

## Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer



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Natal dispersal (i.e. movements between the natal range of an individual and its first breeding site) is a complex process which can have profound impacts on population dynamics. In most species, only a proportion of juveniles actually disperse, but few empirical data are available on the factors that drive the decision to disperse. To understand the behavioural ontogeny of the decision to disperse, we investigated the ranging behaviour of 66 juvenile roe deer, *Capreolus capreolus*, monitored with GPS collars prior to and during the dispersal phase. We compared the number and features (distance and duration) of exploratory movements during the period prior to dispersal between philopatric individuals and dispersers. Overall, 76% of the juveniles that dispersed during their first spring performed exploratory movements prior to the dispersal period. Indeed, exploration prior to the dispersal phase was much more common among future dispersers than among future philopatric individuals, suggesting that dispersal of juveniles is facilitated to some degree by predispersal exploration forays. Furthermore, the direction of the dispersal event was correlated with the direction of previous exploration, although there was no relationship between exploration distance and subsequent dispersal distance. Thus, it appears that individuals that subsequently disperse first explore their environment, prior to definitively leaving their natal range, probably to obtain information on potential suitable adult ranges. Exploratory movements prior to dispersal can thus provide information that influences an individual's decision on whether or not to disperse and, if so, in which direction.

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Animal movements can affect many important ecological processes such as gene flow (Bohonak 1999) and metapopulation dynamics (Hastings & Harrison 1994). Natal dispersal, defined as the net movement between the natal area and the site of first breeding (Howard 1960), is characterized by long-distance movements which, for nonmigratory species, are usually the longest performed during an individual's lifetime. Not all individuals within a given population disperse (Bowler & Benton 2005; Ronce 2007), but the factors that influence this decision at the individual level are poorly understood, despite the fact that natal dispersal decisions can have profound consequences for population dynamics (Clobert et al. 2001). Dispersal is a complex process, and a variety of factors can

affect the decision to leave the natal area (e.g. sex, developmental stage, body size, density, etc.; i.e. condition-dependent dispersal sensu Bowler & Benton 2005). Investigating the behavioural ontogeny of this decision could help us understand why some individuals disperse while others do not. In particular, exploratory movements (i.e. movements outside an individual's home range) performed prior to true dispersal may play a role in the dispersal decision (Selonen & Hanski 2006). Indeed, such movements can provide information on the surrounding environment which can be used by individuals to decide (1) whether or not to disperse and (2) for dispersers, how far and in which direction to disperse during the transition phase (Stamps & Krishnan 1999). Despite this, very few studies have investigated between-individual differences in exploration behaviour and its impact on the dispersal decision.

Exploration behaviour prior to dispersal has been documented in several species and seems to be a common behaviour associated with dispersal. For instance, a peak of exploratory activity was detected 1 week before dispersal in male Belding's ground

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squirrels, *Spermophilus beldingi* (Holekamp 1986). This exploratory activity has also been recorded in Eurasian lynx, *Lynx lynx* (Samelius et al. 2011) and in eagle owls, *Bubo bubo* (Delgado et al. 2009), and systematically precedes dispersal in badgers, *Meles meles* (Roper et al. 2003). However, Doerr & Doerr (2005) noticed a high level of individual heterogeneity in exploratory behaviour prior to dispersal in two species of treecreepers (*Climacteris picumnus* and *Cormobates leucophaea*), suggesting that not all dispersers first explore their surrounding habitat before dispersing. A similar pattern has been observed in wolverines, *Gulo gulo* (Vangen et al. 2001) and in North American red squirrels, *Tamiasciurus hudsonicus* (Haughland & Larsen 2004). Exploration is thus a highly variable behaviour among species, but also among individuals within populations. More generally, exploration behaviour may be part of a complex of interindividual behavioural variation which, when coupled with other traits, describes a behavioural syndrome (Sih et al. 2004), also called personality. Indeed, exploration is listed as one of the five main behavioural gradients that commonly describe animal personalities (Réale et al. 2007). Hence, we might expect that dispersal should be related to a particular personality type which is characterized, among other behavioural traits, by more pronounced exploratory behaviour, as was found in a population of great tits, *Parus major* (Dingemanse et al. 2003). However, studies considering exploration as a personality trait have usually been conducted under experimental conditions, and the link between exploratory movements and dispersal could differ between experimental and natural populations. In particular, exploration is forced rather than voluntarily expressed in an experimental set-up. Hence, in the following, when possible we refer to studies that investigated exploratory movements in wild populations.

It has also been demonstrated that exploration has the potential to influence certain features of the dispersal movement. For example, exploration distance and direction seem to determine, at least in part, the subsequent direction and distance of the dispersal movement in North American red squirrels (Haughland & Larsen 2004). If exploratory movements are linked to dispersal, we can expect exploration propensity and features to differ between dispersers and philopatric individuals. The only study, to our knowledge, that has investigated this question did not find any difference in exploratory behaviour of disperser and philopatric individuals in flying squirrels, *Pteromys volans* (Selonen & Hanski 2006). Differences in exploratory behaviour are also expected between short- and long-distance dispersers or between early and late dispersers, assuming that the underlying behavioural mechanism for dispersing differs between these categories of individuals (e.g. Selonen & Hanski 2004). For example, if juveniles that disperse late are forced to do so, whereas early dispersers leave voluntarily, we might expect that the former would engage in less predispersal exploratory behaviour than the latter. Also, as suggested by Wigggett et al. (1989), individuals that undergo long-distance dispersal movements are unlikely to be able to familiarize themselves with potential home ranges during exploration, which generally involves shorter movements. Hence, long-distance dispersers may benefit less from exploratory movements compared to short-distance dispersers and, as found by Selonen & Hanski (2006), may thus explore less. However, to date, few studies have compared these categories of individuals.

