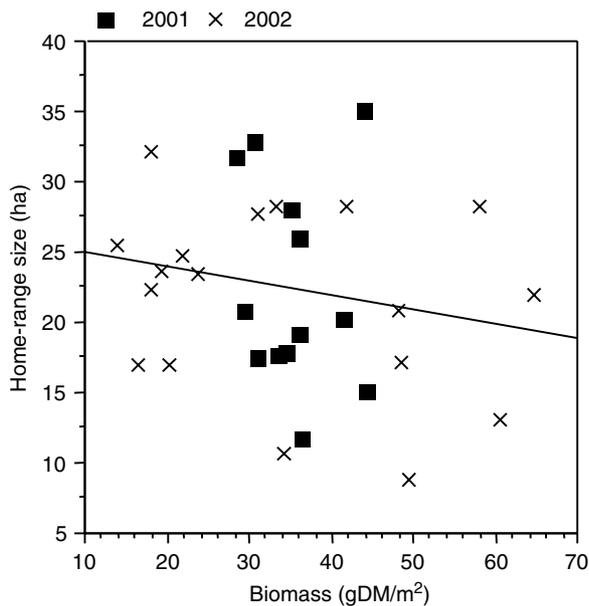
### RESULTS

The estimated mean monthly home-range size was 21.7 ha (SE = 0.48). From the model including additive fixed effects of year, month, age, biomass, body mass and reproductive success as well as a random effect of female identity (AIC = 905.11), the year of study, the female age and her body mass did not influence home-range size. The home-range size was only 0.74 ha (SE = 1.03) larger in 2002 than in 2001 ( $P = 0.475$ ). Although the home-range size tended to increase with increasing body mass (prediction 1.1), the trend was very weak (slope of 0.37, SE = 0.49,  $P = 0.45$ ) and showed a very weak trend to decrease with increasing age (slope of -0.57, SE = 0.36,  $P = 0.12$ ). Therefore, the year, the female body mass and the female age were dropped to get a better model (AIC = 903.53). As expected (prediction 1.2), female home-range size varied greatly among months: from an average of 27.15 ha in April, the home ranges declined by c. 5.6 ha (SE = 1.14,  $P = 0.001$ ) in June (21.54) and then increased in July and August (average size of 24.75 ha and 24.89 ha, respectively) (Fig. 2).

Support was found for an increasing home-range size with increasing reproductive success (our second prediction). Home-range size tended to increase from 0 to 1 fawn (increase of 1.60 ha, SE = 1.78,  $P = 0.37$ ) and markedly increased from 1 to 2 fawns (increase of 3.74 ha, SE = 1.37,  $P = 0.007$ ). Likewise, in support of our third prediction, female home-range size decreased with increasing plant biomass ( $P = 0.002$ ) but the slope differed from -1 (-0.14, SE = 0.04) indicating that female roe deer adjust the size of their home range to the resources available only partially (Fig. 3). When looking at possible interactions among fixed factors and covariates, evidence was only found for interactive effects between month variation and reproductive success (AIC = 876.38). Indeed, while all females showed the lowest home-range size in June irrespective of their reproductive success, females with fawns at heel had larger home-range sizes than females without fawns in April and August and females with two fawns at heel had much larger home



**Fig. 2.** Changes in mean ( $\pm$  SE) home-range size (ha) during spring and summer periods for female roe deer *Capreolus capreolus* at Chizé, France.



**Fig. 3.** Relationship between home-range size (ha) in July and biomass (gDM/m<sup>2</sup>) for female roe deer *Capreolus capreolus* in the deciduous forest of Chizé (France) during 2001 and 2002.

ranges than any other female category during the intensive period of maternal care (i.e. May to July; Fig. 4).

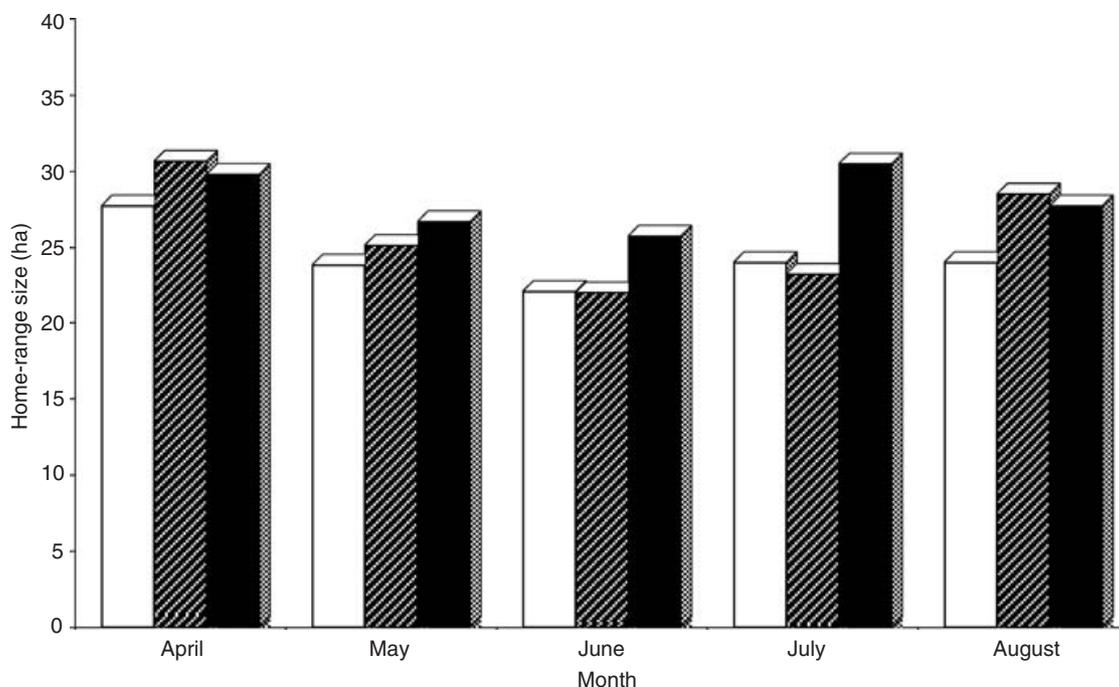
Lastly, in support of the expected marked spatial heterogeneity in roe deer resources at the scale of home range, strong among-female variation was found in home-range size when other sources of variation were accounted for (from 20.86 ha for female 3 to 32.04 ha for female 19; Table 1).

