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What shapes intra-specific variation in home range size? A case study of female roe deer

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Spatial distribution in mammals, and thereby home range size, is influenced by many different factors including body size, sex, age, reproductive status, season, availability of forage, availability of water, fragmentation of landscape, trophic level and intra- and inter-specific competition. Using linear mixed models, we looked for factors shaping the variation in size of spring-summer and winter home ranges for 51 radio-collared adult female roe deer at Trois Fontaines forest, Champagne-Ardenne, France (1996–2005). Home range size of females was larger in winter than in spring-summer, decreased with age, and decreased with increasing quality. Females in low quality areas adjusted the size of their home range to include more patches of habitat so that all female deer obtained similar amounts of food resources (total biomass of 6.73 ± 2.34 tons (mean \pm SE) for each home range). Such adjustments of home range size in response to patchiness of resources led to marked between-female variation in home range size. Our results demonstrate that roe deer females have different tactics of habitat use according to spatial variations in habitat quality so that females get similar food resources in highly productive environments such as the Trois Fontaines forest.

Assessing home range characteristics and identifying factors that shape variation in home range size is a popular topic in vertebrate ecology. Variations of home range size have been related to body size (Peters 1983), sex and age (Relyea et al. 2000), reproductive status (Bertrand et al. 1996), season (Nicholson et al. 1997), availability of forage (Relyea et al. 2000) or water (Bowers et al. 1990), fragmentation of landscape (Kie et al. 2002), trophic level (Harestad and Bunnell 1979), taxonomy (Kie et al. 2002), and intra- (Riley and Dood 1984) and inter-specific competition (Loft et al. 1993). However, while allometric constraints and diet have been shown to account for most inter-specific variation in home range size (Lindstedt et al. 1986), our understanding of intra-specific variation in home range size remains poor. Indeed, several studies have reported large variation within and among different populations (Kie et al. 2002), but most studies have focused on habitat use and selection, so that the mechanistic causes for observed variation in home range size have not been clearly identified. We aim here to fill this gap by providing a comprehensive analysis of among-individual variation in home range size of female roe deer according to reproduction, intra-specific competition, and habitat quality. Indeed, according to the concept of the ideal free distribution (IFD,

Fretwell and Lucas, 1970) the size of an animal's home range should be determined by the balance between population density and resource availability.

Roe deer *Capreolus capreolus* are selective feeders that experience large fluctuations in the distribution and abundance of forage over time and space (Duncan et al. 1998). Female roe deer allocate high levels of resources to reproduction compared to most other large herbivores (Andersen et al. 2000), and early survival of fawns is strongly influenced by climatic conditions during spring-summer and by population density (Gaillard et al. 1997). Moreover, roe deer females do not store body reserves (Andersen et al. 2000) so that the extra-energy required to raise fawns is largely met during the late gestation-early lactation period (income breeder tactic, Andersen et al. 2000). With such a life history tactic the reproductive status of roe deer females strongly depends on resource availability during spring-summer (McLoughlin et al. 2007). We thus expect to find strong links among home range patterns, resource availability, and female attributes in roe deer.

From the intensive monitoring of roe deer females over a period of 10 years (ca 80 female-years) in the well-studied population of Trois Fontaines (Gaillard et al. 1993), we tested the following hypotheses:

- (H1) As previously reported in another roe deer population (Saïd et al. 2005a) and considering both the spatial constraints of nursing fawns and the marked decrease in resource availability during winter in temperate areas, we expected to find seasonal variation in home range size, with largest home range in winter and smallest ranges in spring–summer.
- (H2) For a given home range quality and population density, home range size should increase with individual body mass (as a result of larger absolute needs, Peters 1983) and
- (H3) Decrease with age (as a result of increased experience and/or knowledge of the habitat).
- (H4) The high energy allocation of female roe deer to reproduction and their income breeding tactic (Andersen et al. 2000) should lead them to increase home range size during the rearing period when the number of fawns to raise, and thereby the energy requirements, increases.
- (H5) As previously reported in other roe deer populations (Kjellander et al. 2004), we expected home range size to decrease with increasing of both density and
- (H6) Resource availability or quality (Saïd et al. 2005a).
- (H7) Lastly, habitat structure such as habitat openness and habitat fragmentation is expected to influence home range size (Tufto et al. 1996). As increased openness and/or visibility in forested habitat correspond to more clearings and thus more food for roe deer, we expected to find a negative relationship between these habitat variables and home range size.
- (H8) As an increase in the amount of edge (or number of habitat patches) is related to an increase in the availability of resources (Saïd and Servanty 2005) this should also result in a decrease of home range size.

