Evidence for exploration behaviour in young roe deer (*Capreolus capreolus*) prior to dispersal

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Natal dispersal is a three-phase process: the decision to leave the natal range, the search phase and finally the settlement phase. Not much is known about the search phase in large herbivores. We quantified the search behaviour of young roe deer from two contrasting populations, using different measures: search area, search rate, search intensity and philopatry of the search. A Principal Component Analysis showed that most measures were highly correlated. Comparing the first axis from this analysis between adult and young roe deer from the two different populations while controlling for habitat quality, we found that the young occupied a larger area, ranged on average farther away and performed more excursions than adults, regardless of their sex. These findings support the hypothesis that young roe deer explore their environment before definitively leaving their natal home range and settling in their adult range.

KEY WORDS: Ungulates; home range; search behaviour; habitat use.

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INTRODUCTION

Habitat use shapes the survival and reproductive patterns of animals, hence individual fitness, and has thereby major consequences for population and ecosystem dynamics (MORRIS 2003). Most animals restrict their habitat use, activities and movements to a certain range, usually referred to as the home range (BURT 1943). Spatial information and familiarity play an important role in the formation of the home range (GAUTESTAD & MYSTERUD 2005) and its use (HOWERY et al. 1999). When animals disperse from their natal range to establish a new home range, we can expect the acquisition of information through exploration also to play a role.

Several mechanisms might promote natal dispersal, i.e. the movement from the natal home range towards a different adult home range. Kin interactions, inbreeding avoidance, local mate and resource competition, and temporal and spatial heterogeneity are all suggested as driving forces in the evolution of dispersal (CLOBERT et al. 2001). However, dispersal has costs; a higher mortality rate during the dispersal phase has been shown in several species (NORRDAHL & KORPIMAKI 1998, YODER et al. 2004). This higher mortality may be caused by a higher predation risk, higher energy expenditure during movement or accidents due to unfamiliarity with new terrain. Animals can be expected to show behaviour that will increase the benefits and decrease the costs of dispersal. One strategy to improve the cost-benefit balance of dispersal is based on obtaining information prior to settlement. This information may provide cues as to whether it is really worthwhile dispersing in the first place. Animals are thus expected to explore the environment before definitive dispersal, as has been reported for badgers (*Meles meles*) by ROPER et al. (2003).

Natal dispersal is a three-phase process (STENSETH & LIDICKER 1992, CLOBERT et al. 2001) involving the decision to leave the natal home range, the search phase, and settlement in the adult home range. Most research has been focused on the leaving and the settlement phases, but the intermediate search phase has been largely neglected (WIENS 2001, DOERR & DOERR 2005). In the present study of roe deer dispersal behaviour, we focus therefore on this second phase, the period in which the animal moves beyond the borders of its home range in order to explore the surrounding environment. DOERR & DOERR (2005) proposed different measures of the dispersal search process (see Table 1 and DOERR & DOERR 2005 for a detailed description). Here, we adopt their methodology to look at the exploration behaviour of young roe deer.

Roe deer are relatively small cervids (20-30 kg; ANDERSEN et al. 1998). Births take place in spring (May-June) and are highly synchronised (LINNELL et al. 1998). Females live with their offspring in small home ranges (in forests: 42-128 ha; HEWISON et al. 1998). There is a close association between fawn and mother, until the fawn is one year old when it may disperse in late spring

and early summer (LINNELL et al. 1998). The use of the home range is characterised by high sedentarity in both sexes (WAHLSTRÖM & LIBERG 1995).

Habitat use and dispersal have been intensively studied in roe deer in which rates of natal dispersal are highly variable (20 to 95%; LINNELL et al. 1998). Different factors have been identified to affect home range size in roe deer: habitat quality (TUFTO et al. 1996, SAID et al. 2005a, SAID & SERVANTY 2005), the presence of dependent young (TUFTO et al. 1996, SAID et al. 2005a), population density (VINCENT et al. 1995, KJELLANDER et al. 2004) and age (STRANDGAARD 1972, BIDEAU et al. 1993, VINCENT et al. 1995). In particular, BIDEAU et al. (1993) found that the home range of young male roe deer was larger than that of adults. This finding is compatible with a higher rate of exploration by the young before dispersal. However, these authors found this difference in males only, whereas in roe deer there are no major between-sex differences in dispersal rates (LINNELL et al. 1998, COULON et al. 2006). Hence, it would be expected that both males and females show exploration behaviour prior to dispersal. Indeed, VINCENT et al. (1995) reported larger home ranges for the young of both sexes.

