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Ranging behaviour and excursions of female roe deer during the rut

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ABSTRACT

Anecdotal evidence has suggested that, during the rutting period, female roe deer may undertake short excursions, outside of their normal home range, possibly to mate with a reproductive partner. To address this question, we analysed the ranging behaviour of 27 female roe deer *Capreolus capreolus*, equipped with GPS collars, inhabiting a fragmented landscape in France. We compared female movements during the rutting period with a non-rutting period over two summers using a recently published approach. Search intensity and home range size were significantly greater during the rutting period. The difference in home range size between the two periods was significantly greater in 2006 compared to 2005 and in open compared to closed habitat. We were not able to identify any influence of body mass on the difference in ranging behaviour between the two periods. Visual analysis of movement trajectories for 11 females revealed that 5 (45%) performed an excursion for a duration of a few hours to several days. We speculatively suggest that female rut excursions provide an opportunity for active mate choice in roe deer, where males are territorial, although we cannot rule out the alternative explanation that these movements are a means to avoid male harassment.

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According to Darwin (1871), sexual selection arises from competition over mates leading to selection on individual traits of one sex that influence reproductive success. He proposed two main mechanisms for this process: competition among males for access to females and competition among males to attract females. The second of these implies that females may express a choice over their reproductive partner (female mate choice). In polygynous large mammals, while evidence for male–male competition over mates is widespread (e.g. Arnould and Duck, 1997 in fur seal *Arctocephalus gazella*, Hogg and Forbes, 1997 in bighorn sheep *Ovis canadensis*, McElligott et al., 2001 in fallow deer *Dama dama*), there is as yet less evidence for mate choice (but see Byers et al., 1994 in pronghorn *Antilocapra americana*, Amos et al., 2001 in grey seal *Halichoerus grypus*, Brø-Jorgensen, 2002 in topi *Damaliscus lunatus*, Charlton et al., 2007 in red deer *Cervus elaphus*). Theoretically, the potential for female mate choice is expected to be higher for species where males form leks or defend territories compared to those where males defend harems or tend females because, in the former, females have greater opportunity to assess the quality of individual males or their territories (Min, 1997).

The roe deer (*Capreolus capreolus*) is a medium size cervid, exhibiting low sexual size dimorphism (Danilkin and Hewison, 1996). Males are strongly territorial from early spring to late summer (Bramley, 1970) and the mating system has been described as resource defence polygyny (Liberg et al., 1998). Territoriality could have evolved as a mating tactic because it may allow males to monopolise reproductive females during the summer rut (Liberg et al., 1998). However, female home ranges commonly overlap the territories of several males and so males cannot completely monopolise females within their territories (Hewison et al., 1998) and there is a potential for the evolution of female mate choice. The variation in the number of female ranges partially overlapped by a male's territory is low, generally less than five (Hewison et al., 1998), so that there is a general prediction of low variance in reproductive success among males (Vanpé, 2007). However, this variance could potentially be greater if females were to express an active choice of mating partner. In a system of resource defence polygyny, female choice is not expected to be oriented directly towards the male himself, but rather towards the quantity or quality of resources defended by him. Indeed, Johansson (1996) suggested that territory quality, and not territory size, influenced male reproductive success in roe deer, although this was not supported by more recent work (Vanpé et al., 2008).

Most animals concentrate their activities within a limited area called the home range (Burt, 1943). In mammals, variation in the size of the home range has been attributed to many factors, includ-

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ing reproductive status (Bertrand et al., 1996). In roe deer, female and male home ranges over the whole summer period are globally of similar size (Danilkin and Hewison, 1996; Liberg et al., 1998). However, there are some indications that some females may range more widely during the short mid-summer rut (San José and Lovari, 1998; Melis et al., 2005), sometimes moving outside their normal home range for a short interval, potentially visiting neighbouring male territories or even crossing several territories (Liberg et al., 1998). This suggests that females may leave their normal home range for reasons of mate choice (i.e. to mate with a male of perceived superior quality or with an unrelated male in the case of inbreeding avoidance) or interference (to find a male that is not occupied with another oestrus female) (Linnell, 1994). Despite recent anecdotal observations (Liberg et al., 1998; Börger, 2006), to our knowledge no detailed published study has yet investigated the importance of this behaviour in roe deer, although Liberg et al. (1998) suggested that as many as 30–50% of females may undertake an excursion during oestrous. If these excursions are accompanied by successful mating and fertilisation, they would constitute a form of breeding dispersal (i.e. movement between two successive breeding areas or social groups, sensu Clobert et al., 2001) and could support the idea that females play an active role in the search for and choice of sexual partner (Liberg et al., 1998).