In this study, we used an especially detailed GPS monitoring of juvenile roe deer, *Capreolus capreolus*, to investigate the influence of exploratory movements on dispersal behaviour in this species. More precisely, we looked for evidence of exploration behaviour and contrasted the exploration frequency and features (distance and duration) of philopatric individuals with those of individuals that subsequently dispersed. Van Moorter et al. (2008) previously showed that juvenile roe deer are more mobile than adults, but

these authors did not compare the behaviour of future dispersers with future philopatric animals. Based on this observation, together with the fact that outside the juvenile dispersal phase, roe deer are generally highly sedentary (Hewison et al. 1998), this species thus provides a pertinent study system for exploring the link between predispersal exploration behaviour and dispersal outcomes, thus contributing to a better understanding of the behavioural ontogeny of the dispersal decision.

The aim of this study was to investigate whether exploration influences dispersal behaviour in roe deer. To do so, we investigated the spatial behaviour of roe deer prior to the dispersal period, in particular, by comparing the behaviour of future dispersers and future philopatric individuals. Assuming that predispersal exploration forays increase the likelihood of subsequent dispersal, we expected that future dispersers should be more mobile and should perform more exploratory movements prior to dispersal than future philopatric individuals. In addition, landscape structure has been shown to influence the spatial behaviour of roe deer (Hewison et al. 2001; Lamberti et al. 2006; Morellet et al. 2011) and we recently showed in the same population that forest deer disperse less than those living in more heterogeneous habitats (Debeffe et al. 2012). We thus controlled for the effect of landscape structure in all analyses. Based on previous studies showing that neither natal dispersal (Coulon et al. 2006; Gaillard et al. 2008) nor juvenile mobility (Van Moorter et al. 2008) is sex biased in roe deer, we expected the pattern of predispersal exploration to be similar between the sexes. Moreover, since body mass has the potential to affect dispersal behaviour (Debeffe et al. 2012), we also tested for an effect of individual body mass on predispersal exploratory behaviour. Assuming that exploratory movements allow individuals to obtain information on the surrounding environment and so to inform their future dispersal decisions (Stamps & Krishnan 1999; Stamps 2001; Selonen & Hanski 2006), we expected exploration and dispersal events to have similar features. We expected exploration distance to be positively correlated with dispersal distance and exploration and dispersal directions to match for a given individual. Finally, we expected differences to occur in exploratory movements (both distance travelled and duration time) between individuals performing long versus short dispersal and between dispersers leaving their natal range early in the season versus those leaving late, with short-distance dispersers and early dispersers engaging more in exploratory movements (i.e. longer distance and duration).

## METHODS

### Study Area

The study was conducted in a hilly (260–380 m above sea level) and heterogeneous agricultural landscape in the Comminges region of southwest France (43°13'N, 0°52'E) covering around 10 000 ha. The climate is oceanic, with an average annual temperature of 11–12 °C and 800 mm precipitation, mainly as rain. The area is a mixed landscape of open fields and small woodland patches (average size of 3 ha) dominated by oaks, *Quercus* spp., with 23.7% woodland, 36.1% meadows, 32.1% cultivated fields and 4.3% hedgerows (see Hewison et al. 2009 for further details). We identified three sectors of contrasting landscape structure based on woodland extent. The first sector included two forest blocks (100% of woodland cover); the second and third sectors were composed of a more open landscape of fragmented woodland, with the second sector corresponding to a partially wooded area (around 30% of woodland cover) and the third sector to an open agricultural area with highly fragmented woodland (around 12% of woodland cover; see Morellet et al. 2011 for further details).

### Capture and Monitoring

Roe deer were caught from 2002 to 2011 during winter (from 16 November to 27 March, with around 75% of individuals captured between 5 January and 9 February) using large-scale drives of between 30 and 100 beaters and up to 4 km of long nets positioned at one of 11 capture sites. For each captured animal, we recorded its body mass to the nearest 0.1 kg and its sex, and we attributed an age class before fitting it with a collar and releasing it on site. Juveniles (less than 1 year old) are distinguishable from older deer by the presence of a tricuspid third premolar milk tooth (Ratcliffe & Mayle 1992). During the nine winters of sampling (2002–2011), 102 juveniles were captured and fitted with a Lotek 3300 GPS or a Lotek Small WildCell GSM collar (<http://www.lotek.com>). Collars were programmed to calculate the roe deer location every 4 h in 2002–2004 (first two winters) or every 6 h (following winters) over approximately 11 months. We performed differential correction to improve fix accuracy (Adrados et al. 2003). Capture and handling can temporarily affect roe deer behaviour; hence, as recommended by Morellet et al. (2009), location data for the first week after release were excluded from the analyses.

The roe deer is a medium-sized (20–30 kg), slightly dimorphic and weakly polygynous species; adults of both sexes are highly sedentary (Andersen et al. 1998). Natal dispersal is highly synchronized in time, occurring only in juveniles, during their first spring, when the mother–juvenile bond breaks down before the mother gives birth to her next litter (Wahlstrom & Liberg 1995; Linnell et al. 1998). Since juvenile roe deer disperse in early spring, their dispersal status can be accurately determined by the end of May. Indeed, GPS data were recovered for 91 of the 102 individuals (the other data were missing either because the GPS collar did not work properly or because the collar was lost), while dispersal fate could be determined for 75 of these which were monitored from their capture in winter to at least the end of May. However, for nine of these, the GPS monitoring had more than 48% of missing GPS data over this period, leading to a poor representation of the individual trajectory. Hence, of the 102 juveniles captured, only 66 individuals were used in the following analyses. We chose a threshold value of less than 48% for missing GPS data because it represented, for our data set, the best compromise between the number of individuals retained for the analyses and the quality of the GPS monitoring. In addition, for one individual, body mass at capture was not recorded.

