

A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic

Lucie Debeffe · Stefano Focardi · Christophe Bonenfant · A. J. Mark Hewison · Nicolas Morellet · Cécile Vanpé · Marco Heurich · Petter Kjellander · John D. C. Linnell · Atle Mysterud · Maryline Pellerin · Pavel Sustr · Ferdinando Urbano · Francesca Cagnacci

Received: 17 December 2013 / Accepted: 30 June 2014 / Published online: 17 July 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Breeding dispersal, defined as the net movement between successive breeding sites, remains a poorly understood and seldom reported phenomenon in mammals, despite its importance for population dynamics and genetics. In large herbivores, females may be more mobile during the breeding season, undertaking short-term trips (excursions) outside their normal home range. If fertilisation occurs, leading to gene flow of the male genome, this

behaviour could be considered a form of breeding dispersal from a genetic point of view. Here, we investigated ranging behaviour of 235 adult roe deer using intensive GPS monitoring in six populations across Europe within the EURODEER initiative. We show that excursions are common from June to August among females, with 41.8 % (vs. 18.1 % of males) making at least one excursion. Most individuals performed only one excursion per season and departure dates for females were concentrated in time, centred on the rutting period, suggesting a link with reproduction. The distance females travelled during excursions was significantly greater than the site-specific average diameter of a male home range, while travel speed decreased once

Communicated by Göran C. Ericsson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-014-3021-8) contains supplementary material, which is available to authorized users.

L. Debeffe (✉) · A. J. M. Hewison · N. Morellet
CEFS-INRA, B.P. 52627, 31326 Castanet-Tolosan, France
e-mail: lucie.debeffe@gmail.com

L. Debeffe · C. Bonenfant · C. Vanpé
UMR 5558, Laboratoire Biométrie et Biologie Évolutive,
Université Claude Bernard Lyon 1, 43 boulevard du 11 novembre
1918, 69622 Villeurbanne Cedex, France

S. Focardi
Istituto Dei Sistemi Compessi, Sezione di Firenze, Via Madonna
Del Piano 10, 50019 Sesto Fiorentino (FI), Italy

M. Heurich
Department of Research and Documentation, Bavarian Forest
National Park, Freyung Str 2, 94481 Grafenau, Germany

P. Kjellander
Grimsö Wildlife Research Station, Department of Ecology,
Swedish University of Agricultural Science, 73091 Uppsala,
Sweden

J. D. C. Linnell
Norwegian Institute for Nature Research, PO Box 5685, Sluppen,
7485 Trondheim, Norway

A. Mysterud
Centre for Ecological and Evolutionary Synthesis, Department
of Biology, University of Oslo, P.O. Box 1066, Blindern,
0316 Oslo, Norway

M. Pellerin
Centre d'Etudes Biologiques de Chizé, CNRS, B.P. 14,
79360 Beauvoir-sur-Niort, France

M. Pellerin
ONCFS-CNERA Cervidés Sanglier, Au Bord Du Rhin,
67150 Gerstheim, France

P. Sustr
Department of Biodiversity Research, Global Change Research
Centre AS CR, Na Sádkách 7, České Budějovice, Czech Republic

F. Urbano
Iuav School of Doctoral Studies, New Technologies
and Information for the Region and Environment, Venice (VE),
Italy

F. Cagnacci
Research and Innovation Centre, Fondazione Edmund Mach, Via
Mach 1, 38010 San Michele all'Adige (Tn), Italy

they progressed beyond this diameter, indicating search behaviour or interaction with other male(s) outside the resident male's territory. Because adults are normally highly sedentary, the potential for mating with relatives is substantial; hence, we conclude that rut excursions could be an alternative tactic enabling females to avoid mating with a closely related male. To understand better the ultimate drivers at play, it will be crucial to explore the genetic causes and consequences of this behaviour.

Keywords Mate choice · Inbreeding avoidance · GPS telemetry · Rut excursion · Ungulate

Introduction

Dispersal refers to movements of individuals from a source location or social group (e.g., birth or breeding site) to another location or group where establishment and reproduction may occur (Clobert et al. 2001). Hence, dispersal is a necessary, but not sufficient, condition for generating gene flow through space (Ronce 2007). Natal dispersal refers to net movement between the natal area and the site of first breeding, while breeding dispersal refers to movement between successive breeding sites (Greenwood 1980; Clobert et al. 2001). Dispersers may seek to alter their ecological context (e.g. density-dependent resource competition, predation risk) and/or their social context, notably in terms of mating opportunities (i.e. mate choice, Daniels and Walters 2000), targeting good genes (Hamilton 1990), compatible genes (Zeh and Zeh 1996), or inbreeding avoidance (Greenwood 1980; Pusey and Wolf 1996). Dispersal is believed to be an adaptive behavioural tactic that enhances lifetime reproductive success (Calabuig et al. 2008), as it can potentially affect most components of fitness (Danchin and Cam 2002).

Breeding dispersal has mostly been described in birds and, more specifically, colonial birds (Paradis et al. 1998). For example, in blue tits *Cyanistes caeruleus* one-third of birds change territory between consecutive breeding seasons (Garcia-Navas and Jose Sanz 2011). Studies on mammals remain scarce (Greenwood and Harvey 1982; Berteaux and Boutin 2000). In North American red squirrels *Tamiasciurus hudsonicus*, breeding dispersal is common, with 15 % of females bequeathing their territory to their offspring, and has been interpreted as a form of parental investment (Berteaux and Boutin 2000). In feral horses *Equus ferus*, 11 % of adults moved to a different social group between breeding attempts (Marjamaeki et al. 2013).

The availability of increasingly detailed monitoring of individual behaviour (e.g. satellite telemetry) is beginning to reveal unusual, reproductively motivated, movements beyond the regular home range in a wide array of species.

For instance, in the common yellowthroat, *Geothlypis trichas*, females performed short distance forays to neighbouring male territories during the reproductive period, resulting in extra-pair paternity (Pedersen et al. 2006). In large herbivores, some reports have suggested that females may be more mobile during the breeding season (Byers et al. 1994, in pronghorns *Antilocapra americana*; Labisky and Fritzen 1998, in white-tailed deer *Odocoileus virginianus*; Fisher and Lara 1999, in wallabies *Onychogalea fraenata*; Lovari et al. 2008; Richard et al. 2008, in roe deer *Capreolus capreolus*; Stopher et al. 2011, in red deer *Cervus elaphus*), undertaking unusual short-term trips outside their normal home range. If fertilisation occurs during these excursions, this could lead to substantial gene flow of the male genome through space, albeit mediated by the female's behaviour. From this genetic viewpoint, excursion movements could thus be considered a form of breeding dispersal motivated by the female's desire to change her mating context through active mate choice (Kolodziniski et al. 2010, in white-tailed deer; Bocci et al. 2013; Richard et al. 2008 and Lovari et al. 2008, in roe deer).

In the European roe deer, anecdotal observations (Lovari et al. 2008; Richard et al. 2008) and genetic evidence suggest a potential role for excursion behaviour in mate choice. Roe deer have a resource defence-based mating tactic (Liberg et al. 1998; Vanpé et al. 2009c), with a low degree of polygyny (Vanpé et al. 2008) and strong male territoriality (Bramley 1970), while adults of both sexes are very strongly sedentary over their lifetime (Hewison et al. 1998, but see Lamberti et al. 2006 for males in a Mediterranean area). This unusually rigid system of space use limits mate access for females, both in terms of number and choice. In addition, females are monoestrous (Hoffmann et al. 1978), with a highly synchronized and short (ca. 36 h) oestrous during the summer rut (mid July–mid August) (Sempéré et al. 1998), limiting their means to exercise mate choice and making them particularly prone to the risk of inbreeding (Kurt et al. 1993). Therefore, from an evolutionary point of view, breeding dispersal should be advantageous, particularly for females that pay most of the costs of reproduction and inbreeding depression (Greenwood 1980). As a result, the roe deer provides an interesting case study to assess whether these exceptional movements constitute a reproductive tactic, potentially leading to significant gene flow, within a breeding dispersal framework.