To clarify this, we looked for exploration behaviour in young roe deer in the spring, prior to the settlement phase of dispersal (LINNELL et al. 1998), and investigated whether this behaviour occurred in both sexes. Natal dispersal by roe deer occurs in yearlings during the spring and summer (LINNELL et al. 1998). LINNELL et al. (1998) remark: "… that if a female yearling does not leave her natal home range during the first summer, she probably never will." (p. 269); males occasionally show dispersal in the following 2 years. Therefore exploration in young roe deer is expected to occur in this period just prior a potential dispersal. Adults are not expected to perform such explorations (but see LIBERG et al. 1998 on female mating excursions and DANILKIN & HEWISON 1996 on male rutting raids). We compared the measures of exploration behaviour of DOERR & DOERR (2005) between adults and young living in the same areas and, therefore, with the same available habitats.

METHODS

Study sites

This study was performed at two sites: the Territoire d'Etude et d'Expérimentation at Trois-Fontaines and Aurignac. Trois-Fontaines is a 1,360 ha enclosed forest organized by the National Forest Office in forest blocks (ca. 7.5 ha), situated in North-East France (Champagne-Ardennes, 48°43'N, 2°61'E). Trois-Fontaines has a continental climate, characterised by cold winters (mean daily temperature in January is 2 °C) and hot, but not dry summers (mean daily temperature in July is 19 °C and total rainfall in July-August is 130 mm). The forest overstory is dominated by oak (*Quercus* spp.) and beech (*Fagus sylvatica*), the coppice by hornbeam (*Carpinus betulus*).

Aurignac is a 7,500 ha area situated in South-West France (Comminges region, 43°13'N, 0°52'E). The climate is oceanic with an average annual temperature of 11-12 °C and 800 mm precipitation, mainly in the form of rain. It is a quite hilly (maximum of 380 m a.s.l) landscape of fragmented oak (*Quercus* spp.) woodland (average woodland patch size of 3 ha), often associated with hornbeam (*Carpinus betulus*), surrounding an 800 ha central forest block of Douglas-fir (*Pseudotsuga menziesii*), pine (*Pinus*

spp.), oak and hornbeam. The understory is dominated by brambles (*Rubus* spp.), common honeysuckle (*Lonicera peryclimenum*), ivy (*Hedera helix*) and butcher's broom (*Ruscus aculeatus*). The primary land use is pastoral for sheep and cattle grazing, with agricultural crops on the increase.

The environment in Trois-Fontaines and Aurignac is contrasting regarding climate (continental versus oceanic), dominant forest species (deciduous versus coniferous), habitat structure (low versus highly fragmented forest) and topography (flat versus hilly). It is therefore interesting to see whether the two study sites differ regarding exploration behaviour in roe deer.

Data collection

In both study sites, the deer were caught during large annual capture sessions in winter (November to February). During these sessions, which lasted approximately three hours, a line of human beaters with some dogs drove the deer into nets to capture them. Upon capture, the deer were placed in wooden dark holding boxes to restrain and calm them, retaining them for later handling; no drugs were administered. After terminating the drive, the deer were measured and equipped with a tracking-collar. In Trois-Fontaines, radio-collars (TXH-3, 350 g) from Televilt, Lindesberg, Sweden were used; in Aurignac, GPS-collars (3300, 300 g) from Lotek, Ontario, Canada were used. After manipulation, the deer were released at the capture site. The weight of the collar never exceeded 2 to 3% of the body weight of the lightest animal (13 and 15 kg for Trois-Fontaines and Aurignac respectively). This weight has no marked effect on the behaviour or performance of the deer. The animals in this study were all almost fully-grown; for the younger animals we ensured that there was room to allow for further growth when putting the collar on, thus an expandable collar was not necessary.