### Ethical Note

All capture, handling and collaring were done according to the French law for animal welfare and procedures were approved by the French administration (prefectural order from Toulouse 'Administrative authorization to inventory and capture wild animals', renewed each year and specifying a species, a date, a place and a method of capture). Animals were captured during drives by human beaters; as these drives did not involve dogs and were carried out during the hunting period, the disturbance caused to roe deer and other wildlife in the area was considerably less than that occurring routinely during regular hunting with dogs. Roe deer were driven for a variable period of time, lasting generally less than 10 min as the mean  $\pm$ SE distance separating a given roe deer's initial location and the net lines was  $513 \pm 186$  m. Once an animal entered a net, it was immediately given an acepromazine intramuscular injection (one dose of 1.65 mg) by a person licensed to do so (Federation of European Laboratory Animal Science Associations (FELASA) category C accreditation) before being isolated in a wooden holding box to allow the tranquillizer to take effect. The acepromazine used was manufactured by Calmivet (Institut de pharmacie vétérinaire, 7,

Avenue Al Majd, 10150 Rabat, Morocco) and the drug dose was calculated for this species following Montané et al.'s (2003) study; acepromazine is a short-acting neuroleptic that reduces the stress response rapidly and prevents any adverse effects in roe deer (Montané et al. 2003), but does not require an antagonist to reverse its rather short-term effects. Subsequently, animals were removed from the box, restrained by the same three highly experienced animal handlers, with their eyes covered to reduce stress while measurements were taken and the collar fitted, before being released on site. GPS and GSM collars weighed a mean  $\pm$ SE of  $370.5 \pm 20.5$  g corresponding to 3.17% of the smallest individual's body mass and 1.94% of the largest individual's body mass. At the time of capture, juveniles were approximately 8 months old with a neck circumference of about 2.5 cm less than that of yearling individuals (mean neck circumference  $\pm$ SE =  $23.6 \pm 2.1$  cm for juveniles,  $N = 140$  and  $25.8 \pm 2.8$  cm for yearlings,  $N = 44$ ). We allowed for this incremental growth of about 10% by fitting the collar slightly looser on juveniles. After 11 months of data acquisition (location of individuals using GPS and GSM systems), the collars fell off the animals thanks to the preprogrammed remote drop-off system and were retrieved for data download. We did not record any adverse effects or behavioural modifications linked to the wearing of the collars during the study.

### Characterizing Dispersal Movements

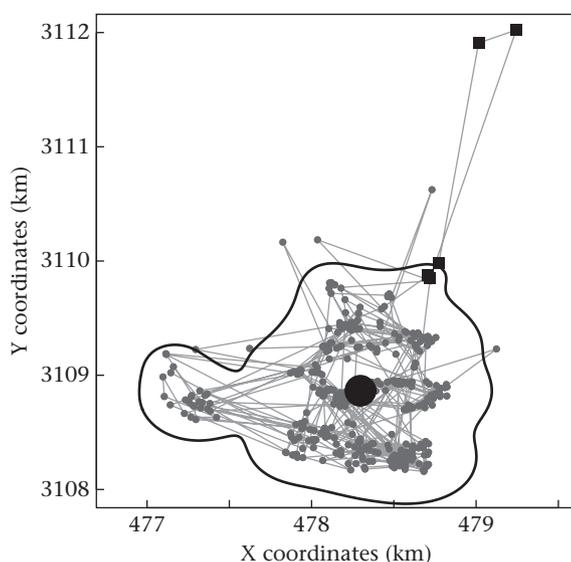
Natal dispersal was defined as permanent emigration from the natal range (predisersal home range) to a distinct adult range (postdispersal home range), such that predisersal locations did not overlap postdispersal locations (Kenward et al. 2002). As described in Debeffe et al. (2012), we used the range stability index proposed by Roshier & Reid (2003) as a measure of this overlap. The range stability index was calculated as the ratio between the seasonal home range (the natal or the postdispersal range) and the annual range (combining the natal and postdispersal ranges for each animal) for each individual and thus allowed us to discriminate dispersers from philopatric animals. As in most studies on dispersal behaviour (Stenseth & Lidicker 1992) and for reasons of simplicity, dispersal was here considered as a binary decision, to disperse or not. Previous analyses on roe deer dispersal have shown that similar patterns are obtained whether dispersal is analysed as either a binary variable (i.e. dispersal versus no dispersal) or as a dispersal distance (e.g. Gaillard et al. 2008; Debeffe et al. 2012).

Dispersal departure date was defined as the last date a deer was located inside its natal range without returning. Dispersal was considered to have ceased when the animal's GPS locations stabilized in space within a postdispersal range (i.e. when the juvenile stopped travelling long distances and restricted its movement to a limited area; in practice this endpoint was easily identifiable). For 90% of dispersers (26 of 29), the dispersal movement ceased abruptly (i.e. within less than 6 h), with the first GPS location inside the future adult range corresponding to the endpoint of the dispersal process. We measured dispersal duration, the total distance travelled during dispersal trajectory, and the distance between the barycentres of the natal range and of the postdispersal range (i.e. dispersal distance). We also measured the direction of the dispersal event, calculated as the mean of the angles defined by the straight line between each location of the dispersal trajectory and the barycentre of the predisersal home range with respect to the east–west axis. We chose to measure the dispersal direction as the mean of successive angles (rather than as the angle between the barycentres of the pre- and postdispersal ranges) as this provided a more accurate evaluation of the overall direction of the dispersal path.

Five of the 66 individuals exhibited a dispersal-type movement (median distance travelled = 15.3 km, range 4.7–32.2 km,  $N = 5$ ), but then returned sometime later during summer (median = 10.7 weeks, range 1.4–28.8 weeks,  $N = 5$ ) to their natal range. Although these five pseudodispersing individuals probably reproduced for the first time within their natal home range, for the subsequent analyses they were considered as dispersers because they left their juvenile area during the natal dispersal period and for a substantial duration. Thus, the behavioural factors that trigger this movement could be assumed to be the same as, or similar to, those for true dispersal movements, even though this attempted dispersal was subsequently aborted.