To explore this behaviour, we analysed the movements of 27 roe deer females monitored using GPS technology in a fragmented landscape. If females actively search for mates, we should expect to observe pronounced movements during the rut, notably an increase in the area of the home range occupied, a preference for particular zones of that range (locations of potential mates) and possibly even excursions of short duration outside of the normal home range (generally < 100 ha during summer, Hewison et al., 1998). Specifically, we aimed to provide evidence for female mate searching using 2 different approaches: in the first, an objective, quantitative analysis was used using a recent and innovative methodological approach (Doerr and Doerr, 2005) and without any *a priori* distinction between individuals, to compare ranging behaviour during the rutting period with that immediately prior to and following the rut; in the second, a more descriptive approach was used to describe, for the first time, the nature (timing, duration, etc.) of rut excursions for those females which performed clear extra-range movements during the rut.

1. Methods

1.1. Study area

The study was carried out in an agricultural landscape located in the south west of France (N 43°23, E 0°52). It is a hilly region, rising to a maximum of 380 m a.s.l. with a mixed landscape of open fields and small woodland patches (average size 3 ha), and a larger central forest of 800 ha. The primary land use is pastoral for sheep and cattle grazing, with agricultural crops on the increase. The total study area covers around 7500 ha with about 25% of that wooded. The human population is present throughout the site, in small villages and farms distributed along the extensive road network which covers the study site. Roe deer were monitored at seven sites across a landscape gradient from forest to open field. Local density of roe deer for the 2 years of study was estimated at around 32 animals/100 ha in the central forest and 7–10 animals/100 ha in the surrounding fragmented landscape using a modified Capture-Mark-Recapture method (Lincoln–Petersen estimator) (see Hewison et al., 2007). The roe deer population is hunted on a regular basis by drive hunts with dogs during winter (September to January) and stalking during summer (June–August, bucks only). Red deer have recently started to colonise this area and wild boar (*Sus scrofa*) are well established. Wild boar hunting starts in the second half of August and hence overlaps somewhat with the end of the rutting period for roe deer, creating a potential source of disturbance during both rutting and non-rutting periods.

1.2. Data collection

During the winters 2004–2005 and 2005–2006 (from October to February), 27 female (3 yearlings of approximately 15 months old and 24 adults of at least 2 years old) roe deer were captured in long nets on the study area. Animals were weighed, sexed and their age class estimated from the eruption and wear of the teeth (Angibault et al., 1993) and then released with a 12 channel Lotek 3300 GPS collar (weight 285 g, advertised accuracy of 35 m, Lotek, 2002). Roe deer were generally monitored for a 46-week period with a schedule of one GPS fix every 6 h (at 06:00, 12:00, 18:00 and 00:00 h). In addition, in order to study reproductive behaviour, during the rutting period of 2006 only, fixes were taken once per hour (note that due to the technical limitations of the collars, we could only programme this fine-scaled tracking for a limited period, i.e. during the 1 month long rut *stricto sensu*). For each fix, satellite configuration (i.e. PDOP), number of satellites and fix status were also recorded. Fix status combines information on whether the fix was 2D (based on three satellites only) or 3D (based on more than three satellites) with an open numeric scale (starting from F0) which may indicate fix quality (see Cargnelutti et al., 2007). We performed differential correction in order to improve fix accuracy (Adrados et al., 2002). All fixes (latitude, longitude) were converted to Lambert III coordinates using pathfinder Office Version 2.7 (Trimble Navigation Ltd., USA).

1.3. Data analysis

1.3.1. Comparing female ranging behaviour between rutting and non-rutting periods

Twenty-seven reproductive females were monitored during one of the 2005 ($N = 16$) and 2006 ($N = 11$) ruts. We visualised the spatial distribution of the data with Arcview 3.2 (Geographical Information System). Extreme fixes outside the study area or isolated fixes with a low index of fix quality (Cargnelutti et al., 2007) which were so far from the previous and/or subsequent fix as to be obviously erroneous were removed from the analysis. More precisely, for the data set with one fix every 6 h, we removed 13 fixes out of a total of 2399 for the non-rutting period and 6 fixes out of a total of 3328 for the rutting period. For the data set with one fix every hour (the 2006 rutting period), we also removed those fixes which were too distant from the previous fix to be biologically plausible (i.e. at a distance that could not be covered by a roe deer in 1 h). We defined the rutting period as running from 20/07 to 23/08 in relation to field observations and published information (Danilkin and Hewison, 1996). During the rutting period, roe deer females become receptive during a single short (approximately 36 h) oestrous (Sempéré et al., 1998). However, as the date of oestrous is not fully synchronous among females (Sempéré et al., 1998), and as we had no information on the timing of oestrous for given individuals, we considered a period of 1 month to define the rutting period. We defined a non-rutting period during the flanking periods, from 5/07 to 19/07 and from 24/08 to 7/09, to avoid the period of intensive maternal care (mainly May–June) and the beginning of the hunting season (mid-September). We selected a non-rutting period of a duration approximately equal to that of the rutting period in order to ensure that derived movement parameters were based on a similar number of GPS fixes in each period. Note, however, that although the time elapsed is approximately equal, the time period spanned by

the non-rutting period is double (2 months) that of the rutting period (1 month). While it is possible that home range size increases with time spanned (for a fixed number of GPS locations), this potential bias would lead us to reject our hypothesis (greater and more pronounced movements during the rut than during the non-rut), hence, our analysis is conservative.