In Trois-Fontaines, 8 young (8-9 months at the age of capture, followed until the age of 14-15 months; 2 males and 6 females) were followed in 1999 and 25 adult roe deer (> 2 year; 2 males and 23 females) were followed in 2003 using radio-collars. The animals were followed from January to at least mid-August of the same year. Although the summer and spring of 2003 were reported to be exceptionally warm (REBETEZ et al. 2006), this is not a major problem; in the other study site no systematic difference in sampling period occurred between adults and young (see below). Moreover, a potential decrease in habitat quality during 2003 caused by the drought should have led to a decreasing power to detect the exploration of young roe deer because roe deer home range increases with decreasing habitat quality (TUFTO et al. 1996, SAID et al. 2005a). Visual inspection of the locations from two young (one male and one female) revealed that these animals used two distinct home ranges during our study period, making comparisons with the other animals that used only one home range more difficult to interpret; hence both individuals were discarded from further analysis. On average 3 fixes per week were taken for the young during this period (on average 102 locations per animal over the study period January/mid-August; SD = 9.5, range: 79-109). The adults were localised on average twice a week over the same period (on average a total of 70 locations per animal; SD = 8.8, range: 60-88). By triangulation the forest block (ca. 7.5 ha) occupied by the animal was determined, hence no higher precision than the forest block was available. The data have thus a relatively low spatial resolution; however the associated error is extremely low.

In Aurignac, from 2003 to 2004, 7 young (4 males and 3 females) and 4 adults (2 males and 2 females) were followed using GPS-collars that were programmed to record a location every 4 hr. We used fix locations over the same period as in Trois-Fontaines (January/mid-August) for the analysis. GPS locations of low reliability were omitted (all 2D fixes were omitted, retaining only 3D fixes for further analysis; CARGNELUTTI et al. 2007). We also omitted all points that were not separated by at least 24 hr to have a

comparable low temporal autocorrelation in both study sites (SWIHART & SLADE 1985). On average 235 locations were available for each animal (SD = 102, range: 81-399). Fix locations were assigned to the centres of cells of a grid with average cell size of 7.5 ha (i.e. about the size of a forest block at Trois-Fontaines) in order to have the same spatial resolution for both study sites; in the following we will refer to both the forest blocks of Trois-Fontaines and the grid cells of Aurignac with the term grid cell. In all the following analyses we used these grid cell data.

Analysis

Comparison of young and adult search behaviour

To account for any confounding effect of habitat quality on our measurements of search behaviour when comparing young and adults, we paired each young with an adult, minimising the distance between the barycentre of the fix locations. Thus, each young was paired with the same-sex adult that had the closest average spatial position (mean distance in metres between two animals of a pair = 593.09, SD = 541.11, range: 37-2039). For Aurignac, the number of available adults was smaller than the number of young, thus the pairing with an adult was carried out with replacement.

To control further for differences in habitat quality that could arise from differences in the timing or exact locations between the young and the adult of the same pair, we entered two measures of habitat quality as covariates in our analysis. For roe deer, food availability and cover are likely to be the most important habitat features determining its space use (MYSTERUD & ØSTBYE 1999). Hence, we assessed food availability by measuring biomass (SAID et al. 2005b) and cover by measuring visibility. Visibility was measured by the proportion of squares (n = 16) that were seen from roe deer height on a vertically placed 100×100 cm white board with 25-cm squares at 5 m in the four primary compass directions. At Trois-Fontaines, sampling was stratified by habitat type (in 2003: 530 stations were sampled in 11 habitats; see SAID et al. 2005b for further details). Using the mean biomass and visibility measures for each habitat type we extrapolated these measures to each grid cell based on the habitat types in the grid cell; habitat types are determined every year for each grid cell. Using the grid cells within the home range of an animal we determined the habitat quality of its home range to account for heterogeneous utilization of the home range, the grid cells were weighted by the intensity of animal use.