Material and methods

Study area

The study was conducted in the Territoire d'Etude et d'Expérimentation of Trois Fontaines (TF), a 1360 ha enclosed forest in north-eastern France (48°43'N, 4°56'E). The climate is continental, characterized by cold winters (mean daily temperature in January is 2°C, data from Météo France) and hot, but not dry summers (mean daily temperature in July is 19°C and total rainfall in July–August is 130 mm, data from Météo France). The forest overstory is dominated by oak *Quercus* spp. and beech *Fagus sylvatica* while the coppice is dominated by hornbeam *Carpinus betulus* (Dray et al. 2008). The soil is fertile and the forest highly productive, with a long-term average of 5.92 m³ of wood annually produced per hectare and high NDVI values during the growing season (Pettorelli et al. 2006). Based on our current knowledge of food habits of roe deer (Duncan et al. 1998), the study site offers rich habitat for roe deer.

The roe deer

Roe deer are generalist herbivores that feed selectively (Duncan et al. 1998). In western Europe, the principal food plants of this browsing ungulate in summer are oak, hornbeam, maple, hawthorn and dogwood; and ivy *Hedera helix* in autumn and winter (Duncan et al. 1998). The availability of ligneous and semi-ligneous plants, which are preferentially eaten by roe deer, increased after a hurricane that impacted the study area in December 1999 (Widmer et al. 2004). For this study, we monitored 51 female roe deer between 1996 and 2005 using radio-telemetry. Only adult (≥ 2 years) females of known age (i.e. previously marked as fawn) were included in the analyses.

The population at Trois Fontaines has been intensively monitored since >30 years using capture–mark–recapture methods (Gaillard et al. 1993). Each year, between 150 and 250 roe deer are caught using driving nets in December–March (about 12 days of capture per year). These operations require 150–200 people per day to drive deer into >3 km-long nets that are set each morning and afternoon. The size of the roe deer population at Trois Fontaines increased more than twofold throughout the study period in response to an experimental density manipulation (Fig. 1). The population has been highly productive with all 2-year-old females breeding in most years (Gaillard et al. 1998), but during the last years when density-dependent responses occurred in both fawn body mass (with a decrease of about 1 kg per increase of 100 deer) and summer survival of fawns (Gaillard and Delorme unpubl.).

Home range size

Female roe deer were monitored throughout each year of study with Televilt TXH-3 radio-collars. Females were tracked using the same sampling design during the entire study period. We used a TONNA five-element antenna attached to Televilt RX 900 or Yaesu FT-290R receivers to approach animals to obtain accurate locations. Equal numbers of observations were made each month around dawn, midday, evening and at night (6 h blocks): dawn: 06:00–09:00 h in P2 and 05:00–8:00 in P3; 07:00–10:00 in P1, midday: 09:00–19:00 in P2 and 08:00–20:00 in P3

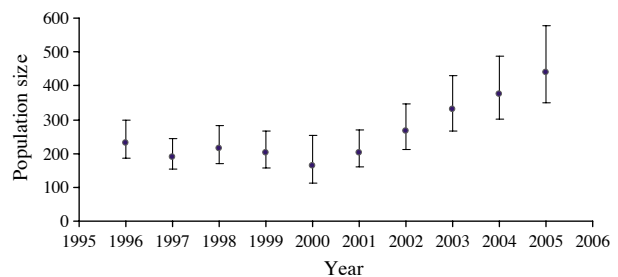


Figure 1. Yearly estimates (with 95% CI) of roe deer population density in March (individuals >1 year) at Trois Fontaines (France) estimated by capture–mark–recapture models (see Gaillard et al. 1993 for further details).