## DISCUSSION

Our results show that female roe deer do not adjust the size of their home ranges according to their age or body mass. The fact that age (and experience) have no effect on home-range size is perhaps not surprising, because it is known that females do not change their habitat during their lives (Holand *et al.*, 1998). Body mass had no influence on home-range size either here or in the study of Tufto *et al.* (1996), indicating that roe deer seem to adjust their home-range sizes in response to factors other than purely metabolic requirements. As expected, the size of the home ranges differed strongly between spring and summer at Chizé. In spring, females occupy small home ranges (Vincent *et al.*, 1983; Chapman *et al.*, 1993; this study). After the high energy expenditure during the strict lactation period, mothers range more widely, and recover their body condition (San José & Lovari, 1997). The interactive effects found between the female reproductive status and the month of monitoring on home-range size nicely fits the between-female differences in energy requirements according to the reproductive output expected to occur in an income breeder such as roe deer.

As expected, females with fawns at heel had larger ranges than females without fawns, and females with two fawns had much larger ranges than other females in the most costly period of maternal care (end of gestation and early lactation). This result requires confirmation with a larger number of females, however, because in this study there were only three females with one fawn and two without fawns. Home-range size increased significantly in July–August, during the rut, which is likely to enhance opportunities for mating, thus allowing a wider male selection (San José, Lovari & Ferrari *et al.*, 1998).

The monthly average spring and summer home-range size (95% kernel) in this study (21.7 ha) was much smaller than the 60 ha reported in the northern site of Storfosna, Norway by Tufto *et al.* (1996). This is consistent with differences in plant biomass, which was almost twice as dense at Chizé (see Tufto *et al.*, 1996), partly accounted for by the much more open habitat on Storfosna. Both San José & Lovari (1997) and Cargnelutti *et al.* (2002) found that home-range size of roe deer individuals increases with the degree of habitat openness. Within each population, home-range sizes increased with decreasing vegetation biomass, supporting our prediction that the availability of resources partly determines home-range size of female roe deer during the spring–summer season, the period of highest energy expenditures. Thus at Chizé, as has been found in other studies of roe deer (Cederlund, 1983; Selas *et al.*, 1991; Wahlström & Kjellander, 1995; Tufto *et al.*, 1996), females do adjust their home-range size to the amount of resources they can obtain. However, as on Storfosna, female roe deer at Chizé did not fully compensate for lower food availability by increasing home-range size; the slope of the regression of home-range size on the biomass of food plants was much higher than  $-1$  (Tufto *et al.*, 1996 and Results above). Therefore, the ideal free distribution can be rejected for female roe



**Fig. 4.** Variations in female roe deer *Capreolus capreolus* home-range size during spring–summer, according to their reproductive success. White bar, no fawn; hatched bar, one fawn; black bar, two fawns. Home-range sizes are the expected values from the selected model (i.e. the model including the fixed effects of plant biomass, the interaction between fixed effects of month and reproductive success and a random effects of female identity).

deer contrary to the report by Wahlström & Kjellander (1995) on a Swedish population. Our finding supports a previous analysis of spatial variation of body mass in the population of Chizé (Pettorelli, Gaillard, Duncan *et al.*, 2001). Factors other than food, perhaps social, seem to be important determinants of home-range size. In white-tailed deer, territoriality of females during the fawn rearing period has been reported (Marchington & Atkeson, 1985) and although little is known about interactions among roe deer females during the rearing period, we hypothesize that similar behaviour occurs in the related roe deer (Kurt, 1968).

For a given month, home-range size varied strongly among females. Individual differences other than age and body mass must account for this variation. Although our sample size was not large enough to look for an effect of spatial heterogeneity in habitat, females in the poor beech stand were expected to have larger ranges than females in the rich oak–hornbeam stand (Pettorelli, Gaillard, Duncan *et al.*, 2001; Pettorelli, Dray *et al.*, 2003). As expected, the females with the smallest home ranges (female identity 1, 3 and 22) were located in the rich oak–hornbeam stand in the north part of the forest, while the females with the largest home-range sizes (female identity 9, 19 and 20) were located in the poor beech stand in the south of the forest (Table 1). Moreover, other sources of inter-individual differences are of the greatest interest, including clan size, local density and rank. Their elucidation requires further detailed investigations on known, recognizable individuals.

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