### Characterizing Exploratory Movements

To detect extrarange movements prior to dispersal, hereafter called exploration, we first calculated the 95% fixed kernel home range with an ad hoc method for the smoothing parameter with the *adehabitat* package of the R software (Calenge 2006). We based this calculation on GPS locations that were obtained during the pre-dispersal period, between 1 January or 1 week after the capture event, and before dispersal initiation for dispersing individuals; and between 1 January or 1 week after the capture event, and before a threshold date randomly chosen from the distribution of dispersal initiation dates for philopatric individuals. An exploration event was defined as at least two successive locations outside the natal home range (to avoid the detection of false exploration events due to a single GPS location error) to which we added the departure and the arrival locations inside the home range (Fig. 1). By using this definition, we assumed that exploration events lasted at least 12 h, which may have led to a degree of underestimation for the number of exploration events performed per individual. For individuals performing more than one exploration event, we defined the main exploration event as that with the longest duration; when specified (using the term main exploration event), analysis concerned this event only. We characterized the features of the exploration event (duration, total distance, maximal distance and direction) in an analogous way to that used for dispersal features (see above).



**Figure 1.** Example of space use for a juvenile roe deer prior to dispersal. The 95% kernel home range contour is drawn in black, grey points indicate GPS locations within the natal home range, black squares represent exploration locations (including the departure and arrival locations of exploration events within the natal home range). The large black dot indicates the barycentre of the home range.

### Statistical Analyses

To test whether exploration occurred at regular intervals through time prior to the dispersal period, we performed a two-sample Kolmogorov–Smirnov test comparing the observed distribution of exploratory movements with a uniform distribution (i.e. a distribution assuming that exploratory movements have a constant probability of occurring through time, without any peak at a given period). To test for differences in exploration features (duration length and distance travelled) in relation to the timing of exploration, we performed linear regressions. We tested whether individuals were more likely to explore or disperse in a given direction, that is, whether the direction of both the main exploration event and of the dispersal event were directionally biased at the population level. To do so, we compared the distribution of observed angles with a uniform distribution using the Rayleigh test for uniformity (Batschelet 1981). We also performed a Wallraff test to compare the angular dispersion between exploration and dispersal directions at the population level (Batschelet 1981). We also analysed differences in exploration features (duration and distance travelled) between the sexes using Student's *t* tests. When required based on inspection for normality of model residuals, exploration distance and exploration duration were log-transformed (Shapiro–Wilk test:  $W = 0.98$ ,  $N = 22$ ,  $P = 0.89$  for distance;  $W = 0.92$ ,  $N = 22$ ,  $P = 0.07$  for duration).

To answer the question whether exploratory behaviour is more common among dispersers than philopatric individuals, we built several candidate models and we then performed a model selection procedure to retain the best one. As dispersal propensity depends on individual body mass and landscape openness (Debeffe et al. 2012), we controlled for these two effects in the models. We used a logit link function for explaining dispersal propensity while taking into account possible between-sector differences (included in the models as a random factor). Based on our explicit hypotheses, we worked with a restricted set of a priori selected variables (i.e. exploration propensity, number of exploration events, sex and body mass), so that 14 candidate mixed generalized linear models were fitted (Table 1). Starting from the basic model in which dispersal propensity (entered as the dependent variable) depends on body mass only (entered as a covariate), we added the effect of exploration (entered as a two-level fixed factor describing whether or not a given individual performed an exploration event or as a covariate describing the number of pre-dispersal exploration events; because these two variables are highly correlated, we never included both in a single model) and the effect of sex (entered as a two-level fixed factor). The most complex model also included the two two-way interactions between exploration (propensity or number) and body mass and between exploration and sex, allowing us to test for the influence of sex and individual body mass on pre-dispersal exploratory behaviour. We selected the best model with the lowest Akaike's information criterion (AIC) value (AIC<sub>c</sub>, i.e. AIC corrected for small sample size), reflecting the best compromise between precision and complexity of the model (Burnham & Anderson 2002). According to the rule of parsimony, when the AIC<sub>c</sub> of two competing models differed by <2, we retained the simplest one. We also calculated AIC<sub>c</sub> weights as a measure of the likelihood that a given model was the best among the set of fitted models. We also investigated the differences in exploration features (duration and distance travelled) between dispersers and philopatric individuals using Mann–Whitney *U* tests.

We then investigated the influence of exploration features (distance and direction) on the features of the subsequent dispersal trajectory at the individual level: first, we compared the distances travelled during exploration and dispersal for a given juvenile using linear regression; second, we tested whether the direction of the

**Table 1**

Logistic regression explaining dispersal status (disperser/philopatric) for juvenile roe deer ( $N = 65$ ) in relation to exploration behaviour and sex using the Akaike's information criterion corrected for small sample size (AICc) for model selection

Associated hypothesis	Models	K	AICc	$\Delta$ AICc	AICcWt
(1)	Nb_Explo+BM	4	73.01	0	0.25
(1)+(3)	BM*Nb_Explo+BM	5	73.51	0.49	0.2
(1)+(2)	Sex+Nb_Explo+BM	5	74.04	1.03	0.15
(1)+(2)	Sex*Nb_Explo+BM	6	74.35	1.34	0.13
(1)+(3)+(2)	BM*Nb_Explo+Sex+BM	6	74.96	1.95	0.09
(1)+(3)+(2)	Sex*Nb_Explo+BM*Nb_Explo+BM	7	76.12	3.11	0.05
(1)	Explo+BM	4	76.47	3.46	0.04
(1)+(2)	Sex+Explo+BM	5	77.71	4.7	0.02
(1)+(3)	BM*Explo+BM	5	78.7	5.69	0.01
(1)+(2)	Sex*Explo+BM	6	79.61	6.6	0.01
(1)+(3)+(2)	BM*Explo+Sex+BM	6	80.08	7.07	0.01
Null hypothesis	BM	3	81.38	8.37	0
(1)+(3)+(2)	Sex*Explo+BM*Explo+BM	7	82.1	9.09	0
Null hypothesis	Constant	2	90.98	17.97	0