We described the ranging behaviour of females during these two periods using the DRAP program (Dispersal Range Analysis Program) proposed by Doerr and Doerr (2005), as well as an index of forays. The different measures (search area, home range size, search rate, thoroughness, search intensity and the foray index) allowed us to compare mobility and exploration behaviour for each individual female during the rutting and non-rutting periods:

- The *search area* describes the total area explored, while accounting for the temporal sequence of locations, hence it is sensitive to brief forays (such as mating excursions) outside the normal home range (see Doerr and Doerr, 2005). It is derived with the Assessment Corridor (AC) method which describes a corridor of a given width linking all consecutive fixes in a chronological manner to describe the animal's trajectory. The width of the corridor corresponds to twice the maximal distance at which an individual may detect another. This distance was fixed at 100 m in our study (see Pays et al., 2007), although the absolute value used is unlikely to be important (see Doerr and Doerr, 2005), particularly as our main purpose was to compare ranging behaviour of the same animal between periods.
- The *home range size* defines the area traversed by an individual in the course of its normal activities (Burt, 1943) and is the metric most commonly used to describe ranging behaviour. In order to include potential excursions which may be represented by relatively few fixes outside of the normal home range, we used the minimum convex polygon (MCP) method and considered 100% of all fixes (Mohr, 1947).
- The *search rate* gives an estimation of the rapidity of movement, calculated as the total path length for an individual divided by the number of monitoring days. Females which undertake rut excursions to search for mates over a wider area should have a higher search rate than those that remain within their normal range. Note, however, that our fix interval of 6 h means that the absolute search rate was certainly under-estimated, but this should not bias the comparison of this metric between periods.
- *Thoroughness* was calculated as the AC/MCP ratio which gives an estimation of the level of use of each part of the total home range. A low ratio indicates that only part of the total range has been used/searched, for example, in the context of rut excursions, locations of potential mates.
- The *search intensity* measures the distribution of the search effort among the areas actually used by the individual. Given that an individual visits a certain number of areas within its search area, it may distribute search intensity equally among them, or it may intensify its search in just a few of those areas, again, in the context of rut excursions, perhaps in relation to the locations of potential mates. The search intensity is measured by the coefficient of variation of the average number of times random points fall within the Assessment Radius (see search area) of the individual's movement path (see Doerr and Doerr, 2005).
- We also constructed a *foray index* to identify movements outside the normal home range which may indicate that individuals were making forays to search for mates, as suggested by Doerr and Doerr (2005). Because, during the rut, females have a short period of receptivity (36 h) and because our GPS collars were scheduled to take a fix every 6 h, we considered the six fixes which were the farthest from the centre of the home range for both the rutting and the non-rutting periods and considered the mean distance between these fixes and the centre of the home range as the foray index.

All parameters were calculated with a fix every 6 h ($n = 27$ females). As we expected that females, if they actively search for mates, should move more during the rutting period compared to the non-rutting period, possibly including rut excursions outside their normal home range, we predicted that the search area, the search rate and the foray index would be greater and that the home range would be larger during the rut than during the non-rutting period. In addition, because females should concentrate their effort in certain areas in order to find and select a mate during the rut, we expected to find low values of thoroughness and high values of search intensity during the rutting period compared to the non-rutting period.

1.3.2. Description of rut excursions

As excursions may last only a few hours, to directly describe this behaviour we considered only those 11 does from 2006 for which one fix per hour was available during the rut (a total of about 800 fixes per individual). With R 2.4.2 software (R Development Core Team, 2006), we graphically represented the trajectories of females (package Adehabitat 1.5–3) in order to describe the frequency and extent of marked rut excursions. We considered an excursion as a series of sequential fixes which fell outside the cluster made up of all other fixes and were clearly not part of the normal home range.

1.4. Statistical analysis

To detect a potential difference between the rutting and non-rutting periods in terms of movements and ranging behaviour of does, we compared the search area (AC), the home range size (MCP), the search rate, the search intensity and the foray index between these two periods. As these values were repeated measures for each individual (rut and non-rut), we performed paired *t*-tests for each variable independently. To investigate the variation of the thoroughness (AC/MCP ratio) variable between the two periods which was non-normally distributed, we used a Spearman rank correlation between AC and MCP.

