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Despite the importance of conservation and management of the European hare, a game species that has declined throughout Europe, little is known about its natal dispersal process. To date, only one radio-tracking study in a mixed cropping-farmed landscape provides a fine description of the dispersal pattern of this species. The study shows in particular a negative density dependence dispersal, juvenile hares dispersing more in a low-density hunting zone rather than in a high density non-hunting zone. Unfortunately, the effect of conspecific density on dispersal remains ambiguous due to the confounding effect of hunting. To provide more insight into the influence of conspecific numbers on the dispersal propensity in hares, we renewed the study in a harvested high density population.

Our results confirmed the known sex-biased and age-related dispersal in this species but we did not find any effect of the birth site density on either the propensity to disperse or the distance moved in juvenile hares. Overall, the dispersal rate and bias were equal to those previously found in the high density non-hunting zone, where density was almost the same as in our population even though hunting pressure differed. Our results emphasize that natal dispersal is a ubiquitous feature in this species, which may respond more to density than hunting.

Introduction

Natal dispersal, defined as "the definitive movement of an individual from its birth site to the place of its first breeding attempt" (Howard, 1960), is a key behavioural process with important consequences on genetic structure, demography and evolutionary dynamics of animal populations (Stenseth and Lidicker, 1992; Clobert et al., 2001; Bowler and Benton, 2005). Through simply moving from the birth site and breeding elsewhere, dispersers change the spatial distribution of populations and maintain the gene flow between local populations. From an evolutionary point of view, colonisation of empty habitats through dispersal may buffer local populations from extinction (Hanski, 1999). On the other hand, high rates of movement between populations may also increase the extinction rate of local populations by increasing the synchrony of spatial dynamics (Heino et al., 1997; Hanski, 1999). Because natal dispersal is closely related to the persistence of many species, knowledge of the dispersal abilities and the causes underlying dispersal in declining species are increasingly needed for the development of suitable management plans.

This is particularly true in the European hare *Lepus europaeus*. The European hare is a common game mammal often encountered in farmland habitats. Since the 1960s, populations of European hares have drastically declined in several European countries (Smith et al., 2004, 2005) due to increasing agricultural intensification and loss of habitat heterogeneity (Tapper and Barnes, 1986; Smith et al., 2004, 2005). Although the European hare has both a game and declining species status, natal dispersal in this species has been paid little attention in the past. To date, only the study of Bray et al. (2007) in a patchy mixed cropping-farmed landscape in Chareil-Montord (France) provides pioneer insights into natal dispersal of the European hare.

In particular, they showed that dispersal in hares occurred preferentially when juveniles reach adult size especially in males, as in many other polygynous-promiscuous species (Greenwood, 1980; Dobson, 1982), although females were those dispersing farther. Furthermore Bray et al. (2007) suggested that the natal dispersal rate in this species was inversely related to conspecific density. Indeed, they showed that juveniles dispersed more from a low-density hunting zone (14 hares/km^2) than from a high density non-hunting zone (49 hares/km^2). Unfortunately the causes underlying this phenomenon remained poorly understood due to the confounding of density and hunting factors. Negative density-dependent dispersal is not rare (see Matthysen, 2005 for a review) and one could suggest two non-exclusive mechanisms for explain-

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ing this phenomenon. First, density might reflect the intrinsic quality of the habitat and dispersal at low-density could be viewed as a means of escaping from an unfavourable physical environment (Clobert et al., 2001; Bowler and Benton, 2005). For instance, juvenile hares born in the hunting zone could disperse more than those born in the non-hunting zone in response to a much more stressful environment. In that case, dispersal could be primarily driven by the "physical environment". In the second mechanism, dispersal could primarily depend on the level of social interactions between conspecifics according to density, density being related or not to the quality of the habitat. As Bray et al. (2007) stated, a low rate of dispersal in a saturated environment could result from increased aggressive behaviour of philopatric individuals against dispersers during the transience phase of the dispersal process ("social fence" hypothesis, Hestbeck, 1982). Furthermore, an excess of philopatric individuals in the high density area could also be explained by a natural tendency of the species to aggregate because of the advantages of living in small groups, for instance anti-predator strategy, social foraging which in turn, overcomes potential costs of inbreeding. In these two cases, dispersal of juvenile hares could be directly driven by the "social environment".

Taking advantage of a 3-year radio-tracking study of juvenile hares in a harvested and high density population, (about 41 hares/km^2), the present study aimed at removing the ambiguity between effects of hunting and density *per se* on dispersal in hares. The population being located in an intensive cropping area, a less patchy landscape than the previous one, we first examined whether the previous dispersal pattern could be extended to other population contexts before investigating the influence of conspecific density on dispersal behaviour at a fine spatial scale. More precisely, after testing for the effect of sex and age on both the dispersal probability and dispersal distances, we tested for the effect of local density around the birth site of each juvenile on dispersal decision. According to the negative density dependence dispersal hypothesis, we expected that juvenile hares should disperse less from a densely populated birth site, or move short dispersal distances due to costly confrontations with conspecifics.