In Aurignac, the same procedure was followed except that sampling (in 2004) was not stratified by habitat type (this information was not available due to the absence of the forest block structure with associated habitat types). Instead, biomass and visibility at 5 m were measured at different sampling points (n = 74) in a systematic design and the mean of these values was calculated for a given grid cell. However, for 35% of the locations no habitat data were available. Because of the low spatial autocorrelation in the habitat variables (see results below), we could not interpolate between cells (interpolation requires a sufficiently high autocorrelation; LEGENDRE 1993). Hence, we restricted the analysis incorporating habitat quality to those grid cells for which biomass and visibility data were available; we included the percentage of available habitat information for each individual as a covariate in the analysis.

Characteristics of individual search behaviour

To assess the search behaviour of roe deer we used several measures proposed by DOERR & DOERR (2005): search area, search rate, search intensity, philopatry of search

and timing of exploration (see Table 1). They also proposed thoroughness that we did not consider here because small-scale movements play a major role in its measurement and the temporal and spatial resolution of our data were rather low. Likewise, we did not consider surreptitiousness because it requires the interactions with conspecifics to be identified.

As a measure of the size of the search area we calculated the size of the home range following the method of Badyaev et al. (1996). Due to the low spatio-temporal resolution of our data we did not use the assessment corridor area proposed by Doerr & Doerr (2005). Conventional home range methods as Kernel (Worton 1989) and the Minimum Convex Polygon methods (White & Garrott 1990) are developed for point locations, not for grid cells. We therefore opted to use a variant of the Grid Cell Counts method (GCC; White & Garrott 1990) to determine home range size; the size of the grid cells corresponds to the 7.5 ha cells defined above. We calculated different measures of GCC by counting the minimum number of cells corresponding to 50, 95 and 100% of the animal's grid cell locations. The GCC (100) corresponds to the search area measure proposed by Badyaev et al. (1996). We included the GCC (50) to describe the core range area. The core area is not necessarily affected by explorations at the outer limits of the home range. The GCC (95) estimates the home range area using the traditional 95% level (White & Garrott 1990).

Table 1.

The different components of the search process prior to dispersal adapted from Doerr & Doerr (2005), with the associated measure we used to describe each component. All the search measures are calculated on the grid cell data used in this study.

Feature from Doerr & Doerr (2005)	Short description	Measured by
Search area	The total area explored. A larger search area results in a greater exploration cost, but provides information acquired over a larger area.	Grid Cell Counts (50, 95 & 100%)
Search and foray rate	The speed of exploration; faster searchers can acquire information about sites before other individuals.	Mean speed and proportion of locations outside the normal home range
Search effort and intensity	The spatial distribution of the search effort: whether movements are restricted to certain areas.	Mean number and standard deviation of visits per cell within the search area
Philopatry	The distance between the explored areas and the normal home range; this distance, like the search area, is linked to the cost and the benefit of exploration.	Distance from home range centre (mean and maximum)
Timing	When the animal starts its exploration; as with the search rate, earlier searchers have a head start in acquiring information.	Mean date outside and inside the normal home range

The search rate is measured by the mean speed (the mean distance between the centres of two consecutive observed cells divided by the time between those observations). Another measure for the search rate proposed by DOERR & DOERR (2005) is the proportion of days an animal is observed outside its normal home range. However, for this latter measure, an animal showing more exploration behaviour will also have a larger home range. To exclude the effects of such exploration behaviour on our estimates of normal home range size for the analysis of search rate, we used a standardised home range of constant dimensions for all animals. The centre of this standardised circular home range was defined as the barycentre of the locations (visual inspection of the data did not reveal anisotropy, therefore the circular form of this standardised home range was not a concern). From our data, we estimated the mean (SD) home range size using the GCC (95) of all roe deer analysed here as 60 (26) and 55 (22) ha for Trois-Fontaines and Aurignac respectively, hence, we used a radius of 435 and 420 m for Trois-Fontaines and Aurignac respectively. We then calculated search rate as the proportion of observations outside this standardised home range.

Search intensity was measured as the coefficient of variation of the search effort (the more variable the search effort, the more it is concentrated in certain areas more than others; DOERR & DOERR 2005). We measured the search effort as the mean number of times each grid cell was visited. The smaller the area an animal occupies, the higher the mean number of visits will be, resulting in a higher search effort.