Based on an exceptionally large dataset of 235 GPS-monitored roe deer inhabiting six populations distributed across Europe (EURODEER collaborative initiative: www.eurodeer.org), we first aimed to characterise the spatial behaviour of male and female roe deer during summer and, more particularly, to link observed movement patterns with reproduction. Because males are generally territorial, we predicted that excursions should be more common

among females than males. In addition, for females (but not males), we expected excursions to be highly synchronised around the peak of the rutting period, which may be somewhat later at more northern latitudes (Liberg et al. 1998; Sempéré et al. 1998). Further, we did not expect any variation in excursion probability among age-classes (yearlings, sub-adults and adults) for females, as roe deer females are sexually mature as yearlings (Gaillard et al. 1992). However, we did expect age-related variation in excursion probability for males, as yearling and most sub-adult males are unable to defend a territory and so are frequently forced out of their range temporarily due to harassment by territorial adults (Wahlstrom 1994; Vanpé et al. 2009a).

Subsequently, we focused on the features of female excursions (distance, duration, speed, and sinuosity) during the core of the rutting period to explore potential mechanisms underlying this behaviour. Since the duration of oestrus does not vary among individual females (Sempéré et al. 1998) and all females are potentially reproductive, we expected no differences in excursion duration or distance among age-classes. If excursions are a means for a female to encounter otherwise unfamiliar males, we expected that females of all age-classes should engage in mating excursions that were sufficiently long so as to go beyond the territory boundaries of the resident male with whom their normal home range overlaps; that is, that excursion distance should be positively related to male territory size at the population scale. Finally, if excursions are a means for a female to exercise mate choice, we expected that females should move along a linear trajectory when moving through their home range while in the vicinity of local territorial males, but should decrease their speed and adopt a more sinuous trajectory further from the centre of their home range, particularly when beyond the territory limits of the resident male and interacting with unfamiliar males.

Materials and methods

Study areas, datasets, and sample selection

This study was conducted in the context of the EURO-DEER collaborative initiative (Urbano and Cagnacci 2014), a data-sharing project for roe deer across their distribution range (Fig. 1). Study area characteristics and GPS collar models are summarised in Table S1 (Online Resource 2). The locations of the six study sites involved in this study (Germany-Bavarian Forest, site 1: “Germany”; France-Coteaux de Gascogne, site 2: “France-South”; Italy-Trentino province, site 3: “Italy”; Southern Scandinavia, two sites, site 4: “Sweden” and site 5: “Norway”; France-Chizé, site 6: “France-West”) are presented in Fig. 1. GPS data collection spanned the period 2002–2010 and concerned

247 individuals. Animals were collared during captures that usually occurred in winter. Prior to release, animals were sexed and assigned to three age-classes for the subsequent summer period based on estimated age at winter capture in relation to tooth development and wear (Ratcliffe and Mayle 1992): yearlings (1 year old, $N = 63$), i.e. animals captured as fawns, sub-adults (2 years old, $N = 21$), i.e. animals captured as yearlings, and adults (3 years old or more, $N = 151$), i.e. all animals above 2 years old at capture. All capture, handling and collaring were done according to the appropriate national law for animal welfare and procedures were approved by the pertinent administration.

We retained all GPS locations taken between the 15 Jun and 15 Sept of each year to be sure to include the start and end of all rutting activity, based on the literature (Liberg et al. 1998). Individuals were retained for analysis only if sampling started on 30 Jun at the latest and ended on 1 Sept at the earliest. In a few cases (13.1 %), animals were monitored in more than 1 year, so to avoid pseudoreplication, we randomly selected one of these years. Daily frequency of locations was one every 4 h for 56.73 % of fixes, one every 6 h for 26.85 %, or one every 8 h for 7.07 %; all other locations (9.36 %) were recorded with an inter-location interval between 12 and 72 h, mainly due to GPS failure. Individuals which had one or more inter-location interval greater than 96 h were excluded from the analysis. Similarly, individuals that undertook migratory or natal dispersal movements during the study period ($N = 10$) were removed. In a preliminary analysis, we verified that the varying sampling regimes among study sites did not affect excursion detection probability (Table S2, Online Resource 3). Overall, 235 individuals were retained for subsequent analysis, 141 females and 94 males (Table 1).

Data analysis

Data analysis was performed with the following steps: We first identified excursion movements using appropriate methodology (see below). Second, we tested the effects of age-class, sex, and study site on excursion probability. Third, we analysed temporal synchronisation of excursion departure date within and among study sites. Finally, we analysed excursion features (i.e. average speed, distance, and step speed) and linked this to among-site variation in male territory size.

Identifying excursions

To identify an excursion reliably, we required that a certain set of temporally consecutive locations was spatially separated from the normal home range. To explore spatial separation and temporal consistency, we first used cluster analyses and then performed analyses based on the Net

Fig. 1 Location of the roe deer populations across Europe involved in the EURODEER collaborative project and used in the present study. Partner countries of the EURODEER initiative are represented in grey, and symbols indicate the six study sites included in the current analyses



Square Displacement (Fig. 2, and see Online Resource 1 and Fig. S1 for details). To ensure that detection probability for an excursion was similar across study sites with varying GPS sampling regimes, and to exclude “apparent” excursions that were in fact due to GPS location error, or very short-term excursions that could be due to disturbance, only extra-range movements which lasted more than 24 h were considered true excursions for the following analysis (see Online Resource 3 for more details). Animals from Norway and Sweden were pooled to form a Scandinavian area (“Scandinavia”) because of low sample size and comparable environment/latitude. From this, we generated three excursion parameters: (1) duration, i.e. the time interval between the time stamp of the first and the last locations of the excursion event; (2) distance, i.e. the Euclidean distance between the first and the farthest locations of the excursion event; (3) average speed, i.e. the ratio between the duration and distance, as derived above.

Excursion probability

Excursion occurrence is a binary response variable (excursion vs. no excursion), thus we used logistic regression to determine whether excursion probability varied in relation to sex, age-class, and study area ($N = 235$). In relation to our biological hypothesis, assuming that, globally, females make more excursions than males, but that excursion probability is particularly low for adult males, we expected statistical support for the model including the interaction between sex and age-class. Thus, our most complex model included the sex and age-class interaction with an additive effect of study area. From this, a set of eight candidate models were built (the full model, all the derived models, and a constant model) and ranked according to their Akaike information criterion corrected for small sample size (AIC_c). We retained the model with the lowest AIC_c value, reflecting the best compromise between precision and complexity (Burnham and Anderson 1998).