Material and methods

Species and study site

The study was carried out in the region Centre around Maves (France, 47°44′35″N, 1°21′55″E) from 2003 to 2006. The study area (36 km^2) is mostly characterized by an arable habitat where agriculture is very intense and the average field size is 7.3 ha. Land cover varies from bare soil to large crop fields according to the season. The crops are mainly cereals, such as wheat or corn, but also alfalfa, canola or cabbage. The European hare is a common game species in this area, and hare shooting occurs each year during 3 months, from the end of September to the end of December. The hare is a non-territorial medium-sized mammal (2.5–6 kg) which lives in temporary feeding groups with no stable social structure (Broekhuizen and Maaskamp, 1980). Groups are characterized by a dominance hierarchy for the acquisition of food and mate resources. The mating system is promiscuous-polygynous, but males do not monopolize the females (see Cowan and Bell, 1986 for a review). The breeding season generally starts in midwinter (January–February) and lasts until midsummer, exceptionally until September (Caillol et al., 1992; Marboutin et al., 2003). Females may have two or more litters during the breeding season and an average litter size is 3–5 leverets. Leverets generally reach adult body size at the age of 3–4 months, and physiological sexual maturity between 4 and 6 months (Lincoln, 1976; Caillol et al., 1992). Sexual maturity mostly depends on the photoperiod. Leverets born earlier in the

season may be sexually mature at the age of 4 months, whereas those born at the end of the breeding season may reach sexual maturity the following year (Lincoln, 1976; Caillol et al., 1992).

Radio-telemetry of juvenile hares

Juveniles from litters of different ranks were trapped in the night using unbaited boxes (Bray and Léonard, 2000) during six trapping sessions from April to September each year. Each juvenile hare was sexed, weighed and fitted with ear tags (Presadom) and a radio-collar (TW-5 Biotrack, Wareham, UK and TXH-2, Televilt, Lindsberg, Sweden; 50 g, 1500 m range, battery life 16 months). Age at first capture was known from body mass and skull length and was precisely measured for individuals <90 days old (see Bray et al., 2002, 2007 for more details). A total of 184 juvenile hares were trapped during the 3-year study. Radio-locations were usually recorded once a week by triangulation and always during the day when most of the hares are resting in their den (Tapper and Barnes, 1986).

To analyse the dispersal pattern, we considered only juveniles that were <90 days old at the time of their first capture to exclude immigrants (70% of dispersal events were recorded between the age of 120 and 180 days in the previous study), and they were monitored until at least 150 days old, when both males and females should have reached adult body weight (Caillol et al., 1992). According to these general rules, we selected only individuals that were monitored during 3 months at least and for a minimum of 10 locations (thereby avoiding potential bias in mortality due to capture, and potential ambiguity in movement pattern interpretation, respectively). We also excluded all individuals showing significant departure following the capture to not confound natural dispersal from possible trapping-induced dispersal ($n = 13$). At the end of these steps, the dataset was composed of 95 individuals (47 males, 48 females), their ages at first capture ranging from 28 to 86 days, and monitoring duration from 90 to 305 days. Since the present study concerns only natal dispersal behaviour, we did not consider movements following the 1st March of the year following the birth year because all juvenile hares were supposed to have bred at least once during this time (Marboutin et al., 2003).