Philopatry of the search was measured as the mean and maximum distance of all fix locations to the barycentre of the home range (DOERR & DOERR 2005).

The timing of the search was measured as the mean and the median date of the fix locations that were observed to be outside the standardised home range, as defined above.

Statistical analyses

We used a re-sampling procedure to correct for the difference in the number of fix locations between adults and young. The data for the paired individual (i.e. adult or young) with the largest number of locations were sub-sampled to obtain the same number of fixes as the other paired individual. The behavioural measures were then estimated using this sub-sample; this sub-sampling procedure was repeated 10,000 times and, for each parameter, the mean of these 10,000 values was used in the analyses.

We used nine (GCC50, GCC95, GCC100, mean speed, proportion at 435/420 m or more from the barycentre of the locations, mean number of visits per grid cell, SD number of visits per grid cell, mean and maximum distance to the barycentre) different measures to assess exploration behaviour. Except for the mean and standard deviation of the visits per grid cell (respectively search effort and search intensity), we expected a higher value for the young than for adults. Because adults are expected to visit fewer cells, the mean number of visits per grid cell should be larger; this higher mean should lead to a higher standard deviation as well.

Testing each of the nine measurements separately increased the chance of a type-I error, while Bonferroni correction increased the chance of a type-II error. We therefore chose to test only a synthetic measure of explorative behaviour. We combined the different measures, using a Principal Component Analysis as a variable selection technique (JOLLIFFE 1972) to produce this synthetic descriptor of search behaviour, which was used to test for the existence of a difference between adults and young. The number of principal components retained to describe search behaviour was determined with a 'scree-test' (i.e. using a sharp break in the graph of the eigen-values to determine the principal components; CATTELL 1966).

To compare search behaviour between the two age groups, we calculated the difference in the exploration behaviour component for each young-adult pair. We then used these score differences to test our hypotheses. To control for possible effects of temporal and spatial variability in habitat quality we included our estimates of habitat quality at the GGC (100) as covariates in our analysis, calculating the difference in both plant biomass and visibility for each young-adult pair. The effect of a difference in percentage missing habitat values within a pair was used as covariate to control for this possible confounding effect, also interactions between habitat variables and site were checked.

An a priori set of ten models was fitted (see Table 3). Five models (model 1 to 5) with habitat variables (plant biomass and visibility) were fitted, with the percentage of missing values (model 1) and site (model 2) as additional covariates. Three models (model 6 to 8) investigating a sex and/or site effect were fitted. Model 9 tested the difference between young and adults by fitting an intercept; the null-hypothesis of no effect between young and adults was fitted as an intercept equal to zero (model 10).

To select the model that best described the data, we used the Akaike's Information Criterion corrected for small sample size: AICc (Burnham & Anderson 1998). We retained the model with the lowest AICc-value (i.e. the best compromise between accuracy and precision). When the difference between two models was less than 2, we retained the simplest model according to the rule of parsimony (Burnham & Anderson 1998).

All analyses were performed using the R 2.2.1 statistical package (R Development Core Team 2004).

RESULTS

Descriptive statistics

We used spatial auto-correlation analysis on the measures of biomass and visibility in Aurignac to assess the possibility of interpolating data to grid cells with missing values for habitat quality. Neither of the variables showed an auto-correlation statistically different from zero using a randomization test, although visibility tended to be clustered (Moran I = 0.15, $P = 0.09$). Hence, these results did not allow us to interpolate missing values for the habitat measurements. At Aurignac, visibility and biomass tended to be positively correlated (r = 0.26, t = 1.68, df = 39, $P = 0.10$) over the different grid cells, while at Trois-Fontaines these measures were not significantly correlated for the different habitat types (r = − 0.11, t = − 0.30, df = 7, $P = 0.77$). We therefore kept both habitat quality measures for further analysis.

Visual inspection of the age differences for the different measures of search behaviour revealed that all were in the predicted direction (Fig. 1), although the differences were not consistently large. As discussed above, we did not perform explicit tests on the variables separately due to the relatively small sample size.