Then, only in the case of any significant differences in ranging behaviour between the two periods, to explore which factors might explain these differences, deltas (the difference between rut and non-rut) were calculated for those ranging metrics. As the deltas for search area and home range size were very closely correlated, we did not consider the delta for search area in order to limit the number of tests. Likewise, as the variation of the delta for thoroughness (AC/MCP ratio) was difficult to interpret (the difference between two ratios), this measure was not considered further in these analyses. The deltas were then considered as dependent variables in linear models with year, habitat and body mass as explanatory variables. Year (2005/2006) and habitat were treated as factors, with body mass as a continuous covariate. We considered the habitat as a binary factor, as either open (5–13% of woodland) or closed (at least 25% of woodland), within the local landscape where that animal was caught and ranged. We did not include age in these models because only three individuals in the data set were yearlings (note that, in any case, female yearling roe deer are reproductively active and so should express similar behaviour to that of adults during the rut). We considered body mass of adults at capture (autumn–winter) to be a good indicator of body mass during the following rut as female body mass varies little over the year in roe deer (Hewison et al., 1996).

In preliminary analysis, we verified homogeneity of variances with the Levene's test (Fox, 1997). When variances were homogeneous, we built linear models of the delta of a given measure in

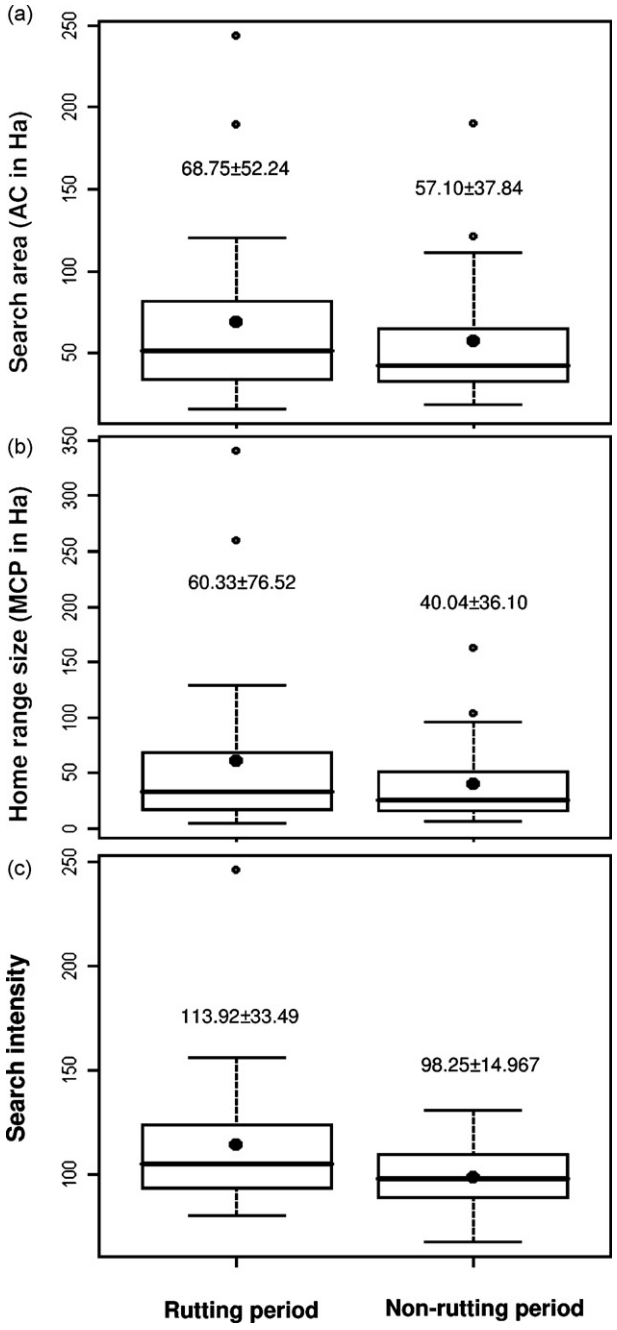

Fig. 1. (a) Search area, (b) home range size and (c) search intensity of female roe deer ($n = 27$) during the rutting and non-rutting periods (with mean ± standard error in brackets). Circles represent outlying data points, the box encompasses the first to the third quartiles, inside the box the horizontal line represents the median and the whiskers are located at 1.5 × IQR (inter-quartile range) below the first quartile and at 1.5 × IQR above the third quartile. The black dot represents the mean.