The basic model includes the fixed effect of body mass ('BM') and controls for differences between sectors by including this factor as a random effect. Exploration behaviour is included as either a two-level fixed factor describing whether or not an individual performed at least one exploration event ('Explo') or as a discrete variable describing the number of exploration events performed ('Nb\_Explo'). All 14 models include the variable 'sectors' as a random effect. The related hypotheses were: (1) influence of predispersal exploration on dispersal propensity (expectation = future dispersers should be more mobile and should perform more exploratory movements prior to dispersal than future philopatric individuals); (2) no sex-biased mobility prior to dispersal (expectation = no difference between the sexes in exploration propensity or in number of exploration events performed); (3) influence of body mass on exploratory behaviour (expectation = positive effect of body mass on exploration propensity and on the number of exploration events performed).

dispersal event was correlated with that of the main exploration event for a given juvenile. A common approach to this is to perform a Rayleigh test of uniformity with specified mean direction ( $V_0$  test), but we obtained too few locations during the exploration event for some individuals to make this test robust (mean  $\pm$ SE number of exploratory locations outside the home range per disperser (i.e. mean number of available locations for a given  $V_0$  test) =  $3.28 \pm 3.01$  locations, range 2–20 locations,  $N = 43$ ). Therefore, to test for the nonindependence of the two directions (main exploration event and dispersal event) for the 22 individuals that performed both types of movement, we used a linear regression. A positive relationship between the two angles indicates that dispersal is oriented towards a previously explored area.

The differences in dispersal features between individuals performing short and long dispersal, and between early and late dispersal events, were investigated using linear regressions between the dispersal distance and date of departure with the number of exploration events performed and exploration features (log-transformed mean distance travelled and mean duration). All statistical analyses were performed with R software version 2.12.1 (R Development Core Team 2010).

## RESULTS

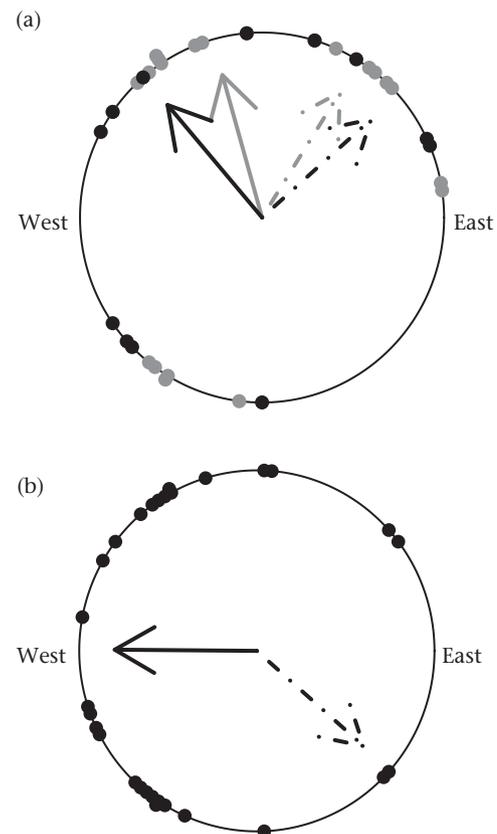
### Exploration Behaviour

Of the 66 juveniles, 34 (i.e. 52%) performed at least one exploration event outside their natal home range prior to the dispersal period (mean  $\pm$ SE =  $1.76 \pm 1.26$  exploratory movements, median = 1, range 1–7,  $N = 34$ ). Thirty-nine per cent ( $N = 15/38$ ) of the females and 68% ( $N = 19/28$ ) of the males performed an exploratory movement. The mean  $\pm$ SE distance travelled during exploration was  $4.79 \pm 4.21$  km (median = 3.7 km, range 0.5–25.0 km) and exploratory movements lasted  $28.5 \pm 21.8$  h

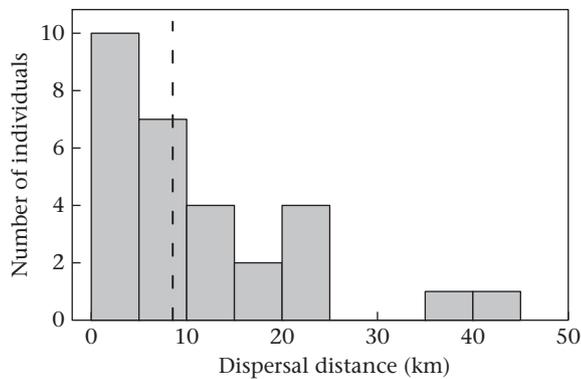
(median = 24.0 h, range 12.0–138.0 h) taking into account all exploration events ( $N = 59$ ). Exploratory movements occurred regularly throughout the predispersal period (two-sample Kolmogorov–Smirnov test:  $D = 0.2$ ,  $N_1 = N_2 = 59$ ,  $P = 0.18$ ; the median  $\pm$ SE exploration date was 17 March  $\pm 34$  days), with no differences in distance travelled or duration in relation to the date of departure (linear regression:  $F_{1,56} = 0.45$ ,  $R^2 = 0.008$ ,  $N = 59$ ,  $P = 0.50$  for distance travelled and  $F_{1,56} = 0.68$ ,  $R^2 = 0.012$ ,  $P = 0.40$  for duration). The mean direction of the exploration events was not uniformly distributed at the population level, but was biased towards the north (Rayleigh's test:  $Z = 0.31$ ,  $N = 34$ ,  $P = 0.03$ ; Fig. 2a). Exploration distance (Student's  $t$  test:  $t_{50.14} = 0.81$ ,  $N_{females} = 24$ ,  $N_{males} = 35$ ,  $P = 0.42$ ) and duration ( $t_{56.34} = 0.50$ ,  $N_{females} = 24$ ,  $N_{males} = 35$ ,  $P = 0.62$ ) did not differ between the sexes.