10:00–18:00 in P1; evening: 19:00–22:00 in P2 and 20:00–23:00 in P3, 18:00–21:00 in P1; night: 22:00–06:00 in P2, 23:00–05:00 in P3; 21:00–7:00 in P1; with a minimum of 1 location made per week and per 6 h block. We divided the year into three different time periods: the autumn-winter period (period 1, from 1 November to 15 April) corresponding to the gestation time, the spring period (period 2, from 15 April to 30 June) corresponding to the fawning time, and the summer period (period 3, from 1 July to 31 October) corresponding to the lactation period. To avoid problems generated by unequal sample size among periods, we randomly drew 17 locations within each period (White and Garrott 1990). Although some authors have previously warned against the use of kernel estimators when less than 30 locations are available (Seaman et al. 1999), empirical analyses have shown that about ten locations (Borger et al. 2006) provide reliable estimates of roe deer home range. We previously showed that using 17 VHF locations to assess home ranges of roe deer females provided similar estimates as using 180 GPS locations over the same period (Pellerin et al. 2008). Radio-tracking data were analysed using the GIS application Arcview 3.2 and the Animal Movement extension (www.absc.usgs.gov/globa/gistools/index.htm) (Hooge and Eichenlaub 1997). We estimated kernel home ranges for each period using the 95% fixed kernel estimator (Worton 1989) with h fixed at 60 corresponding to the mean of h -ref values of all animals and months (mean = 62.8 and SD = 25.6). Pellerin et al. (2008) showed that fixing h at the same value for all home ranges (i.e. $h = 60$) provides a reliable way to standardize the estimate of home-range size and thereby provides a better way to compare home ranges of different size and number of locations.

Habitat features at the landscape and home range scale

The study site is divided into 171 numbered forest plots delineated by forest trails. In each plot (average of 7.95 ha), we identified the dominant species and its cover proportion in the coppice wood by using aerial photographs, providing a typology of habitat at the landscape scale at the beginning of the study (1996).

At the home range scale, we used two measures of dry biomass within an individual's home range as a proxy for food resources. We first estimated the dry biomass per m^2 using a field protocol based on the number of plant contacts on a $25 \times 25 \times 165$ cm structure (quadrant-3D; see Saïd et al. 2005b for the calibration of the method). We sampled each female home range every year in May–June according to a systematic sampling design (grid cell of 70×70 m, about 30 points per home range per year). This measure corresponded to the average value of dry biomass per m^2 for a given year. We called it the quality index. We also estimated the total biomass within a home range by using an interpolation method that allowed us to predict unknown values from measures obtained at known locations (Kriging interpolation, Cressie 1993). The Kriging interpolation uses variogram to express the spatial variation. After interpolating the data, we calculated the total food resources within a home range (i.e. total biomass measured

as the sum of dry biomass within a home range calculated with GIS). We called this measure the biomass index.

We measured the visibility within each home range at each point sampled using the quadrant-3D. The visibility corresponded to the proportion of cells (from a sighting card of 16 cells) still visible at 5 m at a height of 50 cm (corresponding to the shoulder height of a roe deer). Lastly, we used a spatial-pattern index (i.e. the total number of patches within the home range; Saïd and Servanty, 2005) as a measure of habitat diversity. We obtained the number of patches within a given period-specific home range using the FRAGSTATS program (McGarigal and Marks 1995) in the Patch Analysis extension for ArcView (Elkie et al. 1999).

Reproductive status

As in most temperate ungulates, virtually all the summer mortality of roe deer fawns occurs within the first weeks of life (Gaillard et al. 2000). Hence, we made observations of each female in late summer, after the hiding phase but before weaning, and counted the number of fawns at heel. We determined the number of fawns by observations of females in September and October. We slowly drove each female to a road where two observers were stationed to record the number of fawns at heel. We repeated this procedure at least three times when a female had less than two fawns, to ensure that a fawn had not been missed.