Dispersal measurements

We identified the four main dispersal patterns described in McShea and Madison (1992) and previously used in Bray et al. (2007). The first ones were philopatric patterns: "stationary" where each successive individual home-ranges highly overlap previous ones; and "explorer" which corresponds to a "stationary" pattern with temporary excursions outside the usual home-range (Fig. 1A). The second ones related to disperser patterns: "shifter" where successive home-ranges gradually shift and move away from previous ones over time (Fig. 1B); and "one-way" where the individual suddenly changes its home-range to establish permanently in a disjunctive one (Fig. 1C). For the sake of objectivity in movement pattern interpretation, we estimated the minimal dispersal distance (DD_{min}) in our population to identify the birth site, exclude possible trapping-induced dispersal and confidently assert dispersal (see Appendix A). Assuming circular home-ranges, we estimated DD_{min} using all locations of stationary adult hares monitored during the 3-year study in our population (Fig. 2A) ($n = 42$, range of number of locations = 10–73, range of monitoring duration = 121–495 days). We chose the 95% quantile from the distribution of the distances of all adult locations from their respective arithmetic centre as the DD_{min} ($DD_{min} = 588$ m) (Fig. 2B). We confidently used a common DD_{min} since adult home-range size was not affected by local density in our population (Appendix B). Furthermore, the birth site of each hare was estimated using the first locations following the
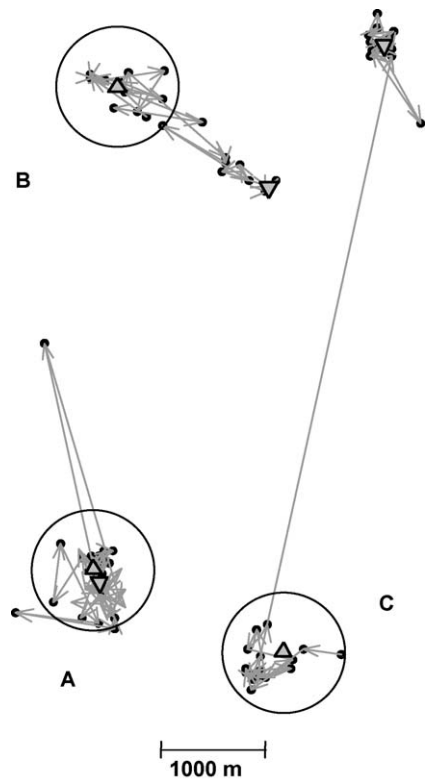
Fig. 1. Examples of dispersal movements in hares in three behavioural groups: A: philopatric «explorer» pattern, B: «shifter» disperser, C: «one-way» disperser. Large circle represents the DD_{min} around the centre of the estimated birth site (point-up triangle). The point-down triangle marks the arithmetic centre of locations used as the settlement place.
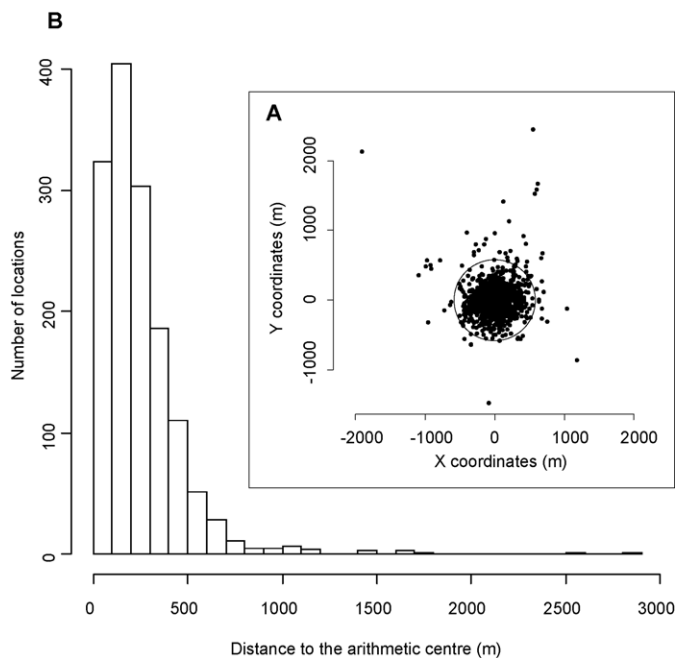

Fig. 2. (A) Graphical representation of all adult locations centred on their respective arithmetic centre. (B) Distribution of the distances of locations of all adults from their respective arithmetic centre ($n = 42$ adults). The circle radius of 588 m centred on the arithmetic centre in A encompasses 95% of the whole set of locations.

capture and remaining within the circle radius equal to the DD_{min} around their arithmetic centre. We also calculated an index of the shift of home-range over time (HRS), which gave the natal dispersal distance (NDD) for disperser patterns (Appendix A).

Local density estimation

Hare densities were estimated each year at the beginning of the breeding season (February) using spotlight point transect which sampled over 94 counting points located on average every 800 m within the study area. Local heterogeneity in hare densities did not allow us to define within the study area clear distinct zones with unambiguous density differences. Hence we chose to estimate local density for each individual using the seven closest count points around the centre of their previously defined birth site. Local density for each juvenile hare reflected the parents' local density in an area of about 200 ha (*i.e.* a circle of radius about 800 m), which represented more than 1.3-fold the DD_{min} in our population.

We used the software DISTANCE to obtain estimates of local density (Laake et al., 1994). Before specifically estimating local densities, we first searched for the best model fitting the detection function to be used within the study area (Buckland et al., 1993; Laake et al., 1994). For this purpose, we divided the study area into two zones by distinguishing the northern part and the southern part that apparently differed in density level. Then, using the Akaike Information Criterion (AIC, Burnham and Anderson, 2002) we selected the best model fitting the detection function in these two zones, taking account of an effect of the year. In each zone the best fits to the detection function were obtained using the "Half-normal" model (Buckland et al., 1993). We thus systematically used that model for each group of seven count points to estimate local density for each individual. Model fits were also looked at using goodness of fit for each group of seven count points. Significant departure from the theoretical estimates given by the model were observed in 14 of the 95 individuals ($P < 0.05$). We re-ran the analyses described below, excluding those 14 individuals, and the effect of the factors remained the same (results not shown).

Statistical analysis

Factors affecting HRS and NDD

We tested for the effect of *Year*, *Density* and *Sex* on the HRS performed by philopatric hares and the NDD for disperser hares separately, using linear models. Because the distribution of original values was highly skewed, data was log-transformed before analysis. Model selection was performed using a backward stepwise procedure, down to the simple effect of the model using *F*-tests and R software 2.8 (R Development Core Team, 2004). We did not test for the three-way interaction terms due to lack of biological relevance and sparseness of the data. The effect of the year was always seen in an additive way only (we assumed that all possible effects interacting with the year would not be of great importance). Overall we only tested for the two-way interaction terms including sex, and the general starting model was *Year + Density * Sex*.