Difference in mean sampling date between young and adults was significantly different from zero (X = 13.11, t = 3.00, df = 5, $P = 0.03$) at Trois-Fontaines; the mean date for fix locations was, however, on average only 13 days earlier for the adults than for the young. In Aurignac, there was no sig-
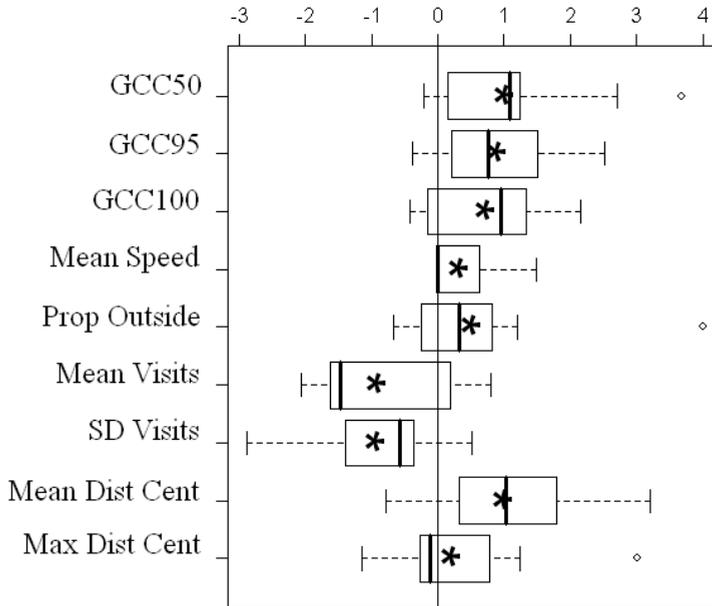
Fig. 1. — Box plots of difference scores for the nine measures of exploration behaviour (see Table 1) after standardization of these measures. The box comprises the first quartile and the third quartile. The line inside the box represents the median and the star the mean. The whiskers extend to the most extreme data point, which is no more than 1.5 times the length of the box away from the box; data points that lie farther away than the whiskers are represented by an open circle. The vertical line at zero in the plot shows where there is no difference between young and adults. Positive difference scores are scores where the young have higher values than the adults. For the details of the different measures in the figure please refer to the text and Table 1.

nificant difference in sampling date (X = 7.06, t = 1.55, df = 6, P = 0.17). Due to the significant difference in sampling date for the two sites pooled (X = 9.85, t = 3.11, df = 12, P = 0.009), we did not use the timing of exploration in further comparisons of search behaviour between adults and young. However, we added a model in our analysis to test for the effect of the difference in sampling date within a young-adult pair on exploration behaviour (model 11 in Table 3). The mean date outside the standardised home range was April 10 and 24 for adults and young, respectively. Due to the relatively small although significant difference in sampling date between age groups, testing the difference of exploration date was meaningless.

In order to generate a synthetic exploration measure and avoid multiple testing, we summarised the nine different search measures using a Principal Component Analysis. The first component accounted for 63% of the total variability, whereas the second component accounted for only 16% of the total variability of the measurements. To assess whether the first principal component only measured variation in home range size, we excluded the direct

measures of home range size (GCC50, GCC95 and GCC100) and performed a second PCA on the six remaining measures of search behaviour. The first axis of this PCA showed a strong correlation with our original exploration behaviour component (r = 0.87, t = 8.88, df = 24, P < 0.0001), indicating that home range size does not account for all the variation in the component.

We thus retained the first component of the PCA, which we further refer to as the exploration behaviour component. As can be seen in Table 2, most variables (GCC95, mean distance to the centre, proportion outside the home range, mean visits per cell, GCC100, GCC50, SD of the visits per cell) contributed substantially (> 0.7) to the exploration component. The contributions of mean speed and maximum distance towards the home range centre to this component were smaller (0.46 and 0.29 respectively). This indicates that these variables are not well represented in our synthetic exploration measure. The second component (see Table 2) was characterized by a high loading of the maximum distance from the home range centre. Most other variables had low loading on this component and, therefore, we did not include the second component of the PCA in our further analysis.