### Dispersal Behaviour

Of the 75 juveniles for which dispersal fate was reliably assessed, 45 were philopatric, 25 dispersed and five left their natal area but then returned sometime later during summer (i.e. pseudodispersal events). When we removed the pseudodispersers, 36% of juveniles in the study population hence dispersed ( $N = 25/69$ ). As nine of 75 juveniles had more than 48% of missing GPS locations, the trajectory of 66 juveniles was retained for the subsequent analyses. The 29 animals that left their natal range travelled a mean  $\pm$ SE total distance during their dispersal trajectory of  $22.02 \pm 16.99$  km before settling in their postdispersal home range (median = 16.1 km, range 0.6–56.7 km; Fig. 3). The direction of dispersal events was not uniformly distributed at the population



**Figure 2.** The directional orientation of (a) the main exploration event for future dispersers in grey ( $N = 22$ ) and future philopatric individuals in black ( $N = 12$ ) and (b) dispersal trajectories ( $N = 29$ ). The arrows show the mean direction and the dashed arrows the median direction.

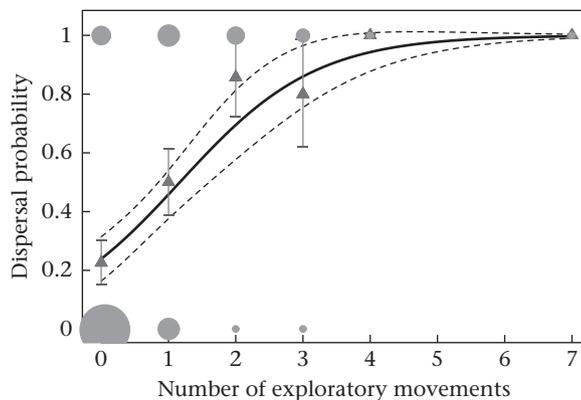


**Figure 3.** Distribution of dispersal distances (i.e. distance between the barycentres of the natal range and of the postdispersal range).  $N = 29$ . The dashed line represents the median dispersal distance.

level, but was biased toward the west (Rayleigh's test:  $Z = 0.38$ ,  $N = 29$ ,  $P = 0.01$ ; Fig. 2b).

#### Link Between Exploration and Dispersal Behaviour

Overall, 76% ( $N = 22/29$ ) of future dispersers performed at least one exploratory movement prior to their dispersal departure, while only 32% ( $N = 12/37$ ) of future philopatric individuals performed at least one exploratory movement during the same period. In the most parsimonious mixed generalized linear model, dispersal propensity was associated with the number of exploratory movements performed, when we controlled for effects of body mass and sector on dispersal propensity (Table 1, Fig. 4). The probability of dispersing increased as the number of exploratory movements prior to dispersal increased and was higher for individuals that performed at least one exploratory movement prior to the dispersal period ( $N = 34$ ; estimated dispersal probability  $\pm$ SE =  $0.65 \pm 0.082$ ) than for individuals that did not explore ( $N = 31$ ; estimated dispersal probability  $\pm$ SE =  $0.23 \pm 0.049$ ). However, there was no difference between future dispersers and future philopatric individuals in terms of either exploration distance (Mann–Whitney  $U$  test:  $W = 363$ ,  $N_{\text{disp}} = 45$ ,  $N_{\text{phil}} = 15$ ,  $P = 0.67$ ) or duration ( $W = 337.5$ ,  $N_{\text{disp}} = 45$ ,  $N_{\text{phil}} = 15$ ,  $P = 1$ ).



**Figure 4.** Relationship between dispersal probability and exploratory propensity, expressed as the number of exploratory movements performed, controlling for variation in body mass ( $N = 65$ ). Circles represent data values with a diameter proportional to the number of individuals for each point, triangles represent the observed probability of dispersing  $\pm$ SE, and the line represents the relationship predicted by the mixed generalized linear model (dispersal propensity ~ number of exploratory movements + body mass) including the effect of landscape sector as a random factor, with body mass set to its mean value; dashed lines represent the 95% confidence interval around the predicted values.

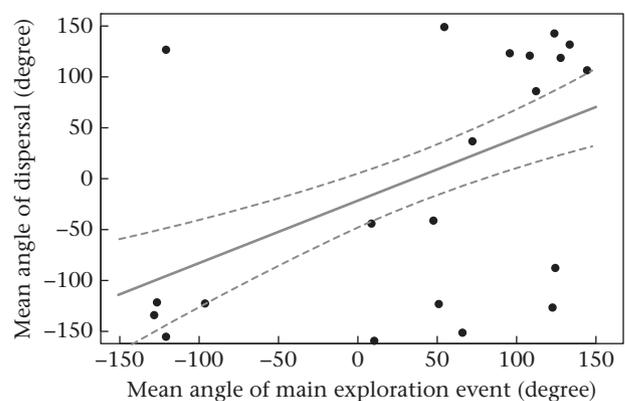
Contrary to expectation, dispersal distance was not correlated with the mean total distance travelled during exploratory movements (linear regression:  $F_{1,20} = 0.04$ ,  $N = 22$ ,  $R^2 = 0.002$ ,  $P = 0.83$ ), nor with the maximum distance recorded from the barycentre of the natal range during exploratory movement (linear regression:  $F_{1,20} = 0.16$ ,  $N = 22$ ,  $R^2 = 0.007$ ,  $P = 0.70$ ).