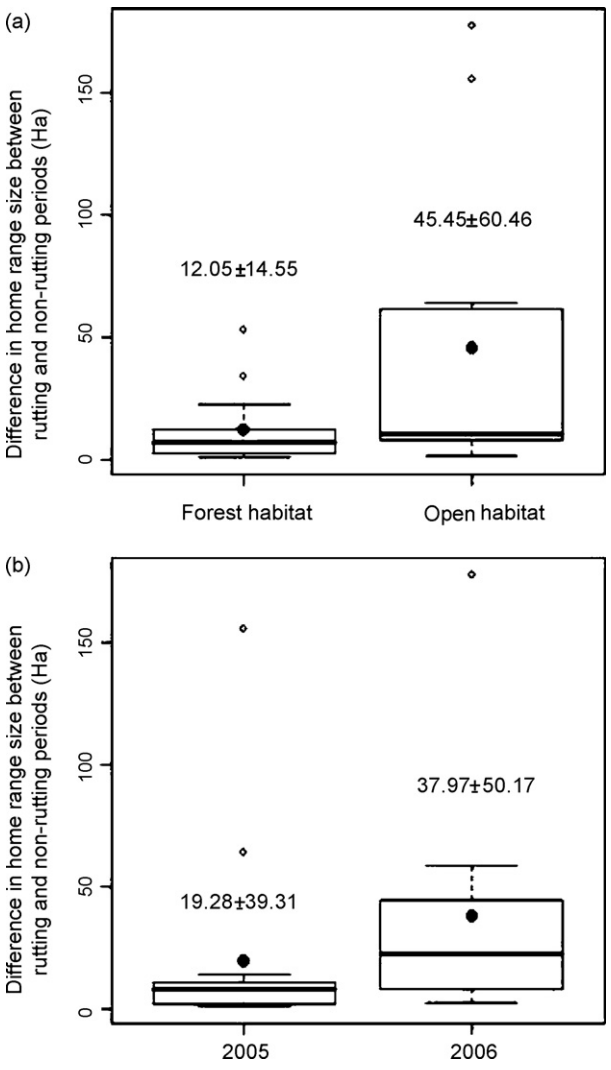

Fig. 2. The difference in female roe deer home range size between rutting and non-rutting periods ($n = 27$): (a) in open and in closed habitats and (b) in 2005 and in 2006 (with mean ± standard error in brackets). Circles represent outlying data points, the box encompasses the first to the third quartiles, inside the box the horizontal line represents the median and the whiskers are located at 1.5 × IQR (inter-quartile range) below the first quartile and at 1.5 × IQR above the third quartile. The black dot represents the mean.

relation to year, habitat and body mass. In this case (homogeneous variances), to select the best model, we used the AIC value corrected for small sample size (AICc, Burnham and Anderson, 1998). When variances were heterogeneous, we used quasi-likelihood models (generalised linear model) in order to take into account the true relation between the mean and the variance of the data (McCullagh and Nelder, 1989). We used the quasi-likelihood with the identity link function and the variance proportional to the square of the mean. In this case (heterogeneous variances), to test the effect of the explanatory variables on the dependent variable, we considered the most complicated model as a starting point and proceeded to simplify it progressively by successive removal of non significant terms at a threshold of 5%. To confirm the pertinence of the quasi-likelihood approach, we compared the residual deviance with the residual degrees of freedom to detect potential over-dispersion in the data.

2. Results

2.1. Comparing female ranging behaviour between the rut and non-rut

The degree of correlation among the different measures of ranging behaviour was highly variable between metrics and between periods ($0.27 < r < 0.98$ during the rutting period; $0.08 < r < 0.99$ during the non-rutting period) except the foray index which is not correlated with others measures. Search area (AC) and home range size (MCP), in particular, were strongly and positively correlated. Indeed, home range size explained 94% of the variability in search

Table 1
Results of model selection performed on search intensity (models and their AICc values)

Model	AICc
Habitat + body mass + year + habitat:body mass+habitat:year + body mass:year	290.15
Habitat + body mass + year + habitat:year + body mass:year	286.29
Habitat + body mass + year + habitat:body mass + body mass:year	286.9
Habitat + body mass + year + habitat:body mass + habitat:year	286.71
Habitat + body mass + year + body mass:year	283.25
Habitat + body mass + year + habitat:year	283
Habitat + body mass + year	280.05
Habitat + year	277.01
Body mass + year	277.3
Habitat + body mass	278.66
Year	274.53
Habitat	275.9
Constant model	273.65