Table 1 Characteristics of female and male roe deer excursions during summer in each study area

Study areas	Female sample size; proportion of females undertaking excursions	Male sample size; proportion of males undertaking excursions	Mean ± SD Euclidean distance (m) of female excursion trajectories	Mean ± SD duration (h) of female excursions	Mean ± SD adult male territory diameter (m)
Germany	$N = 19; 47.4\%$	$N = 19; 10.5\%$	$3,982.8 \pm 2,058.3$	85.8 ± 51.4	$1,649.1 \pm 1,526.9$
France-South	$N = 78; 39.7\%$	$N = 55; 21.8\%$	$1,517.6 \pm 1,045.6$	65.8 ± 53.1	534.7 ± 383.0^a $1,089.7 \pm 1,060.5^b$
Italy	$N = 14; 71.4\%$	$N = 7; 0\%$	$1,540.3 \pm 835.5$	75.1 ± 54.3	677.5 ± 332.7
Norway	$N = 12; 25\%$	$N = 6; 0\%$	$2,686.9 \pm 2,051.9$	40.7 ± 8.1	$1,569.7 \pm 977.4$
Sweden	$N = 5; 40\%$	$N = 7; 42.8\%$	$1,041.7 \pm 893.5$	56.0 ± 42.3	$1,149.2 \pm 773.8$
France-West	$N = 13; 30.8\%$	$N = 0; NA$	$2,203.0 \pm 650.6$	105.0 ± 52.2	947.1 ± 557.6^c

^a France-South_closed habitat

^b France-South_open habitat

^c Estimated

Excursion departure date

The effect of sex, age-class, and study area on excursion departure date was investigated using a log rank test. Log rank tests are usually used for survival analysis from censored data, but can be used for any transition probability between non-reversible states (Fieberg and Delgiudice 2008). In this case, possible states were “no excursion” (coded 1) vs. “at least one excursion” (coded 0). Cumulative probability curves for the status “no excursion” were generated using the Kaplan–Meier estimate, and we tested for differences between curves using the G-rho family of tests implemented in the R “survival” package (Harrington and Fleming 1982; Therneau and Lumley 2010). For this analysis only, sub-adult and adult females were pooled since, almost without exception, females rut for the first time at 1 year old (Gaillard et al. 1992). According to our biological hypotheses, we expected excursions of females to be more synchronised in time and to occur mostly during the peak of the rutting period compared to those of males; further, because of latitude-related variation in the timing of the peak of the rut (Liberg et al. 1998), we expected to observe differences in mean excursion departure date among study areas.

Estimation of male territory size

The summer home range size of each male (assumed equivalent to territory size for adults) was calculated using GPS locations between 15 Jun and 15 Sept and the 90 % fixed kernel method with the locations of the central cluster only (i.e. excluding locations during excursions) (Worton 1989; Börger et al. 2006) with the “adehabitat” R package (Calenge 2006) (Fig. 2). Males with an abnormally large summer home range (>1,000 ha, $N = 2$) were excluded for this analysis because it is unlikely that they could successfully defend a territory of this size (mean territory size ± SD = 121.1 ± 129.3 ha, min = 11.1 ha, max = 685.7 ha, $N = 56$). Individuals from the predominantly forested part of the France-South study area (“France-South_Closed”) were considered separately from those in the more open part of the landscape (“France-South_Open”), because average home range size and landscape structure both differ considerably (Morellet et al. 2011). For the other study sites, landscape structure was relatively homogeneous at this spatial scale so that no site-subdivision was evident a priori. We computed mean male summer home range diameter for each study area and log-transformed it to achieve normality. However, because GPS data were only available for females for France-West, we estimated mean male summer home range size for this site based on the predicted value from the linear regression between female and male summer home range size across

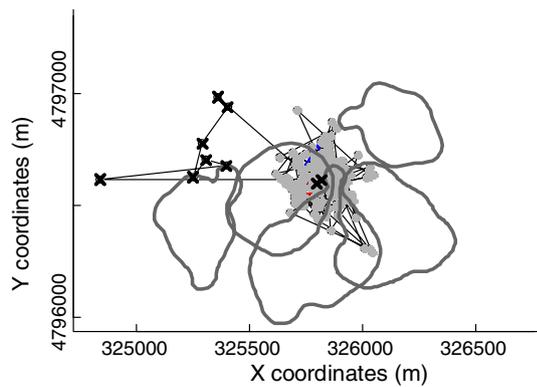


Fig. 2 Example of a typical female's space use during summer with several adult male home ranges (grey circles). Light grey points represent female locations, with black crosses indicating excursion locations

study sites ($N = 6$, $F = 8.34$, $r^2 = 0.68$, $df = 4$, $P = 0.045$; Fig. S2, Online Resource 4).

Excursion distance and speed

Since excursion duration and distance are correlated at the level of the excursion (linear regression: $N = 54$, $R^2 = 0.12$, $F = 7.25$, $df = 52$, $P = 0.009$), these effects were analysed using the compound variable 'average speed' (mean average speed = 0.037 ± 0.03 km/h, min. = 0.005 km/h, max. = 0.12 km/h, $N = 54$). Focusing on the strict rutting period (15 Jul–28 Aug), we analysed the effects of age-class, date of departure, and mean adult male territory size for a given study area on average excursion speed of females across the six populations. If excursion behaviour is motivated by mating opportunity, we expected excursion distance, and therefore, average speed, to increase with population-specific male territory size. As the peak of the rut occurs during the middle of the selected study period, we expected non-linear relationships between average excursion speed and date of departure, thus departure date was modelled with a spline effect using a generalized additive mixed model. We fitted a generalized linear mixed model (GLMM) and a generalized additive mixed model (GAMM) with a Gaussian error distribution for a full model that included the additive effects of all factors listed above (lme4 and mgcv R packages: Bates et al. 2011; Wood 2011) (note that GAMMs and GLMMs are equivalent if no smoothing term is included in the GAMM). Study area was included as a random factor to control for the potential non-independence of individual female behaviour within each study site. We calculated AIC_c values for all possible additive models derived from the a priori full model and ranked the eight candidate models according to their AIC_c values.

Subsequently, to infer whether females performed excursions to increase encounter rates with unfamiliar males, we calculated the number of male territories that a given female potentially crossed during each excursion, dividing the Euclidean excursion distance by the mean male territory diameter for a given study area or sub-area.

Finally, to analyse variation in movement speed during the excursion, we split each excursion into two stages: (1) the portion of the excursion that occurred outside the home range, but within a distance shorter than the mean male territory diameter for that study area, defined as the "near" stage, and (2) the portion of the excursion that occurred at a distance greater than the mean male territory diameter, defined as the "far" stage. We then analysed whether female movement speed ('step speed') differed between the near and far stages of excursions. We predicted that once outside the territory of males overlapping their normal home range, females would decrease their step speed so as to search for, select, and interact with unfamiliar males. More specifically, for each i -th location of the excursion, we computed displacement and duration with respect to the $(i + 1)$ -th location and derived the speed of each step. Step speed was modelled using linear mixed models (PROC MIXED: SAS 9.2, SAS Institute Inc., Cary, NC, USA) with study site and excursion stage (near or far) as fixed effects and animal identity as a random effect. The distribution of step speed was not normal, so this variable was log-transformed. Model selection was based on an AIC approach as described above.

All analyses were run in R version 2.12.1 (R Development Core Team 2010) except where specified. Note that R and SAS software were used exclusively for separate analyses.

Results

Excursion probability

Excursions occurred in all study areas, but were consistently more frequent among females than males (41.8 % of females, $N = 141$ vs. 18.1 % of males, $N = 94$; Table 1). Of the 86 excursions that we identified, 54 were performed by females during the core of the rutting period (i.e. from 15 Jul to 28 Aug). In general, animals performed only a single excursion during a given rut (86.4 % of females, $N = 57$ individuals and 94.1 % of males, $N = 17$ individuals), but in some cases they performed two (eight females and no males) or three (no females and one male). For females that performed two excursions, there was a mean of 25.9 days between the two events.