At the population level, neither the direction of dispersal nor the direction of exploratory movements was uniformly distributed (Fig. 2). The overall population distribution of directions taken during exploratory movements ( $N = 34$ ) was similar to those taken during dispersal ( $N = 29$ ; Wallraff test:  $\chi^2_1 = 1.44$ ,  $P = 0.23$ ). At the individual level, for the 22 individuals performing exploratory movements prior to dispersing, the direction of the dispersal path was positively related to the direction of the main exploration event (linear regression:  $R^2 = 0.22$ ,  $F_{1,20} = 5.6$ ,  $N = 22$ ,  $P = 0.028$ , slope  $\pm$ SE =  $0.61 \pm 0.26$ , intercept  $\pm$ SE =  $-0.38 \pm 0.46$ ), indicating that the two directions were not independent, with dispersers tending to move towards a previously explored area (Fig. 5).

Dispersal distance was not correlated with the number of exploratory movements performed (linear regression:  $F_{1,27} = 0.80$ ,  $N = 29$ ,  $R^2 = 0.03$ ,  $P = 0.37$ ). Similarly, for individuals that explored, dispersal distance was not correlated with either the mean exploration distance (linear regression:  $F_{1,20} = 0.04$ ,  $N = 22$ ,  $R^2 = 0.002$ ,  $P = 0.83$ ) or the mean exploration duration ( $F_{1,20} = 1.11$ ,  $N = 22$ ,  $R^2 = 0.05$ ,  $P = 0.30$ ). Overall, this indicates that individuals that travelled long distances during dispersal did not differ from those that travelled shorter distances in terms of exploration features. Similarly, individuals that initiated dispersal early did not differ from those that left late in terms of exploration behaviour: there was no correlation between the dispersal date of departure and the number of exploration events performed (linear regression:  $F_{1,27} = 0.09$ ,  $N = 29$ ,  $R^2 = 0.003$ ,  $P = 0.77$ ) or, for those making exploratory movements, between departure date and mean exploration distance ( $F_{1,20} < 0.001$ ,  $N = 22$ ,  $R^2 < 0.001$ ,  $P = 0.99$ ) or mean duration ( $F_{1,20} = 1.70$ ,  $N = 22$ ,  $R^2 = 0.08$ ,  $P = 0.21$ ).

#### DISCUSSION

We have shown that exploration behaviour by juvenile roe deer during the predispersal period is common, particularly among males, with more than 50% of juveniles performing at least one exploratory movement in our study population (68% of males and 39% of females). This result is in agreement with Van Moorter et al. (2008) who found that juveniles occupied larger ranges than adult deer during this predispersal phase and interpreted this as



evidence for exploration behaviour. Here, we went one step further by showing that these exploratory movements were much more common among juveniles that subsequently went on to disperse compared to those that remained philopatric, although some future philopatric individuals did explore, but to a lesser extent. This suggests that exploration may provide information that is used by juveniles to inform their decision on whether or not to disperse, and that some individuals may be predisposed to disperse or, at least, that exploration may be a precursor to successful dispersal. In addition, the direction of the dispersal trajectory was correlated with the direction taken during exploration, with a slope slightly lower than one that may be due to the overall bias in direction of both the exploratory and dispersal movements. These observations provide, to our knowledge, the first empirical evidence that exploration of the surrounding environment is a key component in the behavioural ontogeny of the natal dispersal decision in a large herbivore.

Exploratory movement prior to dispersal initiation has been observed in several species of vertebrates, and thus seems to be a widespread behaviour (Roper et al. 2003; Haughland & Larsen 2004; Selonen & Hanski 2006; Delgado et al. 2009; Samelius et al. 2011). Contrary to expectations, in our study population, males performed more exploratory movements than females, possibly linked to the agonistic relationships that juvenile males often have with adult territorial males (Wahlstrom 1994). However, the majority of studies investigating exploration behaviour prior to dispersal have only considered dispersers. For example, a study on Scandinavian Eurasian lynx recorded exploratory movements outside the natal area after the juveniles had separated from their mothers and before dispersal departure (Samelius et al. 2011). Similarly, dispersing badgers first made nocturnal forays into the new area before settling definitively (Roper et al. 2003). Some other studies have assessed the proportion of future dispersers that engaged in exploration behaviour such as in wolverines, where 25% of dispersing individuals performed exploratory movements (Vangen et al. 2001) or in North American red squirrels, where 37% of future dispersers moved around their natal area prior to dispersal (Haughland & Larsen 2004). But few studies have investigated the importance of exploration in the ontogeny of dispersal behaviour by comparing future dispersers with future philopatric individuals (Selonen & Hanski 2006). Our results provide evidence that both future dispersers and future philopatric individuals may perform exploratory movements prior to the dispersal period, in agreement with Selonen & Hanski (2006)'s results. However, in our study population, this behaviour was more pronounced among future dispersers than among future philopatric individuals. Exploratory movements may thus be a way for juveniles, both future dispersers and future philopatric individuals, to evaluate range conditions outside of their natal range and so evaluate the potential gain (for example, in terms of access to resources) if they do disperse. For the individuals that made the decision to disperse, performing more exploratory movements may also allow them to gather information on the surrounding habitat and so choose the dispersal direction.