Table 2
Main characteristics of the excursions observed for five females

Female number	Habitat type	Fawns at heel	Duration (h)	Distance (m)	Dates
234	Closed	1	13	1000	16 and 17 August
			26	1200	22 and 23 August
232	Closed	No data	19	700	19 August
260	Open	1	47	1000	29 and 30 July
			6	1425	16 August
			5	600	18 August
306	Open	2	5	700	29 July
			2	900	15 August
			8	900	17 August
264	Open	1	85	4500	6–10 August

area (Spearman rank correlation: $r_s = 0.97$, $N = 27$, $P < 0.001$). Search area (paired t-test: $t_{26} = 2.61$, $P = 0.015$), home range size (paired t-test: $t_{26} = 2.21$, $P = 0.036$), and search intensity (paired t-test: $t_{26} = 2.26$, $P = 0.032$) were significantly greater during the rutting period than during the non-rut (Fig. 1). In addition, we observed a greater variability among individuals in each of these measures during the rut than during the non-rut (Fig. 1). In contrast, the foray index (paired t-test: $t_{26} = -1.65$, $P = 0.112$), search rate (paired t-test: $t_{26} = -1.41$, $P = 0.171$) and the thoroughness of search (paired t-test: $t_{26} = -1.06$, $P = 0.296$) were not significantly different between the two periods.

2.2. Factors explaining differences in female ranging behaviour

Due to a non-constant relationship between the mean and the variance in the data, we used the quasi-likelihood approach on absolute values of differences in home range size between the two periods. Due to the small sample size and some problems of convergence, we did not attempt to model any interactions between the explanatory variables. The absolute difference in home range size between the two periods was significantly higher in open habitat (ANOVA: $F_{1,26} = 12.327$, $P = 0.002$; Fig. 2a) compared to closed habitat. Furthermore, the variance of the difference was also higher in this habitat. In addition, the difference in absolute home range size between periods was greater (both in mean and variance) in 2006 (ANOVA: $F_{1,26} = 5.6$, $P = 0.026$; Fig. 2b) compared to 2005. In contrast, we did not find a significant effect of female body mass on the degree of difference in home range size between periods (linear least-squares regression: $F_{1,26} = 0.002$, $P = 0.964$). So, the best model describing the absolute difference in home range size between the two periods contained the two main effects of habitat and year (residual deviance of 33.2 for 24 degrees of freedom).

For search intensity, we did not find any significant effect of any of the factors tested on the difference in search intensity between the two periods using a linear model. Indeed, the best model was the constant model, although the model including an effect of year had a very similar AIC value to the constant model (see Table 1). All other models had a difference of AICc greater than 2 compared with the constant model.

2.3. Description of female rut excursions

Visual analysis of female movements during the rut of 2006 revealed that 5 out of 11 (about 45%) individuals performed excursions, leaving their normal home range for a duration of a few hours or days (Table 2 and Fig. 3b), whereas the rest always remained within the same home range area (Fig. 3a). For females living in closed habitat, 2 out of 6 (33%) undertook a rut excursion, while in open habitat 3 out of 5 females (60%) did so (Table 2). Females that performed an excursion had a lower thoroughness value (AC/MCP ratio) than other females (0.95 ± 0.15 vs. 1.43 ± 0.08, respectively, Mann–Whitney test: $U_{11} = 3$, $P = 0.030$), indicating that only part of the total range had been used. Three females performed several excursions, or performed excursions of short distance compared to their home range size, leading to intermediate values of the AC/MCP ratio. Speed during excursions was broadly similar whether the female was leaving her normal home range or returning to it (average = 343.1 m/h, S.E. = 100.5 for the out-going leg vs. 248.3 m/h, S.E. = 78.4 for the incoming leg).

3. Discussion

We showed that ranging behaviour of female roe deer during summer differed markedly between the peak rutting period and the weeks just prior to and just after the rut. Indeed, home range size, search area and search intensity were all higher during the reproductive period. This indicates that females increased their space use during the rut (home range size, search area), and concentrated their space use within specific areas of their range (search intensity). We also found that the difference between rutting and non-rutting periods in home range size was more marked in open habitat compared to wooded habitat and during 2006 compared to 2005. Finally, from visual interpretation of GPS fixes for individuals that were intensively monitored during the 2006 rut (1 fix/h), we were able to describe rut excursions (short duration movements outside the normal home range during the reproductive period) for 45% of our monitored female roe deer.

3.1. Evidence for female mate choice?

Our results indicate that female roe deer are able to increase their space use (home range size, search area) during the rutting period, but we were not able to show that they increase their overall movements in terms of distance covered per day (search rate). This is consistent with the fact that females concentrated their activity within certain sectors of their range (increase in search intensity) during this period. A first interpretation of these patterns is that females alter their ranging behaviour during the rut for reasons of mate choice (San José and Lovari, 1998; Rossi et al., 2001 in roe deer; Dahle and Swensson, 2003 in brown bear *Ursus arc-*