Tests of hypotheses

We tested our hypothesis using the difference between scores of the exploration behaviour component for each young-adult pair. The AICc values of the different models are shown in Table 3. We tested whether a difference in the exploration behaviour component could be explained by our two measures of habitat quality (models: 1 to 5). As the inclusion of the habitat quality measures did not decrease the AICc of the models (biomass: X ± SE = − 0.26 ± 0.36, P = 0.47; visibility: X ± SE = − 0.61 ± 1.06, P = 0.58), we retained the model with only the intercept since it is characterised by the smaller AICc

Table 2.

The loadings for the nine search behaviour measure (based on DOERR & DOERR 2005) for the first and second component from a PCA of these variables. These loadings are the correlations between each variable and the different components. See Table 1 for a detailed description of the measurements.

Search behaviour measure	Component 1	Component 2
GCC95	0.96	0.16
Mean desistance to the centre	0.95	0.07
Proportion outside the normalized home range	0.87	0.18
Mean visits per home range grid cell	− 0.87	0.11
GCC100	0.87	0.39
GCC50	0.86	− 0.24
SD of the visits per home range grid cell	− 0.74	0.49
Mean speed	0.46	− 0.58
Maximum distance from the centre	0.29	0.76

Table 3.

The different models fitted to predict the difference within adult-young pairs of the exploration behaviour component from the PCA including nine measures of search behaviour based on DOERR & DOERR (2005). The AICc-value is given and the dAICc for model selection. Models 1 to 5 test the influence of habitat quality (the within-pair difference in visibility and biomass within the home range, respectively Δ vis and Δ biom), with interactions from the site (model 1) and from the percentage of missing values (% missing; model 2). In models 6 to 8 sex and site effects are tested. Model 9 tests the age difference in exploration behaviour, whereas model 10 tests the null-hypothesis of no such age-effect. Model 11 is added to the a priori model set to correct for the difference in sampling date we found in Trois-Fontaines between young and adults (Δ sample period). The retained model for the exploration behaviour component is the simplest one, with only an intercept different from zero.

No.	Model	AICc	dAICc
9	*Intercept*	63.02	*0.00*
11	Intercept + Δ sample period	64.72	1.69
8	Intercept + site	64.80	1.78
4	Intercept + Δ biom	65.22	2.20
5	Intercept + Δ vis	65.48	2.45
7	Intercept + sex	65.66	2.64
6	Intercept + sex + site	67.26	4.24
3	Intercept + Δ vis + Δ biom	68.53	5.51
10	Intercept = 0	69.75	6.73
1	Intercept + Δ vis * site + Δ biom * site	79.35	16.33
2	Intercept + Δ vis * % missing + Δ biom * % missing	81.27	18.25

value. According to our definition of the variables (Fig. 1) an intercept with a positive value indicates that yearlings exhibit a larger value than adults. Indeed, for this model the intercept is significantly different from zero (X ± SE = 2.33 ± 0.67, P = 0.005). Accordingly, the model with the intercept equal to zero ranks much lower (Table 3). This means that the young exhibited more exploration behaviour than the adults did. The distribution of the residuals for the selected model (i.e. model 9) did not differ from normality (Wilk normality test: P = 0.60).

We tested for between-sex and between-site differences in search behaviour by fitting models including these parameters (models 6 to 8). We did not find any effect of either sex (X ± SE = 0.58 ± 1.42, P = 0.69) or site (X ± SE = – 1.29 ± 1.34, P = 0.36) and the AICc value of the simplest model with only the intercept was the lowest.

The added model (model 11) correcting for difference in sample date within the young-adult pair occurring in Trois-Fontaines was not retained, because the effect of the difference in sample date was minimal (X ± SE = – 0.06 ± 0.06, P = 0.34), while the intercept estimated using this model was still markedly different from zero (X ± SE = 2.92 ± 0.90, P = 0.0075).