The above observations indicate that exploration is an integral part of the dispersal process, since it may influence a suite of decisions that individuals make prior to and during their dispersal movements. However, as pointed out by Doerr & Doerr (2005), little is known about how individuals locate and assess their post-dispersal range and there is a need for empirical data on this process across a variety of model organisms. As dispersal should provide greater benefits for individuals that settle in a good-quality range, the process of locating a suitable new habitat is crucial to offset the overall costs of dispersal. When performing exploratory movements individuals can gather information about habitat

quality or availability (Stamps & Krishnan 1999), competitors and/or available future mates (Stamps 2001). Since the costs of dispersal may be reduced by becoming familiar with the habitats around the natal home range (Stamps & Krishnan 1999), exploration may facilitate this familiarization, and thus reduce dispersal costs (Selonen & Hanski 2006). In our study, a few individuals dispersed but then returned to their natal habitat (pseudodispersal events) and we might speculate that these dispersal attempts were aborted because of the specific costs of dispersal (settlement costs in this case). Individuals born in relatively poor habitat may particularly benefit from exploring their surroundings to identify better quality areas in which to settle. In line with this prediction, juvenile North American red squirrels from lower quality habitats (i.e. thinned and edge habitats) performed more exploratory movements towards contrasting habitat (i.e. mature forest; Haughland & Larsen 2004). Furthermore, these benefits obtained during exploration could increase as landscape heterogeneity increases, since the spatial variation in habitat quality is higher in heterogeneous landscapes (North et al. 2011). In heterogeneous landscapes, high-quality ranges may thus be more randomly distributed and harder to locate than in more homogeneous habitats. In this context, dispersal could thus be risky (with a high probability of moving from a good to a poor range) and potentially costly (with marked differences in quality between good and poor ranges; North et al. 2011); as a consequence, because of the information it provides, exploration could be more useful in such landscapes. However, as searching is costly (Stamps 2001), exploratory movements are expected to occur only if they are beneficial. This could explain the observation that individuals in the most fragmented parts of our study site tended to have a higher propensity to explore. Exploratory movements may also provide information on the costs of the projected dispersal movement (Stamps 2001), such that the evaluation of search costs during exploration may determine whether individuals do disperse or not (Stamps et al. 2005). Of the individuals that made at least one exploratory movement in our study, about one-third did not subsequently disperse. We may speculate that this was because the information they obtained during extrarange movements directed their choice towards philopatry.

Individuals differ in their ability to explore and a link between movement behaviour and personalities has been observed in several species (Fraser et al. 2001; Dingemanse et al. 2003; Delgado et al. 2010; Jones & Godin 2010; Wilson & Godin 2010). Exploration behaviour has been found to be a repeatable and heritable trait in a wild population of great tits (Verbeek et al. 1994; Dingemanse et al. 2002). Hence, exploration behaviour seems to be part of a behavioural syndrome (sensu Sih et al. 2004) in a range of species. Furthermore, this behavioural syndrome seems also associated with environmental sensitivity, as in wild starlings, *Sturnus vulgaris*, for which exploratory movements were linked to environmental sensitivity (Minderman et al. 2009). These individuals with high levels of environmental sensitivity should benefit more from these exploratory movements in terms of information gathered. From a more general point of view, exploration behaviour could be part of a behavioural syndrome linked to dispersal, that is, a dispersal syndrome, with certain individuals predisposed to disperse (Clobert et al. 2009).

Although the directions of the exploration and dispersal trajectories were correlated overall, there was no relationship between the distance travelled during exploration and that travelled during dispersal. Indeed, exploration and dispersal did not occur at the same spatial scales, as the mean dispersal distance was four times greater than the mean exploration distance. Similarly, in great tits, postfledging offspring undertook family excursions of substantial distances and these family movements were associated

with future dispersal directions of the juveniles, but not with future dispersal distances (Matthysen et al. 2010). Hence, although individuals might gain information on the surrounding environment during exploration, they are still likely ultimately to settle in an unfamiliar area. Of the 22 dispersers that made an exploratory movement prior to dispersal, only two actually settled in a previously explored area according to our GPS monitoring. This pattern is similar to that observed in several previous studies which did not report a strong predictive relationship between exploration distance and dispersal distance (Holekamp 1986; Wiggett et al. 1989; Vangen et al. 2001). Moreover, phenotypic traits such as body mass or age at dispersal can also generate among-individual variation in dispersal distance and direction (Tarwater 2012), complicating the potential relationship between exploration and dispersal in terms of orientation and distance. However, despite the fact that individuals apparently did not settle in a previously explored area, exploratory movements could still inform individuals about the risks to which they will potentially be exposed when they move outside their familiar range, but also about the relative quality of their natal range (known) compared to that of the (unknown) immediate surrounding area (i.e. spatial sampling). This information could thus be subsequently used as a simple rule of thumb (e.g. if the natal range is of higher quality relative to a sample of the surrounding environment, then stay, but leave if it is of relatively lower quality) on which to base the decision whether or not to leave the natal range.

Individuals that performed long-distance dispersal or left their natal area early were not more likely to explore and they explored over the same range of distance and duration as short-distance dispersers or individuals that left their natal range late. This result contrasts somewhat with Selonen & Hanski (2006)'s findings in flying squirrels that supported the hypothesis that individuals decide to disperse over long or short distances prior to the onset of dispersal. In our study, all dispersers seemed to prepare for their dispersal event in the same way in terms of predispersal exploration. Hence, the hypothesis that long-distance dispersers benefit less from exploratory movements than short-distance dispersers because of the lower probability of settling in a previously explored area was not supported in roe deer, although the sample size was low for this test. However, a directional bias in dispersal direction was observed towards the west. This pattern was unexpected and is difficult to explain, given that there is no obvious directional gradient in habitat composition, fragmentation or quality across this highly fragmented landscape. Hence, it is not clear whether the overall bias in direction of extrarange movements towards the north and west at the population level is more the result of landscape structure or the product of the link in the direction an individual takes during its exploratory and dispersal movements. Further data are required to explore this question.

Our results provide strong evidence that exploration prior to dispersal is a key component of the dispersal process in a large herbivore, the roe deer. Exploratory movements influenced not only the decision whether to disperse or not, but also in which direction the individual dispersed. The factors affecting dispersal departure are expected to play a major role in determining the overall dispersal rate of the population (Bowler & Benton 2005). Hence, a better knowledge of the behavioural ontogeny of the dispersal process will aid our understanding of the causes of variation in dispersal parameters and so improve individual-based models of population dynamics.

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