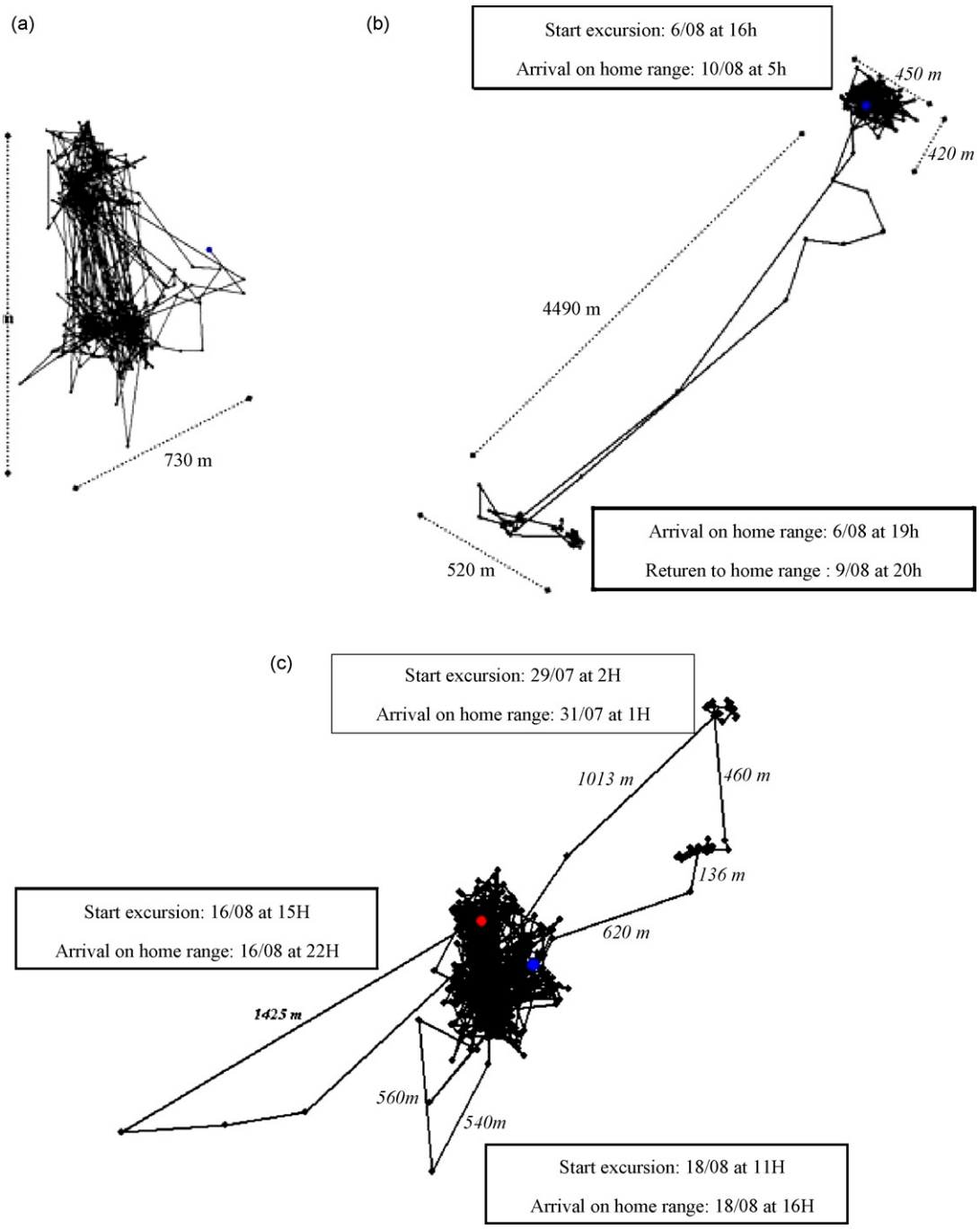

Fig. 3. Examples of movement trajectories of female roe deer during the rut: (a) a female which remained on its home range throughout and (b and c) two females which performed an excursion.

tos). That is, females increase their range size in order to encounter more potential partners, concentrating their movements in certain areas where males have set up their territories and operating some degree of mate choice (Andersson, 1994). Among ungulates, a similar phenomenon has also been observed in a low density population of white-tailed deer (*Odocoilus virginianus*) (Labisky and Fritzen, 1998). These authors suggest that the increase in home range size and rate of travel during the rut was due to females actively searching for mates in instances where hunting leads to a shortage of breeding males. Although, in our study, average differences in ranging behaviour between the periods were not large, they were likely large enough to increase female exposure to alternative mates. In addition, this could be a result of the existence of 2 strategies (stationary vs. mobile) for mate searching in female roe deer which should depend on the distribution of available males.