The most parsimonious model for excursion probability contained the two-way interaction between age-class

and sex, but did not include the effect of study site, indicating that excursions were equally prevalent in all study areas (pseudo- $r^2 = 0.11$ for the best model vs. 0.02 for the model with only study area as a factor) (Table 2). The estimated excursion probabilities from the best model (Fig. 3; Table S3, Online resource 5) showed that females were more likely to perform an excursion than males and that this sex difference increased with age (difference between female and male excursion probabilities: 0.04, 0.17, and 0.34 for yearlings, sub-adults, and adults, respectively). As expected under the hypothesis that rut excursions play a role in reproduction, female excursion probability was not affected by age-class, but male excursion probability was, with younger males more likely to perform excursions than adult males (Fig. 3).

Excursion departure date

As expected in relation to the timing of the rut, female excursions were synchronised in time around the beginning of August, while male excursions were not (Fig. 4a). Indeed, the timing of excursions differed significantly between males and females (log rank test: $N = 235$, $\chi^2 = 12.9$, $df = 1$, $P < 0.001$). There were also differences in excursion timing among age-classes for males (yearlings vs. sub-adults vs. adults; log rank test: $\chi^2 = 13.6$, $df = 2$, $P = 0.001$), because the very few excursions performed by adult males were concentrated at the end of the study period, but this was not the case for females (yearlings vs. adults; log rank test: $\chi^2 = 0$, $df = 1$, $P = 0.95$). There was no significant among-area difference in the timing of excursion departure for females (log rank test: $\chi^2 = 7.3$, $df = 4$, $P = 0.122$), but sample sizes were low for some areas. There was a marked increase in the number of female excursions just after the beginning of August (after Julian day 224, i.e. 1 Aug) (Fig. 4b). The temporal pattern was quite similar across the different study areas, although female excursions were somewhat later in Scandinavia (Scandinavia vs. other areas pooled, Kolmogorov–Smirnov test: $N = 144$, $D = 0.6$, $P < 0.0001$). The mean date of departure of females was correlated with latitude, with later excursions in the more northern latitudes (linear regression: $R^2 = 0.74$, $F = 11.31$, $df = 4$, $P = 0.028$).

Excursion distance and speed

For the analysis of excursion distance and average speed, we focused on the core rutting period (15 Jul–28 Aug, Fig. 4b), involving 54 excursions performed by 51 females. Of the eight candidate models, the most parsimonious included the effect of age-class and of male territory size on average female excursion speed, with study area as a random effect (pseudo- r^2 best model: 0.17) (Table 3). As

Table 2 Performance of the eight candidate logistic regression models estimating the probability of excursion occurrence in roe deer in relation to the individual’s sex, age-class, and study site of origin

Excursion probability	<i>K</i>	<i>AIC_c</i>	ΔAIC_c	<i>AIC_cWt</i>
Age + sex + age: sex	6	280.6	0	0.74
Age + sex	4	284.61	4	0.1
Sex	2	284.61	4	0.1
Age + sex + site + age: sex	11	286.17	5.56	0.05
Age + sex + site	9	289.19	8.58	0.01
Constant	1	297.84	17.23	0
Age	3	298.93	18.32	0
Site	6	303.13	22.52	0

Age age-classes (yearlings, sub-adults, adults), *K* number of parameters, *AIC_c* Akaike’s Information Criterion corrected for small sample size, *AIC_cWt* Akaike weights

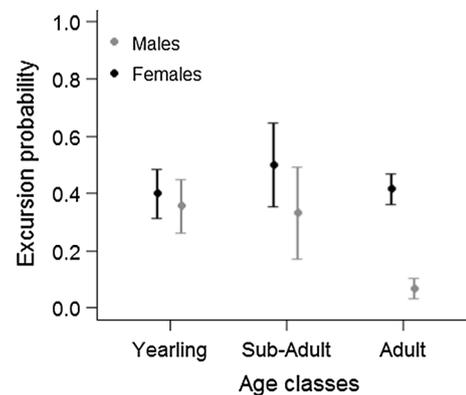


Fig. 3 Estimated excursion probabilities for the three age-classes (yearlings, sub-adults, and adults) in male and female roe deer. Males are in grey and females are in black ($N = 141$ and 94, respectively). Error bars represent the associated standard error

expected, average excursion speed increased with mean male territory size, both for adult and yearling females (slope mean \pm SE = 0.64 ± 0.12); in addition, yearling females had a lower average excursion speed than adults (for a given male territory size, estimated average excursion speed was 0.59 m/min lower for yearling females compared to adults) (Fig. S3; Table S3, Online resource 5).

The distance travelled during an excursion was almost always greater than the mean diameter of a male territory in the given study area (Fig. 5). The mean \pm SD distance travelled during an excursion was 2.15 ± 1.54 km, representing a mean (\pm SD) of $1.99 (\pm 0.29)$ male territories crossed, which was significantly greater than one (Student test: $N = 54$, $t = 6.77$, $df = 53$, $P < 0.001$). Significant variability in excursion distance among study sites was observed (ANOVA: $F = 3.24$, $df = 4$, $P = 0.019$) such that females crossed 1.31 male territories, on average, in Scandinavia, but 2.89 territories, on average, in Germany (Fig. 5).

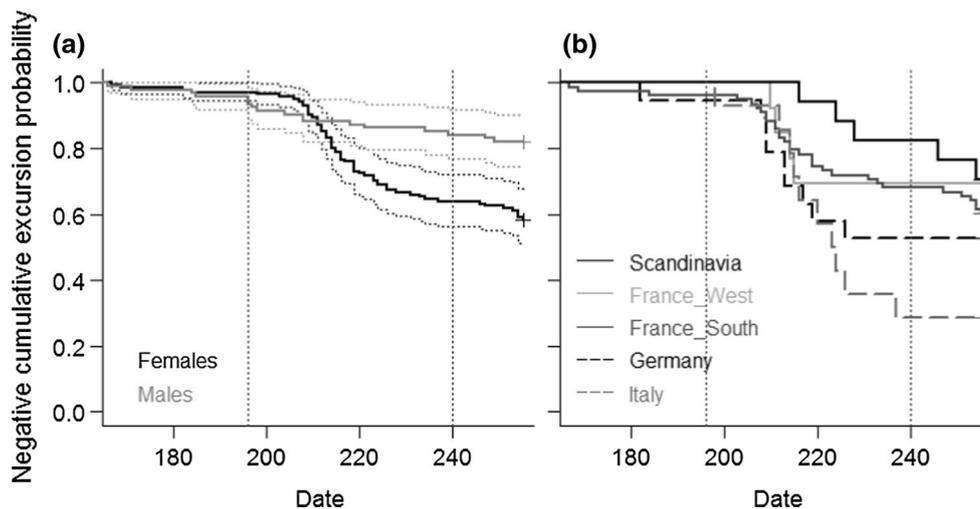


Fig. 4 Estimated negative cumulative excursion probability of **a** roe deer excursions for males and females and **b** female roe deer excursions for the six study areas, using the Kaplan–Meier estimator. Note that the graph presents the negative excursion probability in that 1 codes for the state “no excursion”, while 0 codes for “excursion.” **a** Males are in grey ($N = 94$) and females are in black ($N = 141$). Dashed lines represent associated confidential intervals. **b** The differ-

ent lines represent the six study areas: Italy in *dashed grey*, $N = 14$; Germany in *dashed black*, $N = 19$; France-West in *light grey*, $N = 13$; France-South in *grey*, $N = 78$; and Scandinavia (Norway and Sweden) in *black*, $N = 17$. The *dotted vertical lines* correspond to the 15 Jul and the 28 Aug, delimiting the core of the rutting period in all study areas with the exception of Scandinavia (end = 15 Sept)