Factors affecting dispersal rate

We specifically looked for the effect of *Year*, *Density*, *Sex* and *Age* on the probability for a hare to disperse. We modelled the age as a two-level factor. The first age-class was constituted of hares of <5 months. Before this age most juveniles were reproductively inactive while most of them had reached adult size. The second age-class was composed of juveniles of more than 5 months old and most of them reproductively mature (Lincoln, 1976; Caillol et al., 1992). Since the age effect might be confounded with plausible hunting-induced dispersal, we also took into account the *Period* of the year (hunting *vs.* non-hunting). The period was modelled as a

two-level factor. March–September was the non-hunting period, and October–February corresponded to the hunting period (hare shooting and roe deer drive hunts). We analysed the determinism of dispersal probability in two separate analyses since we were not able to estimate either an age or a period for the timing of dispersal in "shifter" dispersers.

In the first analysis, we tested for the effects of *Year*, *Sex* and *Density* on dispersal probability using logistic regression models (GLM) with a binomial response variable (1, "shifter" and "one-way" dispersers; 0, philopatric hares). Model selection was performed using a backward stepwise procedure and χ^2 tests to select or remove factors starting from the general model *Year + Density * Sex*.

In the second analysis, we modelled the probability for a hare to make a "one-way" movement, adding the age and the period to the previous factors and excluding "shifter" hares from the dataset. We used the time corresponding to the last location recorded at <588 m (*i.e.* <DD_{min}) from the centre of the birth site as the date of "one-way" dispersal. In this second analysis, the response variable was the presence–absence of a "one-way" movement for a given combination of period and age. Hence, there could be up to three successive observations per hare. Hares that had dispersed were removed from the dataset because "one-way" movement only occurred once.

Given that the dataset was made of repeated measures we should have used Generalized Linear Mixed Models (GLMMs) or Generalized Estimating Equations (GEEs, Liang and Zeger, 1986) to take into account correlation of observations within a same individual. However, using GEEs with either an "exchangeable" or "unstructured" correlation matrix gave similar parameter estimates and standard errors than a standard logistic regression or its equivalent GEEs with an "independent" correlation matrix (Appendix C). Actually, this was mainly due to the fact that the correlation parameters estimated with an "exchangeable" (ρ_{exch}) or "unstructured" correlation matrix (ρ_{unst}) were weak ($\rho_{exch} = 0.001$; $-0.033 < \rho_{unst} < 0.046$, respectively), thus suggesting that correlation among individuals was negligible in our dataset. We therefore used a standard logistic regression to fit the data for practical reasons. Model selection was performed using a backward stepwise procedure starting from the model *Year + Period + Density * Sex + Density * Age*, and the well-known Likelihood Ratio Test (*LRT*) to select or remove factors. We did not test for all the two or all the three-way interactions due to the lack of biological relevance and the sparseness of the data. In particular, we did not test for the interaction *Sex * Age* because the dataset was highly unbalanced between the levels of those factors ("one-way" movements occurred mainly in males). The effects of *Year* and *Period* were seen in an additive way. For the two analyses, we used R software 2.8 (R Development Core Team, 2004) to perform model selection and the "Geepack" package for R software 2.8 (Halekoh et al., 2006) to estimate correlation of observations within individuals.

Results

Patterns of dispersal and NDD

Among the 95 selected individuals, eight were excluded from the analyses because they were recorded beyond the DD_{min} during the 2 months preceding the end of the monitoring and we could not reliably classify the last movement into temporary excursion or late dispersal (Appendix A). Among the 87 remaining individuals, 57 displayed philopatric patterns (either "stationary"; $n = 26$ or "explorer" $n = 31$). Seven individuals exhibited a "shifter" pattern, leaving gradually the birth site. Finally, 23 juvenile hares performed a sudden "one-way" movement and settled in a disjunctive home-range.
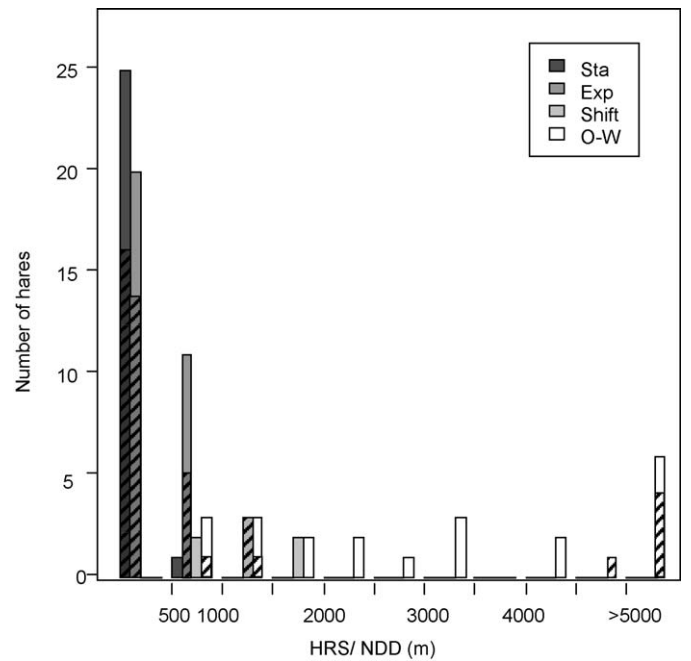

Fig. 3. Shift of home-range (*HRS*) around the birth site for philopatric hares (-Sta- "stationary" and -Exp- "explorer" patterns) and Natal Dispersal Distances (*NDD*) in dispersing hares (-Shift- "shifter" patterns and -O-W- "one-way" disperser patterns). Hatched bars indicate females.