Statistical analyses

To test our predictions about the sources of variation in female home range size we fitted linear mixed-effects (LME) models ('lmer' function in the 'lme4' R package, Pinheiro et al. 2005). LME models were run using the period-specific 95% kernel home range of a given female in a given year as the dependent variable, and the year (1996 to 2005), the period (autumn-winter, spring and summer), and the reproductive status (0, 1, 2 and 3 fawns) as fixed factors; female age (from 2 to 10 years), quality index (from 30.4 to 39.21 g m^{-2}), biomass index (from 2.9 to 14.3 tons in home range), number of patches (from 9 to 85), and visibility (from 0 to 38%) within the home range as covariates; and female identity as a random factor. To account for possible non-linear effects of covariates, we fitted quadratic terms. We used restricted maximum likelihood (REML) and tested the significance of the model terms for fixed effects using Wald-tests. To select the best model, we used the Akaike information criterion adjusted for sample size (AICc) as recommended by Burnham and Anderson (2002). We retained the model with the lowest AICc score (i.e. the best compromise between accuracy and precision). When the difference between two models was less than 2, we retained the simplest model according to parsimony rules (Burnham and Anderson 2002). All the analyses were performed using the R 2.5.0 statistical package. Parameter estimates are given ± 1 SE but when indicated otherwise. We checked the normality of residuals of the selected model of home range size variation (Shapiro–Wilk test: $W = 0.99$, p -value = 0.80).

Table 1. Top models ($\Delta\text{AICc} < 4$) of variation in home range size for 51 female roe deer according to habitat variables and reproductive status between 1996–2005 at Trois Fontaines, France. Predictors include year, reproductive status (RS), periods of annual life cycle (P), number of patches (NP), quality index (QI), biomass index (BI), age of roe deer (age), visibility (vis), body mass (BM) and the interaction between reproductive status and period of the year (P.RS). AICc corresponds to the Akaike information criterion adjusted for sample size, ΔAICc refers to the change in AICc between a given model and the best model (i.e. the model with the lowest AICc score), K is the number of model parameters, and w_i corresponds to the AICc weight of a given model.

Model	Model predictors	k	AICc	ΔAICc	w_i
	Initial model: age+P+QI+NP+RS+BM+ BI+vis+year+density+P.RS	36	1378.39	30.706	0.00
1	age+P+QI+NP	8	1347.69	0	0.22
2	age+P+QI+NP+vis	9	1348.88	1.197	0.12
3	age+P+QI+NP+BI	9	1349.53	1.841	0.09
4	age+P+QI+NP+BM+vis	10	1349.76	2.072	0.05
5	age+P+NP+vis	8	1350.29	2.605	0.06
6	age+P+QI+NP+density	15	1350.65	2.96	0.05
7	age+P+QI+NP+BI+vis	10	1350.78	3.096	0.05
8	age+P+NP+BI+vis	9	1351.54	3.852	0.03

Results

We found statistical support for 8 of the 25 candidate models (Table 1). However, the best model was the simplest one and all factors included occurred in all models that received some support. Based on the parsimony principle, we retained the simplest model as the best descriptor of home range size variation (Table 2). Female roe deer had a mean home range size of 28.79 ha (± 0.977) in autumn–winter, 20.18 ha (± 1.02) in spring, and 22.26 ha (± 1.19) in summer in support of H1. Females showed considerable variation in home range size (from 16.79 ha to 39.41 ha for a given period). We found only very weak support for H2 as larger females only showed a small trend to have larger home range (slope of 0.283 ± 0.217). In support to H3, home range size decreased with increasing age (slope of -0.384 ± 0.137), so that a female will have a home range smaller by about 4 ha at 12 than at 2 years of age. However, these age-specific changes accounted for $< 1\%$ of the observed variation in home range size. On the contrary to the expectations, neither H4 nor H5 were supported: female home range size did not change according to changes of reproductive success (slope of 0.214 ± 0.398) or of population density (slope of 0.0002 ± 0.0058). While the biomass index (that averaged 6.73 tons (SE = 2.34), slope of 0.07, SE = 0.036) did not influence the home range size of female roe deer, the quality index (that averaged 33.77 g m^{-2} (SE = 1.35), slope of -0.011 , SE = 0.005) did, leading to support H6. On the other hand, H7 was not supported as the visibility did not have

Table 2. Parameter estimates, standard errors (SE) and statistical significance under model 1 in Table 1. The model describes the effects of period of annual life cycle (P), number of patches (NP), age of roe deer and quality index (QI) on home range size of female roe deer ($n = 51$) at Trois Fontaines, France 1996–2005.