Table 3 Performance of the candidate models for explaining variation in average excursion speed of female roe deer during the rut in relation to the individual’s age-class, the date of departure, the size of the average male territory, and the study site of origin

Type	Excursion average speed	K	AIC_c	ΔAIC_c	$AIC_c Wt$
GLMM	Age + log_mHR	5	106.73	0.00	0.72
GAMM	Age + s(date) + log_mHR	13	109.31	2.58	0.20
GLMM	Log_mHR	4	111.33	4.60	0.07
GAMM	S(date) + log_mHR	12	114.71	7.98	0.01
GLMM	Age	4	120.12	13.39	0.00
GAMM	Age + s(date)	12	122.74	16.01	0.00
GLMM	Constant	3	126.38	19.65	0.00
GAMM	S(date)	11	129.82	23.09	0.00

‘Study area’ is included as a random effect in all models, *Age* age-classes (yearlings, sub-adults, adults), *log_mHR* mean size of an adult male territory in that area or sub area, *s(date)* date of departure with a spline effect, K number of parameters, AIC_c Akaike’s Information Criterion corrected for small sample size, $AIC_c Wt$ Akaike weights

The most parsimonious model for describing variation in step speed during female excursions included the interaction between study site and excursion stage (i.e. near and far stages, as defined above), with animal identity as a random effect (Table S4, Online resource 6). As expected, if females slow down to search for mates once they have

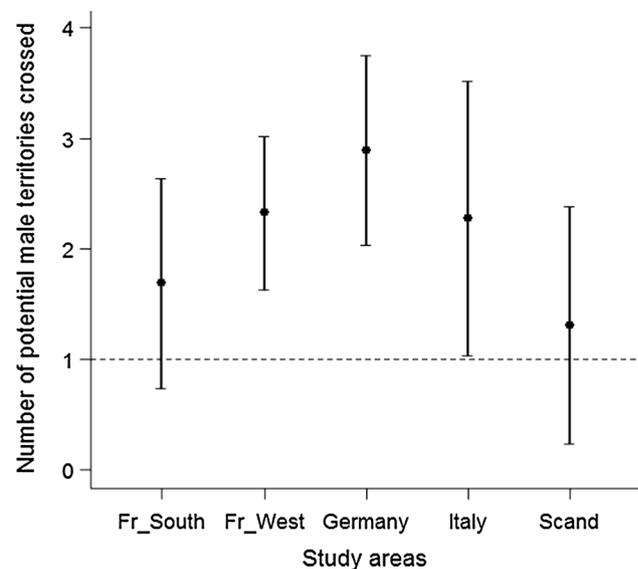


Fig. 5 Number of potential male territories crossed by roe deer females during rut excursions in each study area. The number of potential male territories crossed by females during rut excursions is defined as the female excursion distance divided by the diameter of the mean male territory size for that study area. Study areas are: France-South (noted Fr_South), France-West (noted Fr_West), Germany, Italy, and Scandinavia (pooling Norway and Sweden, noted Scand). The *dashed line* represents the distance required to cross the territory of one male. *Error bars* represent the associated standard deviation

travelled a certain threshold distance, mean (\pm SD) excursion step speed was 1.13 (\pm 2.1 m/min, $N = 365$) and 1.69 (\pm 2.51 m/min, $N = 211$) for the far and near stages, respectively (50.9 % difference: Fig. S4, Online resource 6). We also observed some variability in step speed among study sites: females moved faster in the Scandinavian and German study sites compared to the other sites (mean \pm SD speed for Scandinavia and Germany: 0.89 ± 0.63 m/min vs. 0.47 ± 0.36 m/min in the other sites). In addition, for the France-South study site, excursion speed was lower in the closed than in the open sector of the landscape (mean \pm SD: 0.21 ± 0.23 m/min and 0.57 ± 0.40 m/min in closed and open sectors, respectively).

Discussion

Our detailed study of movement behaviour from fine-scaled analysis of GPS locations clearly indicates that unusual extra-range movements are common among roe deer females during the reproductive period. The synchronicity of these movements, during the core rutting period, and the fact that the large majority (86 %) of females performed only a single excursion suggest that these movements represent a reproductive tactic in this monoestrous species. We also showed that during these excursions, females generally travelled far enough to go beyond the territory of the resident male, enabling them potentially to encounter unfamiliar mates. Moreover, travel speed decreased as they progressed beyond this threshold distance. Typically, the female moved faster when close to her normal summer range, suggesting that she was initially seeking to move quickly away during the first stage of her excursion, but subsequently, her speed slowed when above a certain threshold distance (Fig. S4, Online resource 6), suggesting that she had begun to search for, or interact with (e.g. courtship behaviour), an unfamiliar male. Hence, these exceptional out and back reproductive movements potentially allow females to manipulate their mating opportunities while maintaining familiarity with their natal site for the key parturition and maternal care phases of their life cycle. Because this reproductive behaviour of females could result in gene flow of the male genome over significant distances (average of 2.15 ± 1.54 km, maximum of 7.28 km) if mating is successful, we suggest that it could thus be considered as a form of breeding dispersal, at least from a genetic point of view.

Rut excursions as a reproductive tactic

Excursion movements were prevalent among females in all study areas considered here, highlighting the generality of this behaviour in roe deer across Europe. A similar type

of unusual movement during reproduction has been documented in several bird species (nightingales *Luscinia megarhynchos*: Naguib et al. 2001; common yellowthroats: Pedersen et al. 2006), but only recently in a few mammalian species (e.g. red fox *Vulpes vulpes*: Soulsbury et al. 2011; short-beaked echidna *Tachyglossus aculeatus*: Nicol et al. 2011). Rut excursions have also been recently reported in white-tailed deer, where 40 % of females performed a single, long-distance movement outside of their normal home range during the rut (Kolodzinski et al. 2010), and red deer, where 43 % of females changed harems (Stopher et al. 2011). In roe deer, we found that a remarkably similar proportion of the female population (42 %) performed at least one excursion during the summer. In other species, genetic-based evidence showed that genetic dispersal distances were higher than individual dispersal distances, suggesting that this pattern could also be the result of reproductive excursions (Winters and Waser 2003, in banner-tailed kangaroo rats *Dipodomys spectabilis*; Sillero-Zubiri et al. 1996, in Ethiopian wolves *Canis simensis*).

During excursions, roe deer females travelled an average distance of between 1.54 km (in Italy) and 4.76 km (in Germany), which is of a similar range to that moved by female white-tailed deer (3.23 ± 1.11 km) (Kolodzinski et al. 2010), but somewhat higher than the mean distance moved by female red deer during oestrus (around 0.7 km) (Stopher et al. 2011). The facts that, in our study, excursion probability was much higher in females compared to males, that it occurred during the core of the rutting period, and that the vast majority (86 %) of females made only one excursion in a given year are in agreement with the hypothesis that excursions could play an important role for reproduction in the monoestrous roe deer. Indeed, female (but not male) excursions were consistently synchronised in time around the beginning of August across all study sites, with a peak corresponding to the core of the rutting period as reported in the literature and which is slightly later in the more northern latitudes (Liberg et al. 1998). Excursions of adult males were rare in comparison, presumably linked to the constraint of summer territoriality and potential loss of mating opportunities (Vanpé et al. 2009a). Yearling and sub-adult males are unlikely to hold a territory and probably do not reproduce (Vanpé et al. 2009a); hence, the higher frequency of excursions of these younger males is in line with their presumably non-territorial status and is likely linked to agonistic interactions with territorial males (Wahlstrom 1994). Because females appear to cue on the size of a male's territory to choose their mate (Vanpé et al. 2009c), whether a given male mates exclusively with local females or females on excursions, the territory itself still plays a critical role in determining male reproductive success through female mate choice so that territoriality is maintained through sexual selection.