An alternative explanation of our results could be that females increase ranging behaviour in response to male harassment during the rut (cf. Sundaresan et al., 2007 in Grevy's zebra *Equus grevyi*). Testosterone production peaks in male roe deer in July and August (Sempéré et al., 1998) and males actively seek out copulations at this time, potentially leading to increased female harassment. Indeed, behavioural observations have shown that females may continue to move in order to avoid a mating (Börger, 2006). Thus, females may increase their home range size to avoid insistently sex-

ual males. A similar increase in female home range size and activity during the reproductive period has been reported in alligators (*Alligator mississipiensis*) (Rootes and Chabreck, 1993) and wallabies (*Onychogalea fraenata*) (Fisher and Lara, 1999). Sundaresan et al. (2007) also observed increased movement rates among lactating Grevy's zebra females and suggested that this was linked to sexual harassment. In contrast, Fisher and Lara (1999) noted a moderate speed and repetitive movements of the wallaby females and suggested that this indicated that they were not attempting to escape harassment. The fact that, during the rut, the female roe deer in our study did not increase their movements per day, despite ranging over a greater surface area, suggests that male harassment is not a major determinant of changes in ranging behaviour of roe deer females at this time.

The rut excursions that we documented directly through intensive GPS monitoring supports the observations of Rossi et al. (2001) who noted that some roe deer females retained a stable home range during the rut, while others extended their pre-rutting home range. Our data showed that slightly less than half of all females (45%) undertook a rut excursion, which agrees with the other available observations from Scandinavia (Liberg et al., 1998). Roe deer bucks compete for sites to establish their zone of dominance and, classically, their territories overlap the home range of several females (Bramley, 1970), but males do not defend females directly (Börger, 2006). We suggest that the most likely explanation for these excursions is that the female is attempting to locate, choose and mate with a particular male in preference to the territorial male present on her home range (Linnell, 1994; Liberg et al., 1998). We speculate that this behaviour may be motivated by a desire to select a partner of superior quality or in order to avoid inbreeding (Linnell, 1994; Coulon, 2006). Alternatively, the male present on the female's home range could be already engaged in courting another oestrus female (interference). Since roe deer females are monoestrus, with a short period of receptivity (ca. 36 h, Sempéré et al., 1998), the observed excursions could thus be the result of a search strategy to find a free male (Linnell, 1994). Among well-studied ungulates, this behaviour seems largely specific to roe deer, perhaps because of the marked male territoriality in this species (but see Labisky and Fritzen, 1998).

3.2. Factors influencing spatial behaviour of females during the rutting period

We found that the degree of difference in home range size of female roe deer between the rut and non-rut was more pronounced in open habitat. This is likely related to the fact that roe deer home ranges are larger in more open landscapes in general (Hewison et al., 1998) and specifically in our study site (Cargnelutti et al., 2002). However, it is also worth noting that population density is also considerably lower in the more open landscapes of our study site (Hewison et al., 2007), implying that male territories are more widely spaced, so that females would have to range more widely to find an alternative mating partner. In this context, Melis et al. (2005) have shown that small woods seem to act as focal points for male territories in open habitats. Indeed, population density is predicted to substantially affect the sexual selection process (Kokko and Rankin, 2006). Further data are required before we can conclude as to whether females in open landscapes travel further than those in more forested areas during rut excursions (see Table 2).

We also found that the degree of difference in the size of the rutting and non-rutting ranges of females was particularly large in 2006 compared to 2005. Environmental conditions are known to affect ranging behaviour in a wide variety of large mammals (e.g. Ferguson et al., 1999 in polar bear *Ursus maritimus*) and roe deer in particular (Danilkin and Hewison, 1996), The summer of 2006 was unusual in that there was a marked contrast in climate, with an exceptionally hot July (pre-rut, mean daily temperature: 26 °C; mean daily maximal temperature: 32.2 °C), a rather cool August (rut, mean daily temperature: 20.8 °C; mean daily maximal temperature: 25.9 °C) and a hot September. The unusually hot non-rut may have constrained female movements as it seems likely that roe deer modify their ranging behaviour during the summer months in relation to temperature in southern latitudes.

We were unable to identify an influence of body mass on ranging behaviour during the rut, contradicting our expectation that bigger females in better condition would be able to allocate more energy to searching for mates. Instead, it is possible that females in better condition allocate more energy to maternal investment rather than mate searching (Hewison et al., 2005), although the small sample size and consequent lack of power means that we cannot exclude the existence of these effects. Similarly, the presence of a fawn at heel does not appear to interfere with the propensity to perform a rut excursion, as at least four of the five females who did so in our sample were known to have fawns (see Table 2), although it is not yet clear whether fawns accompany their mothers during excursions. To explore the reasons that provoke females to undertake rut excursions, it would be illuminating to combine field observations and paternity analyses to determine on which male attributes females base their choice of mating partner and to verify that these excursions do indeed lead to successful reproduction.

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