Parameter	Estimate	SE	t-value
(Intercept)	20.307	3.675	5.146
Period2	-2.193	0.572	-3.833
Period3	-1.157	0.567	-2.039
NP	0.439	0.023	19.456
Age	-0.375	0.138	-2.722
QI	-0.010	0.003	-3.151

any effect on home range size (slope of -0.375 , SE = 0.382). Lastly, contrary to H8 female home range increased with the number of patches (slope of 0.441 ± 0.023). Note that the biomass index and the number of patches varied independently (slope of 24.35 ± 27.89 , $p = 0.35$).

Our selected model had high explanatory power ($R^2 = 0.78$). From standardized slopes (sts), the influence of the number of patches in a home range (sts = 5.96) was about seven times higher than that of the quality index (sts = -0.930) and that of age (sts = -0.800). The number of patches in a home range accounted for the largest part of the observed variation in home range size (33%), followed by female identity (28.9%).

Discussion

We aimed to assess what factors shaped the variation observed in the home range size of female roe deer. Our results supported four out of the eight hypotheses we tested (Table 3). Although our study took place in an enclosed area, we are confident that the presence of a fence did not influence our results for two main reasons. First, roe deer are extremely sedentary in forested areas (Strandgaard 1972) and our study area was large relative to the home range size, so that most roe deer we monitored were likely to never face with the fence. Second, as we assessed home range variation from the study of environmental factors and of female attributes within the enclosure only, we accounted for possible confounding effects of fencing that could have occurred by using a transversal approach (i.e. comparing home range variation between our fenced population and open populations).

Most previous studies of home range variation at the intra-specific level did not assess possible influence of the reproductive status. We did not provide evidence of home range size variation among females of different yearly reproductive success. The high productivity of the forest at Trois Fontaines might provide enough resources during year so that roe deer do not need to increase their home range size when females have fawns.

Contrary to previous reports (Mares et al. 1982) animals living at high density at Trois Fontaines did not decrease their home range size. In fact, such a negative relationship

Table 3. Synthesis of hypotheses tested from the monitoring of 51 female roe deer over 10 years at Trois Fontaines, France.

	Hypothesis	Support
H1	seasonal variation in home range size (largest home range in winter and smallest ranges in spring-summer)	yes
H2	home range size increases with individual body mass	no
H3	home range size decreases with age	yes
H4	home range size increases with increasing reproductive success	no
H5	home range size decreases with increasing density	no
H6	home range size decreases with increasing resource availability or quality	yes
H7	home range size decreases with increasing openness and/or visibility in forested habitat	no
H8	home range size decreases with increasing in the amount of edge	no

may be attributed to resource availability (Mares et al. 1982) or to interactions among individuals restricting each other's movement at high densities, although in most studies it has been difficult to tease apart these effects. Therefore, the absence of between-year variation we reported is probably due to the high habitat quality that resulted from the marked forest opening performed by the hurricane Lothar (Widmer et al. 2004).

We found that female roe deer do not adjust the size of their home ranges according to their body mass. The relationship between home-range size and body size at the intra-specific level varies from positive (e.g. male Egyptian mongooses *Herpestes ichneumon* – Palomares 1994) to negative (e.g. female Egyptian mongooses – Palomares 1994). Although for a given season the size of home ranges varied strongly among females at Trois Fontaines, such variation was not accounted for by differences in body mass. Females in this highly productive forest are likely to be able to adjust their home range size for compensating changes in resources that are likely to be much more variable than female body mass. This is different from other studies performed in poorer Mediterranean habitats (e.g. Italian roe deer: Focardi et al. 2006).

On the other hand, home range size decreased with increasing age. Cederlund and Sand (1994) found a positive relationship between age and home range size in male but not female moose *Alces alces*, but Saïd et al. (2005a) did not report a relationship between age and home range size in another population of roe deer, maybe as a result of low sample size. Previous researchers have often found that territory size is a function of individual quality (Kodric-Brown and Brown 1978) so that the most likely interpretation of the age effect we report involves increased experience.