The *HRS* for philopatric hares was generally <600 m (median = 258.1) (Fig. 3). Fifty-three individuals out of the 57 philopatric hares performed movements of <600 m on average around the birth site, whereas four individuals performed temporary excursion leading to a greater expansion of home-range around the birth site (range 901–954 m). On average, females tended to perform movements around the birth site of smaller amplitude than males (median = 210 and 339 m for females and males, respectively), but the difference only approaches significance ($F = 4.895$, $df = 1$, $P = 0.07$). On the other hand, we did not find any effect of *Year*, *Density* and all the two-way interactions terms on the *HRS* (all $P > 0.23$).

Concerning disperser hares, the median of their *NDD* was 1096 (range 846–1770 m) and 3469 m (range 704–8916 m) for "shifter" dispersers and "one-way" dispersers respectively (Fig. 3). We did not find any significant effect of *Sex*, *Density*, *Year* nor of the two-way interactions terms on the *NDD* (all $P > 0.27$). However, keeping in mind that philopatric females tended to perform movement around the birth site of smaller amplitude than males, one should note the reverse tendency in dispersing hares (median *NDD* = 3002 and 2040 m, for females and males, respectively) (Fig. 3).

Factors affecting natal dispersal rate

In the first analysis, modelling the dispersal probability using "one-way" and "shifter" dispersers and starting from the model with the two-way interaction terms *Year + Density * Sex*, showed a significant effect of the sex ($\chi^2 = 6.286$, $df = 1$, $P = 0.012$). Neither *Density*, nor *Year*, nor the two-way interaction terms were significant (all $P > 0.39$). The best model showed that natal dispersal was mainly sex-biased, with a greater propensity to disperse in males (0.48 ± 0.08, 0.22 ± 0.06 for males and females, respectively).

The second analysis, modelling the probability for a hare to make a "one-way" movement and adding the age-class and the period when dispersal occurred, confirmed the previous effect of the sex ($\chi^2 = 5.95$, $df = 1$, $P = 0.015$; Table 1) and we found a highly significant effect of the age-class ($\chi^2 = 8.18$, $df = 1$, $P = 0.004$; Table 1), most

Table 1
Effects of the *Year*, *Sex*, *Age*, *Density* and *Period* on the proportion of "one-way" dispersal movements. Tests for the effect of the factors were performed using the likelihood ratio test (*LRT*), following a backward stepwise procedure. Significant effects (*P* < 0.05) are shown in bold characters.

Model	Specific LRT for	LRT (df) *p*-value
Logit(Disp.) ~ *Year* + *Period* + *Density* * *Sex* + *Density* * *Age*	*Density* * *Age*	0.01 (1) *P* = 0.92
Logit(Disp.) ~ *Year* + *Period* + *Age* + *Density* * *Sex*	*Density* * *Sex*	0.31 (1) *P* = 0.58
Logit(Disp.) ~ *Year* + *Period* + *Density* + *Sex* + *Age*	*Density*	0.05 (1) *P* = 0.83
Logit(Disp.) ~ *Year* + *Period* + *Sex* + *Age*	*Year*	3.86 (2) *P* = 0.15
Logit(Disp.) ~ *Period* + *Sex* + *Age*	*Period*	0.55 (1) *P* = 0.46
Logit(Disp.) ~ *Sex* + *Age*	***Sex***	**5.95 (1) *P* = 0.015**
Logit(Disp.) ~ *Sex* + *Age*	***Age***	**8.18 (1) *P* = 0.004**

of "one-way" movements occurring before the age of 5 months. In contrast, neither the *Year*, nor the *Period*, nor *Density*, nor the two-way interactions terms were significant (all *P* > 0.15). The absence of significant increase in the proportion of "one-way" movements during the hunting period ensures that the previous effect of the age cannot be confounded with plausible hunting-induced dispersal (Table 2). Overall, natal dispersal probability in juvenile hares was mainly explained by the sex and the age-class in an additive way, with dispersal events occurring preferentially in males and in the first age-classe (<5 months).

Discussion

Natal dispersal in our population of hares was male-biased. Males dispersed twice more than females on average (48% *vs.* 22%, respectively), regardless to the time of year (hunting *vs.* non-hunting period), whereas females moved the farthest although the between-sex differences were not significant. In addition, all juvenile hares dispersed before reaching sexual maturity (*i.e.* <5 months). These results are conclusive with the main findings of Bray et al. (2007) in Chareil-Montord, despite differences in habitat structure and farming practices between the two areas. The study area in Chareil-Montord was characterized by a matrix of crop fields, grassland and groves, whereas the study area in Maves was almost exclusively composed of crop fields. However, contrary to Bray et al. (2007), we did not find any evidence for a relationship between density of birth site and dispersal. Since both the rate, the sex-bias and local density were similar to that found in the high density non-hunting zone of Chareil-Montord, our results indicate that the natal dispersal pattern in hares is influenced by density rather than hunting.