DISCUSSION

As expected, in both populations we found a clear difference in space use between young and adults, which we interpret as evidence for exploration behaviour by young roe deer prior to dispersal. This difference occurred when we controlled for differences in habitat quality, which is known to influence home range size, suggesting a real influence of age on search behaviour. This finding supports earlier studies of roe deer that reported that young males occupy a larger home range than adult males (BIDEAU et al. 1993) or suggested that both sexes of young ranged over a large area (VINCENT et al. 1995), although neither of these studies controlled for possible confounding effects of habitat quality. Exploration behaviour in the young of both sexes could be expected in roe deer given the observed absence of marked sex differences in dispersal rates (LINNELL et al. 1998, COULON et al. 2006). It should be noted that our analysis might have suffered from a lack of power to detect an effect of sex or site due to its relatively small sample size; nevertheless we found a consistent effect of age for both sexes and both study sites.

Animal movements occur within a spatio-temporal hierarchy (SENFT et al. 1987); the low spatial resolution of our data did not allow us to investigate the smallest scales of this hierarchy. We are dealing, however, with explorative movements; these movements are expected to occur mostly on a larger spatial scale. In exploration fine-grained heterogeneity is of only limited importance, most important are more global differences that indicate home range suitability. Low resolution in movement data will, however, result in an underestimation of the movement rate (TURCHIN 1998); we thus most likely underestimated the age-effect that we report here.

A possible alternative interpretation for the age-related patterns of space use we found could involve agonistic behaviour between adults and young, following a general increase in adult aggression in spring (MELIS et al. 2005), causing the young to move away and thereby range over a larger area. Around March, after the bucks have acquired hard antlers, they begin to exhibit territorial behaviour, including marking and an overall increase in aggression (DANILKIN & HEWISON 1996, MELIS et al. 2005). This aggression is primarily directed towards other adult males, but secondarily also towards young males, especially those showing stronger signs of sexual maturity (WAHLSTRÖM 1994). Occasionally, adult bucks may also show aggressive behaviour towards adult and young females (DANILKIN & HEWISON 1996). Thus the territoriality of males in spring increases their aggressiveness not only towards the young but especially towards other adults. Indeed, the frequency of adult aggression towards the young is likely to be lower than towards other adults, which makes this alternative interpretation less plausible as an explanation of the age-related differences in space use that we observed.

However, the young and the adults might respond differently to adult aggression. HOEM et al. (2007) have shown young roe buck more often retreat from aggressive interactions with adult roe buck; the spatial consequences of this retreat behaviour remain, however, unclear. One could speculate that this retreat results in the young buck getting pushed around more often; this does however not explain our findings, as supported by two observations. First, as

discussed above, the frequency of such aggressive interactions with young individuals seems to be relatively low. Second, our analyses do not support sex differences in exploration behaviour. Further research will be required to assess the respective role of aggression and exploration to account for the different space occupation exhibited by young roe deer in both sexes.

It is noteworthy that two measures did not show a strong correlation with the explorative behaviour component: the mean speed and the maximum distance from the home range centre. The spatial and temporal coarse measure of movement speed can lead to an underestimation of small-scale movements (Turchin 1998). The under-representation of mean speed in the exploration component suggests that exploration does not result in an increase in the rate of large-scale movements; however, our data did not allow us to generalize this for small-scale movement rate. The maximum distance from the home range centre showed a higher correlation with the second component from the PCA (see Table 2). The biological interpretation of this component was, however, not straightforward. The low number of variables loading on this factor indicates that it is not an important aspect of exploration.

A strict interpretation of our results in terms of exploration behaviour would imply that young voluntarily prospect over larger areas in order to gather information about potential post-dispersal home ranges (Schjörring 2002). This is something we cannot definitively prove from our analysis and, indeed, it will be difficult to show. As we discussed above, it seems, however, unlikely that the wider ranging and the more frequent excursions of the young that we observed can be accounted for by external forces such as habitat quality or agonistic behaviour from conspecifics. The choice of home range will have an important impact on the fitness of an individual (McLoughlin et al. 2006, 2007). It seems thus likely that, prior to the settlement phase of dispersal, animals will try to minimise uncertainty by exploring the surrounding environment (Roper et al. 2003).

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