We observed the expected negative relationship between home range size and quality index (measured here by the average value of dry biomass per m²) so that the amount of food has a marked influence on home range size as has been commonly reported (Relyea et al. 2000). Resource availability is considered to be the single most important factor influencing animals' home-range size (Mares et al. 1982). Forage availability within a given home range has to satisfy energy and nutritional requirements; otherwise home range size has to be increased.

As a result of the influence of forage availability on home range size, roe deer living in temperate areas range over larger areas in winter than in summer. In winter, there are energetic but not social constraints to movement. As food is depleting throughout winter there is little need for roe deer

to revisit patches. In summer, food is renewed and there are social (territoriality, rearing of offspring) but not energetic constraints to movement (Mysterud 1999). Interestingly, roe deer have been reported to increase home range size in summer when food resources are scarce in Mediterranean areas (Carvalho et al. 2008), suggesting that energetic constraints are more important than social constraints to shape seasonal differences of home range size in roe deer.

That the biomass index (a measure of the total biomass measured as the sum of dry biomass in a home range) did not change in relation with home range size and remained quite constant among females was an unexpected but key result of our analyses. Roe deer females are thus able to compensate for poor home range quality by enlarging home range size. This mirrors results obtained in experimental settings for rufous hummingbirds *Selasphorus rufus* (Kodric-Brown and Brown 1978) where the amount of nectar that each territory contains remains constant despite great variation in size of feeding territories and flower composition. In American red squirrels *Tamiasciurus hudsonicus*, home range size is positively correlated with the number of pine cones within a territory, and thereby to the absolute amount of food energy available to individuals (Smith 1968). Moreover, the home range size of roe deer females was positively correlated with the number of patches. This might be related to the fact that roe deer are browsers (Duncan et al. 1998) for which principal food occurs in edge habitat. Home ranges with few patches (≤ 15) in rich habitat such as areas of fallen trees were smaller than home ranges with many patches (≥ 50) in poor quality as old thickets. Roe deer females have thus two tactics of habitat use to obtain resources (Fig. 2). In this study, the number of patches included habitat heterogeneity, edge density and contact areas between patches of landscape in the home range. At the habitat scale (i.e. rich vs poor habitat), this interplay between home range size and number of patches was obvious (Fig. 2). Our study therefore supports previous works showing that the landscape structure is more complex than the simple consideration of edge length, patch size, or edge density (Kie et al. 2002, Saïd and Servanty 2005). At Trois Fontaines roe deer females could add patches and thereby increase the home range size in order to compensate for a low average quality.

The relationship between home range size and habitat is bounded by a well-defined constraint in space, supporting and extending arguments for constraints on geographic range size (Brown and Maurer 1987) and various other ecological and life history traits (McLoughlin et al. 2007). These constraints almost certainly are a consequence of



Figure 2. (A) Distribution of forest plots, roads, trails and vegetation associations within the forest of Trois-Fontaines. (1360 ha in eastern France, map year 2002). (B) An illustration of three contrasted home ranges size (HR) (in terms of number of patches: NP) of roe deer females and three different tactics of habitat use according to spatial variations in habitat quality so that females get similar food resources in highly productive environments. Home range size has been standardized for year and reproductive status (RS). An example of home range is presented in the east of map (trait thick). Different gray scale shadings illustrate heterogeneity in forest types (McLoughlin et al. 2007) with richest habitat in white and poorest habitat in black.

energetic limitations reflecting the metabolic needs. The number of patches a home range contains and the female identity accounted for most observed variation in home range size of roe deer females at Trois Fontaines. On the other hand, female body mass, population density and

female reproductive success did not influence markedly home range size of roe deer in this productive forest. Our results demonstrate that roe deer females have different tactics of habitat use according to spatial variations in habitat quality so that females get similar food resources in

highly productive environments. In addition we provide here one of very few evidence that older females occupy smaller home range as a likely result of increased experience and/or better knowledge of their environment.

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