Although we observed some differences in excursion probability among areas, with a higher excursion rate for females in Italy and for males in Sweden (Table 1), overall, excursion probability was similar across study sites. However, this result may be due to low statistical power given the rather low sample size available for some areas. Indeed, we might expect excursion probability to vary among study sites in relation to landscape structure, predator presence or population density. A preliminary analysis contrasting excursion probability at sites where predators are present (i.e. the two Scandinavian sites and Germany) with those where predators are absent revealed no difference in female excursion probability in relation to predation risk (Chisquared test: $N = 235$, $\chi^2 = 0.29$, $df = 1$, $P = 0.59$). Future work should focus on the role of environmental factors for explaining variation in female excursion behaviour at both the within- and among-population scales.

Rut excursions as breeding dispersal

These unusual movements during excursions allow females to manipulate their mating context in terms of available mates, without modifying the ecological context of the subsequent critical phases of parturition and lactation. Because this female reproductive tactic should lead to substantial gene flow of the male genome through space, we suggest that it could be considered a form of breeding dispersal. Under the classical definition of breeding dispersal, females change sites between successive breeding attempts, and hence may pay substantial costs during the birth and maternal care phases due to the loss of site familiarity. These costs may be particularly high for the roe deer because it has very high levels of maternal investment and is an income breeder (Andersen et al. 2000), relying on current energy intake to offset reproductive costs, hence detailed knowledge of local environment may be critical. Therefore, we suggest that roe deer females that perform an excursion gain the fitness benefits associated with a change of mating context [e.g. mate choice for good or compatible genes, for greater genetic diversity of offspring (Vanpé et al. 2009b), or for inbreeding avoidance] without paying the associated costs of true dispersal (unfamiliarity with the environment, e.g. resource distribution, exposure to predators, mate availability: Pusey and Wolf 1996; Danchin and Cam 2002). Note, however, that excursions may entail short-term costs, for example, an increased risk of predation in an unfamiliar environment during the excursion event itself. Excursion behaviour was not a repeatable behaviour across years ($N = 21$ females, with 46 observations, repeatability estimate $R = 0 \pm 0.11$, $CI = [0, 0.37]$, $P = 1$). This result suggests that females change mating sites between successive reproductive events which is in agreement with our interpretation of female excursion behaviour as a form of breeding dispersal.

During excursions, females may benefit through exercising mate choice on the basis of the male's genetic quality (e.g. heterozygosity), phenotypic quality (e.g. body mass and/or antler size, since these traits are honest signals of quality in roe deer: Vanpé et al. 2007, 2010), and/or territory characteristics (territory size is correlated with male reproductive success in roe deer: Vanpé et al. 2009c). Ultimately, this should result in the production of offspring of higher phenotypic and/or genetic quality, hence, with higher fitness. Because excursion behaviour during the reproductive period appears to be widespread in ungulates [e.g. red deer (Stopher et al. 2011), white-tailed deer (Kolodzinski et al. 2010), pronghorn (Byers et al. 1994)], as well as in other taxa [e.g. banner-tailed kangaroo rats (Winters and Waser 2003), Ethiopian wolves (Sillero-Zubiri et al. 1996), red foxes (Soulsbury et al. 2011), short-beaked echidna (Nicol et al. 2011)], this reproductive tactic seems to be common among polygynous mammals. To assess the impact of this behaviour at the genetic level, it would be interesting in the future to test whether the occurrence of breeding dispersal movements generates genetic distances that are longer than expected, as found in banner-tailed kangaroo rats and in Ethiopian wolves (Winters and Waser 2003; Sillero-Zubiri et al. 1996).

Rut excursions as an inbreeding avoidance mechanism?

Because roe deer adults have an extremely sedentary life history (Hewison et al. 1998) with a low degree of polygyny (Vanpé et al. 2008), and because a variable, but high, proportion of juveniles remain philopatric (Debeffe et al. 2012), they appear particularly prone to the risk of inbreeding (Kurt et al. 1993). The female excursions that we report here may offer the opportunity to minimize the probability of mating with a related male and so provide a mechanism for efficient inbreeding avoidance (Greenwood 1980). Since female mammals invest more in their offspring than males (Clutton-Brock 1991), the costs of inbreeding are likely greater for females (Greenwood 1980), and, indeed, we have shown that excursions were much more prevalent in females than males. Breeding with a related male can have major fitness consequences (Morton et al. 1956) through the production of offspring with low levels of genetic variation, leading to the expression of deleterious recessive alleles and promoting inbreeding depression which, in turn, may lower reproductive success (Cohas et al. 2009; Da Silva et al. 2009). In roe deer, Vanpé et al. (2009b) found that parents who were strongly related produced offspring with lower individual heterozygosity that survived less well during their first summer compared to fawns whose parents were unrelated. Rut excursions of female roe deer may thus provide the opportunity to minimize the probability of mating with a related male

(Greenwood 1980). A link between rut excursion behaviour and inbreeding avoidance has previously been inferred in a red deer population (Stopher et al. 2011) and was explicitly demonstrated in Antarctic fur seals *Arctocephalus gazelle* (Hoffman et al. 2007).

As described above, we also found that the distance covered during excursions allowed females to go beyond the territory of the local territorial male, potentially providing access to unrelated and/or unfamiliar mates (Bonnot et al. 2010). Since genetic distance and geographic distance among individuals are correlated (Coulon et al. 2004), the probability of mating with an unrelated male likely increased with distance travelled away from a female's home range. Furthermore, the fact that females slowed down once beyond the limit of local male's territory suggests that the female engaged in courtship with the first unrelated male encountered, rather than exercising choice based on her assessment of the quality of several alternative mates, providing further support for the hypothesis that excursions constitute an inbreeding avoidance mechanism. In the future, it would be interesting to link female excursion behaviour to natal dispersal behaviour; indeed, we might expect female breeding excursions to be more prevalent among the philopatric segment of the population, as the risk of inbreeding is likely higher for these individuals compared to those that dispersed natively and so have access to unrelated sexual partners.

Conclusions

Female rut excursions can be considered a form of breeding dispersal and may have evolved as an inbreeding avoidance tactic in roe deer. In this context, by combining behavioural data with genetic information, it would be interesting in the future to investigate (1) whether the male that a given female visits during her excursion is less related to her than the resident male with whom her normal home range overlaps; and (2) if the local level of genetic relatedness affects the probability that a female undertakes an excursion. A recent study on group-living ungulates highlighted that, at the inter-specific level, the occurrence of natal dispersal is linked to the risk of inbreeding. That is, in plural breeders, the probability for female philopatry depends on the risk that a female's father is reproductively active in her group when she starts to breed (Lukas and Clutton-Brock 2011). The authors suggested that sex-biased female dispersal has evolved to minimize the risk of inbreeding. At the intra-specific level, increased mobility during the reproductive period combined with active mate choice could help minimize this risk. For example, in Antarctic fur seals, females move further to maximize the probability of mating with highly heterozygous males and with individuals

of low relatedness (Hoffman et al. 2007). The ubiquity of rut excursions in roe deer and, more generally, in other large mammals, strongly suggests that accentuated female mobility during reproduction is a form of breeding dispersal potentially driven by inbreeding avoidance.