Sex-biased and age-related dispersal in hares

The observed male-biased dispersal in our study was consistent with most studies on polygynous-promiscuous mammals (Gundersen and Andreassen, 1998 in root voles *Microtus oeconomus*; McLellan and Hovey, 2001 in the brown bear *Ursus arctos*; Devillard et al., 2004 in feral cats *Felis silvestris catus*; Macdonald et al., 2008 in the European badger *Meles meles*) and lagomorphs (Kunkele and vonHolst, 1996; Gillis and Krebs, 1999; Bray et al., 2007). Indeed, a sex-bias is expected to avoid inbreeding with kin, whereas the identity of the main dispersing sex should depend on between-sex asymmetries in the intra-sexual competition for resources (Greenwood, 1980; Dobson, 1982; Perrin and Goudet,

2001). Hares are solitary mammals except during the mating season. Males do not monopolize females and do not provide parental care but they do face numerous sexual competitors as is well illustrated by males chasing one another to attain dominance and access to breeding females (Cowan and Bell, 1986). Thus, consistently with Bray et al.'s conclusions, inbreeding avoidance and mate competition are likely to be the main ultimate causes of dispersal in males. In contrast, females do not compete with other females for mating opportunities but they do devote more in reproduction as they may have several litters in the year. Hence, even if inbreeding avoidance may also play a role in female dispersal, local competition for non-sexual resources, such as food and shelter for instance, probably exert more influence on their decision to disperse (Perrin and Mazalov, 1999; Perrin and Goudet, 2001). Distances to attain breeding sites with different ecological characteristics compared to that of the birth site are expected to be at least greater than the distances travelled to avoid the social context of the birth site and interactions with relatives (Ronce et al., 2001). Bray et al. (2007) suggested that the "ecological" natal environment should influence more female dispersal than male dispersal since females were shown to move farther than males and well beyond the minimal dispersal distance required to avoid interactions with relatives (10-fold more). We did not find that females dispersed significantly farther than males in our population. However, the greatest NDDs were always recorded for females (*e.g.* 5/10 females dispersed over 4000 m *vs.* 4/20 in males) which reinforces the idea that females should avoid both the social context of their birth site and probably other factors working at the level of the distances moved, such as particular ecological characteristics of the habitat.

Among the proximate factors influencing the decision of juvenile hares to disperse, disturbances related to hunting of hares and other game species did not affect the dispersal rate, which corresponds to Bray et al.'s findings (2007). On the other hand the timing of dispersal was strongly linked to the age-class. In our population, juvenile hares dispersed preferentially before the age of 5 months (78%, range = 66–114 days), when they were not yet reproductively mature. Most hares were born after April so that they should reach puberty only the following year (Lincoln, 1976; Caillol et al., 1992). Thus, proximate factors related to competition with conspecifics for sexual resources should probably exert poor influence on the timing of departure. In contrast attainment of a threshold body mass or sufficient body reserves remain the most likely factors triggering dispersal (Holekamp, 1986; Dufty and Belthoff, 2001).

No evidence for density-dependent dispersal

Contrary to our expectations, neither dispersal rate nor dispersal distances were affected by local density. First, one obviously plausible reason for lack of density dependence in our population may be the lack of strong heterogeneity in local densities especially during the last 2 years of the study. Nevertheless, during the first year of the study, when local density showed the greatest heterogeneity within the study area (range = 14–70, 27–46, 32–53 hares/km^2

Table 2
Proportion of "one-way" dispersal events according to the age-class and the period of the year (non-hunting and hunting period).

	<5 months	≥5 months
Non-hunting	18% (*n* = 87)	0% (*n* = 26)
Hunting	10% (*n* = 42)	5% (*n* = 51)

during year 2003, 2004, 2005, respectively), dispersing hares were recorded over the whole range of local densities, which could suggest therefore that local density has no strong effect on the dispersal propensity in our hare population.

Second, lack of density effect may depend on the spatial scale used for estimating densities. Good fits of the "half-normal" model and good coincidence with raw data counts confirmed the reliability of our results. On the other hand, one may also discuss the biological relevance of the spatial scale used. Our choice was guided by the particular spatial distribution of hares, which tend to aggregate (Marboutin and Aebischer, 1996; Marboutin and Péroux, 1999). Since the area used to estimate local density (200 ha) was greater than an adult home-range size (Reitz and Leonard, 1994; Marboutin and Aebischer, 1996; Bray, 1998; Rühe and Hohmann, 2004), and since it always encompassed the entire set of locations used for defining the birth site, we emphasize that the spatial scale used has strong biological meaning and may not explain the absence of any relationship between conspecific density and dispersal in our population.

Third, another explanation might be that March counts used for estimating local density around the birth site of each hare, gave a biased picture of the real density context encountered by hares at birth or at the time of dispersal, especially for those born late in the season (*e.g.* May–July). For instance, since adult home-ranges may shift by about 200 m for a 6 month period (Reitz and Leonard, 1994; Rühe and Hohmann, 2004), local densities in March may poorly reflect the true social context of each juvenile hare. We removed this potential bias, since adults monitored in our population were highly stationary. On the other hand, local differences in adult mortality and fecundity following March counts could also give a false picture of each juvenile hare's density context. For instance, spatial heterogeneity in fecundity and increasing density along the season would probably distort the range of densities during the study period.

However, under the hypothesis that local density would not show too great a fluctuation in time during the months following March counts, natal dispersal rates (48% *vs.* 22% for males and females, respectively) remain comparable with estimates of Bray et al. (2007) in the non-hunting zone (41% *vs.* 26% for males and females, respectively), where density was nearly equal to the average density in our population over the study period (49 hares/km^2 *vs.* 41 hares/km^2 respectively). Since the non-hunting zone of Chareil-Montord and our study area differ mainly in hunting pressure and in the habitat matrix, our results suggest that the natal dispersal rate in European hare is not affected by those factors.

Conclusions and future directions

Our study strengthens the idea that natal dispersal in the European hare is a ubiquitous and common process, which occurs mainly in immature individuals and twice more in males than in females. Inbreeding avoidance and mate competition appear as the main ultimate causes of dispersal in males, whereas local resource competition should probably exert more influence on female dispersal. However, proximate causes of dispersal in females remain poorly understood. Habitat suitability might be an important factor driving female dispersal. In particular, availability of shelters such as hedges or groves could be of particular interest to females for protecting newborns from predation, especially in species such as the European hare living in open landscapes. We did not take into account the ecological characteristics of the habitat in the analysis of the dispersal pattern. The fields were the smallest landscape entity in the study area, and we assumed that the overall habitat diversity encountered over the study area was homogenous from one hare to another at least in terms of

resource availability or landscape elements, since a hare home-range overlapped about 3–8 different fields. On the other hand, anthropogenic disturbances (road traffic, hunting pressure) are probably more heterogeneous over the study area, even locally at the level of a hare home-range and could influence the dispersal process.

Furthermore, we did not find any relationship between local density and dispersal of juvenile hares. Dispersal in hares seems to respond more to the "social environment" rather than hunting pressure. The dispersal rate in our population was indeed similar to that found in the non-hunting zone of Chareil-Montord which showed similar hare density, but it remained lower than the dispersal rate found in the low-density hunting zone of Chareil-Montord (Bray et al. 2007). Nevertheless, the lack of density effect could arise either from a lack of strong heterogeneity in local densities, a biased picture of each hare's density context or both. Hare densities show high variability both at small spatial scales and fine temporal scales (Kovacs and Heltay, 1981). For instance, density may increase along the season due to recruitment of individuals (birth and immigration). Including variations in density during the breeding season and taking into account the litter rank of each individual would be of great interest to provide more insight into the mechanisms underlying a hypothetic density-dependent dispersal in hares and in the broader context of the dynamics of populations in species with a long breeding season.

Appendix A. Birth site, movement pattern classification and dispersal distances

A.1. Birth site

We used DD_{min} to estimate the birth site which was unknown and could not be summarized to the trapping location both because the animal may have been trapped during temporary excursion and because the trapping location was a nocturnal point. We used the first locations (minimum number of locations = 2; trap location and first relocation) remaining within a circle radius of 588 m from their arithmetic centre to define the birth site for each juvenile hare. Hence, the circle worked as a confidence interval for the estimated centre of the birth site. Using this approach, locations outside a circle radius of DD_{min} around the birth site, *i.e.* beyond 588 m from the arithmetic centre of the birth site, were interpreted as unordinary or dispersal movements. To take into account possible trapping-induced dispersal, we excluded individuals that were relocated at more than 588 m from the trapping point and that were always seen beyond 588 from the birth site soon after ($n = 13$).
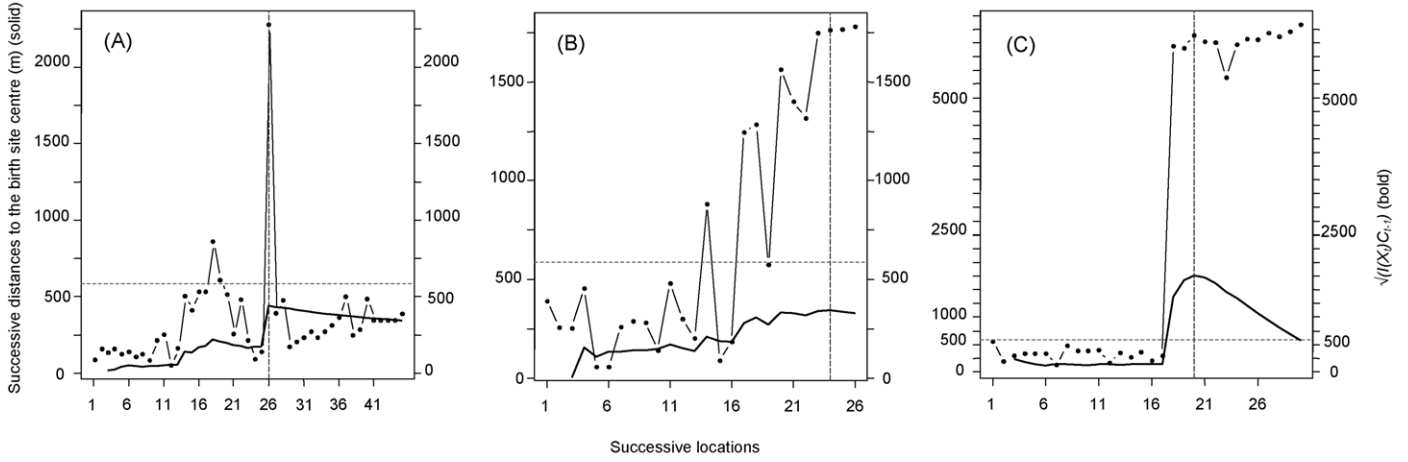
Fig. 4. Evolution of the distances of the successive locations (solid line) from the birth site centre, and successive variances of the distances of all locations at t from the preceding arithmetic centre at $t-1$ ($\sqrt{(I(X_t)_{Ct-1}}$ bold line) in the three behavioural groups shown in Fig. 2: A: Philopatric "explorer"; B: Disperser "shifter"; C: Disperser "one-way". Horizontal dashed line indicates the DD_{min}. The arithmetic centre of locations following the inertia peak (*i.e.* following the vertical dashed line) was used to define the settlement place.