Acknowledgments This paper was conceived and written within the EURODEER collaborative project (paper 3 of the EURODEER series; www.eurodeer.org). Co-authors are grateful to all members for their support for the initiative. We also thank two anonymous referees and the handling editor for constructive comments on an earlier version of this paper. The EURODEER spatial database is hosted by the Edmund Mach Foundation. GPS data collection of the Edmund Mach Foundation was supported by the Autonomous Province of Trento under Grant N. 3479 to F. Cagnacci (BECOCERWI–Behavioural Ecology of Cervids in Relation to Wildlife Infections). F. Cagnacci thanks the Wildlife and Forest Service of the Autonomous Province of Trento and the Hunting Association of Trento Province (A.C.T.) for support and help during captures. Financial support for GPS data collection in the Bavarian Forest was provided by the EU-programme INTERREG IV (EFRE Ziel 3) and the Bavarian Forest National Park Administration. The Swedish study was supported by grants from the private foundation of “Marie Claire Cronstedts Minne”, The Swedish Environmental Protection Agency and The Swedish Association for Hunting and Wildlife Management. M. Hewison and N. Morellet would like to thank the local hunting associations, the Fédération Départementale des Chasseurs de la Haute Garonne, as well as numerous co-workers and volunteers for their assistance and, in particular, B. Cargnelutti, J.M. Angibault, B. Lourtet, D. Picot and J. Merlet. The France South study was partly funded by the INDHET ANR grant (ANR-12-BSV7-0023-02). C. Vanpé and L. Debeffe were supported by the PATCH RPDOR ANR project (ANR-12-PDOC-0017-01) attributed to CV from the French National Research Agency (PATCH project). The Norwegian study was financed by the Research Council of Norway, the Directorate for Nature Management, and the county governor's office in Buskerud county. The authors declare that they have no conflict of interest.

References

- Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using Eigen and S4 classes R package, Version 0.999375-39
- Berteaux D, Boutin S (2000) Breeding dispersal in female North American red squirrels. *Ecology* 81:1311–1326. doi:10.1890/0012-9658(2000)081[1311:BDIFNA]2.0.CO;2
- Bocci A, Aiello V, Lovari S (2013) Excursion behaviour of female roe deer may depend on density. *Behav Processes* 97:18–20. doi:10.1016/j.beproc.2013.03.004
- Bonnot N, Gaillard JM, Coulon A et al (2010) No difference between the sexes in fine-scale spatial genetic structure of roe deer. *PLoS One* 5:e14436. doi:10.1371/journal.pone.0014436
- Börger L, Franconi N, De Michele G et al (2006) Effects of sampling regime on the mean and variance of home range size estimates. *J Anim Ecol* 75:1393–1405. doi:10.1111/j.1365-2656.2006.01164.x
- Bramley PS (1970) Territoriality and reproductive behavior of roe deer. *J Reprod Fertil Suppl* 11:43–70
- Burnham KP, Anderson DR (1998) Model selection and inference. Springer, New York
- Byers JA, Moodie JD, Hall N (1994) Pronghorn females choose vigorous mates. *Anim Behav* 47:33–43. doi:10.1006/anbe.1994.1005
- Calabuig G, Ortego J, Cordero PJ, Aparicio JM (2008) Causes, consequences and mechanisms of breeding dispersal in the colonial

- lesser kestrel, *Falco naumanni*. *Anim Behav* 76:1989–1996. doi:10.1016/j.anbehav.2008.08.019
- Calenge C (2006) The package "adehabitat" for R software: a tool for the analysis of space and habitat use by animal. *Ecol Model* 197:516–519. doi:10.1016/j.ecolmodel.2006.03.017
- Clobert J, Danchin E, Dhondt AA, Nichols JD (2001) *Dispersal*. Oxford University Press, New York
- Clutton-Brock TH (1991) *The evolution of parental care*. Princeton University Press, Princeton
- Cohas A, Bonenfant C, Kempnaers B, Allaine D (2009) Age-specific effect of heterozygosity on survival in alpine marmots, *Marmota marmota*. *Mol Ecol* 18:1491–1503. doi:10.1111/j.1365-294X.2009.04116.x
- Coulon A, Cosson JF, Angibault JM et al (2004) Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. *Mol Ecol* 13:2841–2850. doi:10.1111/j.1365-294X.2004.02253.x
- Da Silva A, Gaillard JM, Yoccoz NG et al (2009) Heterozygosity-fitness correlations revealed by neutral and candidate gene markers in roe deer from a long-term study. *Evolution* 63:403–417. doi:10.1111/j.1558-5646.2008.00542.x
- Danchin E, Cam E (2002) Can non-breeding be a cost of breeding dispersal? *Behav Ecol Sociobiol* 51:153–163. doi:10.1007/s00265-001-0423-5
- Daniels SJ, Walters JR (2000) Between-year breeding dispersal in Red-cockaded Woodpeckers: multiple causes and estimated cost. *Ecology* 81:2473–2484
- Debeffe L, Morellet N, Cargnelutti B et al (2012) Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *J Anim Ecol* 81:1327–1337. doi:10.1111/j.1365-2656.2012.02006.x
- Fieberg J, Delgiudice G (2008) Exploring migration data using interval-censored time-to-event models. *J Wildl Manag* 72:1211–1219. doi:10.2193/2007-403
- Fisher DO, Lara MC (1999) Effects of body size and home range on access to mates and paternity in male bridled naitail wallabies. *Anim Behav* 58:121–130. doi:10.1006/anbe.1999.1119
- Gaillard JM, Sempere AJ, Boutin JM et al (1992) Effects of age and body-weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Can J Zool-Rev Can Zool* 70:1541–1545. doi:10.1139/z92-212
- García-Navas V, Jose Sanz J (2011) Females call the shots: breeding dispersal and divorce in blue tits. *Behav Ecol* 22:932–939. doi:10.1093/beheco/arr067
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162. doi:10.1016/S0003-3472(80)80103-5
- Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annu Rev Ecol Syst* 13:1–21. doi:10.1146/annurev.es.13.110182.000245
- Hamilton WD (1990) Mate choice near or far. *Am Zool* 30:341–352. doi:10.1093/icb/30.2.341
- Harrington DP, Fleming TR (1982) A class of rank test procedures for censored survival-data. *Biometrika* 69:553–566. doi:10.1093/biomet/69.3.553
- Hewison AJM, Vincent JP, Reby D (1998) Social organisation of European roe deer. *The European Roe Deer: the biology of success*. Scandinavian University Press, oslo
- Hoffman JI, Forcada J, Trathan PN, Amos W (2007) Female fur seals show active choice for males that are heterozygous and unrelated. *Nature* 445:912–914. doi:10.1038/nature05558
- Hoffmann B, Barth D, Karg H (1978) Progesterone and estrogen-levels in peripheral plasma of the pregnant and non-pregnant roe deer (*Capreolus-capreolus*). *Biol Reprod* 19:931–935. doi:10.1095/biolreprod19.5.931
- Kolodzinski JJ, Tannenbaum LV, Muller LI et al (2010) Excursive behaviors by female white-tailed deer during estrus at two mid-atlantic sites. *Am Midl Nat* 163:366–373. doi:10.1674/0003-0031-163.2.366
- Kurt F, Hartl G, Volk F (1993) Breeding strategies and genetic-variation in European roe deer *Capreolus capreolus* populations. *Acta Theriol (Warsz)* 38:187–194
- Labisky RF, Fritzen DE (1998) Spatial mobility of breeding female white-tailed deer in a low-density population. *J Wildl Manag* 62:1329–1334. doi:10.2307/3801998
- Lamberti P, Mauri L, Merli E et al (2006) Use of space and habitat selection by roe deer *Capreolus capreolus* in a Mediterranean coastal area: how does woods landscape affect home range? *J Ethol* 24:181–188
- Liberg O, Johansson A, Andersen R, Linnell JDC (1998) Mating system, mating tactics and the function of male territory in roe deer. In: Andersen R, Duncan P, Linnell J (eds) *The European Roe Deer: the biology of success*. Scandinavian University Press, Oslo, pp 221–256
- Lovari S, Bartolommei P, Meschi F, Pezzo F (2008) Going out to mate: excursion behaviour of female roe deer. *Ethology* 114:886–896. doi:10.1111/j.1439-0310.2008.01549.x
- Lukas D, Clutton-Brock TH (2011) Group structure, kinship, inbreeding risk and habitual female dispersal in plural-breeding mammals. *J Evol Biol* 24:2624–2630. doi:10.1111/j.1420-9101.2011.02385.x
- Marjamaeki PH, Contasti AL, Coulson TN, McLoughlin PD (2013) Local density and group size interacts with age and sex to determine direction and rate of social dispersal in a polygynous mammal. *Ecol Evol* 3:3073–3082. doi:10.1002/ece3.694
- Morellet N, Van Moorter B, Cargnelutti B et al (2011) Landscape composition influences roe deer habitat selection at both home range and landscape scales. *Landsc Ecol* 26:999–1010. doi:10.1007/s10980-011-9624-0
- Morton NE, Crow JF, Muller HJ (1956) An estimate of the mutational damage in man from data on consanguineous marriages. *Proc Natl Acad Sci USA* 42:855–863. doi:10.1073/pnas.42.11.855
- Naguib M, Altenkamp R, Griessmann B (2001) Nightingales in space: song and extra-territorial forays of radio tagged song birds. *J Ornithol* 142:306–312. doi:10.1046/j.1439-0361.2001.01005.x
- Nicol SC, Vanpe C, Sprent J et al (2011) Spatial ecology of a ubiquitous Australian anteater, the short-beaked echidna (*Tachyglossus aculeatus*). *J Mammal* 92:101–110. doi:10.1644/09-MAMM-A-398.1
- Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. *J Anim Ecol* 67:518–536. doi:10.1046/j.1365-2656.1998.00215.x
- Pedersen MC, Dunn PO, Whittingham LA (2006) Extraterritorial forays are related to a male ornamental trait in the common yellowthroat. *Anim Behav* 72:479–486. doi:10.1016/j.anbehav.2006.02.010
- Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206. doi:10.1016/0169-5347(96)10028-8
- R Development Core Team (2010) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Ratcliffe PR, Mayle B (1992) *Roe deer biology and management*. For Commision Bull 105:1–28
- Richard E, Morellet N, Cargnelutti B et al (2008) Ranging behaviour and excursions of female roe deer during the rut. *Behav Processes* 79:28–35. doi:10.1016/j.beproc.2008.04.008
- Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu Rev Ecol Evol Syst* 38:231–253. doi:10.1146/annurev.ecolsys.38.091206.095611
- Sempéré AJ, Mauget R, Mauget C (1998) Reproductive physiology of roe deer. In: Andersen R, Duncan P, Linnell J (eds) *The European*

- Roe deer: the biology of success. Scandinavian University Press, Oslo, pp 161–188
- Sillero-Zubiri C, Gottelli D, Macdonald DW (1996) Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behav Ecol Sociobiol* 38:331–340. doi:[10.1007/s002650050249](https://doi.org/10.1007/s002650050249)
- Soulsbury CD, Iossa G, Baker PJ et al (2011) Behavioral and spatial analysis of extraterritorial movements in red foxes (*Vulpes vulpes*). *J Mammal* 92:190–199. doi:[10.1644/09-MAMM-A-187.1](https://doi.org/10.1644/09-MAMM-A-187.1)
- Stopher KV, Nussey DH, Clutton-Brock TH et al (2011) The red deer rut revisited: female excursions but no evidence females move to mate with preferred males. *Behav Ecol* 22:808–818. doi:[10.1093/beheco/arr052](https://doi.org/10.1093/beheco/arr052)
- Therneau T, Lumley T (2010) survival: Survival analysis, including penalised likelihood R package, Version 2.36-2
- Urbano F, Cagnacci F (2014) Spatial database for GPS wildlife tracking data. A practical guide to creating a data management system with PostgreSQL/PostGIS and R. Springer, Berlin
- Vanpé C, Gaillard JM, Kjellander P et al (2007) Antler size provides an honest signal of male phenotypic quality in roe deer. *Am Nat* 169:481–493. doi:[10.1086/512046](https://doi.org/10.1086/512046)
- Vanpé C, Kjellander P, Galan M et al (2008) Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behav Ecol* 19:309–316. doi:[10.1093/beheco/arm132](https://doi.org/10.1093/beheco/arm132)
- Vanpé C, Gaillard JM, Morellet N et al (2009a) Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. *J Mammal* 90:661–665. doi:[10.1644/08-MAMM-A-137R.1](https://doi.org/10.1644/08-MAMM-A-137R.1)
- Vanpé C, Kjellander P, Gaillard JM et al (2009b) Multiple paternity occurs with low frequency in the territorial roe deer, *Capreolus capreolus*. *Biol J Linn Soc* 97:128–139. doi:[10.1111/j.1095-8312.2009.01196.x](https://doi.org/10.1111/j.1095-8312.2009.01196.x)
- Vanpé C, Morellet N, Kjellander P et al (2009c) Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. *J Anim Ecol* 78:42–51. doi:[10.1111/j.1365-2656.2008.01467.x](https://doi.org/10.1111/j.1365-2656.2008.01467.x)
- Vanpé C, Gaillard JM, Kjellander P et al (2010) Assessing the intensity of sexual selection on male body mass and antler length in roe deer *Capreolus capreolus*: is bigger better in a weakly dimorphic species? *Oikos* 119:1484–1492. doi:[10.1111/j.1600-0706.2010.18312.x](https://doi.org/10.1111/j.1600-0706.2010.18312.x)
- Wahlstrom LK (1994) The significance of male male-aggression for yearling dispersal in roe reer (*Capreolus-capreolus*). *Behav Ecol Sociobiol* 35:409–412. doi:[10.1007/BF00165843](https://doi.org/10.1007/BF00165843)
- Winters JB, Waser PM (2003) Gene dispersal and outbreeding in a philopatric mammal. *Mol Ecol* 12:2251–2259. doi:[10.1046/j.1365-294X.2003.01896.x](https://doi.org/10.1046/j.1365-294X.2003.01896.x)
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Ser B-Stat Methodol* 73:3–36
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168. doi:[10.2307/1938423](https://doi.org/10.2307/1938423)
- Zeh JA, Zeh DW (1996) The evolution of polyandry I: Intra-genomic conflict and genetic incompatibility. *Proc R Soc Lond B Biol Sci* 263:1711–1717. doi:[10.1098/rspb.1996.0250](https://doi.org/10.1098/rspb.1996.0250)