A.2. Home-range shift and expansion

Home-range stability is achieved when the individual performs ordinary movements or when the disperser settles in a new area, that is to say when home-range does not widen or shift anymore over time. To have an index of the shift/expansion of home-range along the radio-monitoring, we computed at each time t the increasing inertia $I(X_t)_{Ct-1}$:

$$I(X_t)_{C_{t-1}} = \frac{1}{N_t}\sum_{i=1}^{N_t}(d(X_t), C_{t-1})^2$$

where N_t, number of locations at t; X_t, locations at t; C_{t-1}, arithmetic centre at $t-1$; $d(X_t)$, C_{t-1}, distances of all locations at t from the arithmetic centre at $t-1$.

As the animal moves away from the previous cloud of locations and its arithmetic centre, *i.e.* its previous home-range, $I(X_t)_{Ct-1}$ increases. Conversely, when the animal performs ordinary movement at t that do not lead to a shift and/or expansion of home-range anymore, $I(X_t)_{Ct-1}$ decreases. Using this measure, we assumed that home-range stability and so settlement start since $I(X_t)_{Ct-1}$ has reached a maximal value until the end of the monitoring (Fig. 4).

A.3. Dispersal classification and Natal Dispersal Distances (NDD)

Once we had defined the birth site for each juvenile hare, we could identify four kinds of movements (Fig. 5). First, a juvenile might remain around the centre of the birth site below DD_{min} throughout the monitoring period, and second, a juvenile could make movements beyond DD_{min} but returns and remains below later on. In those cases, individuals were classified as philopatric "stationary" or "explorer" respectively (Fig. 5). The third and four kind of movements related to individuals recorded beyond DD_{min} from the centre of the birth site at the end of the monitoring. In cases where the individual was recorded beyond DD_{min} for more than two months until the end of the monitoring period, without ever crossing it, we classified it as disperser "shifter" or "one-way" according to the shape of the movement pattern (Fig. 5). We chose a time-span of two months because excursions generally lasted less than 40 days, and hence, dispersal could be confidently disentangled from excursion. On the other hand, when the individual move

beyond DD_{min} for <2 months until the end of the monitoring, dispersal was more ambiguous and we used the home-range shift to rise the ambiguity: when $\max(I(X_t)_{Ct-1})$ was reached before the individual was definitely recorded beyond DD_{min} from the birth site, for instance during temporary excursions preceding the last departure, we assumed that the last locations corresponded to ordinary exploration movements, and hence the individual was classified as philopatric ("explorer") (Fig. 5). In contrast, if $\max(I(X_t)_{Ct-1})$ coincided with the last locations recorded beyond DD_{min}, the individual was non-classified and removed from the analysis because we were unable to disentangle excursion from late dispersal (Fig. 5).

Following this approach, the linear distance between the arithmetic centre of locations defining the birth site and the arithmetic centre of locations following the inertia peak reflected the average shift of home-range (*HRS*) for philopatric hares around their birth site due to temporary excursions for instance, while it measured the natal dispersal distance (*NDD*) for disperser hares.

Appendix B. Does adult home-range size depend on local density?

We reasonably expected a negative relationship between home-range size and density as is commonly shown in home-range studies. We thus tested for the effect of local density on the adult home-range size in our population before using a common DD_{min} to assert excursion or possibly dispersal in the subsequent analyses.

Because of the well known increase of home-range size with increasing number of locations, we first selected all adults with sufficient number of locations to obtain reliable estimates of the home-range size using the incremental area analysis and the Minimum Convex Polygon (*MCP*) (Odum and Kuenzler, 1955; Kenward, 2001). Adults were individuals marked as adults or individuals marked as juvenile and monitored during adult stages (*i.e.* >180 days-old). Among the 44 adult hares, we excluded two adult hares showing two distinct core areas (clearly distinct areas separated by more than 2 km possibly related to breeding dispersal). We then performed the incremental area analysis using the 42 remaining adults. For each of the 42 adults, we performed 100 random samples of k locations (k varying from 10 to the total number of locations, with an increment of five) and for each value of k we computed the mean of the 95% *MCP* over the 100 random samples (Devillard
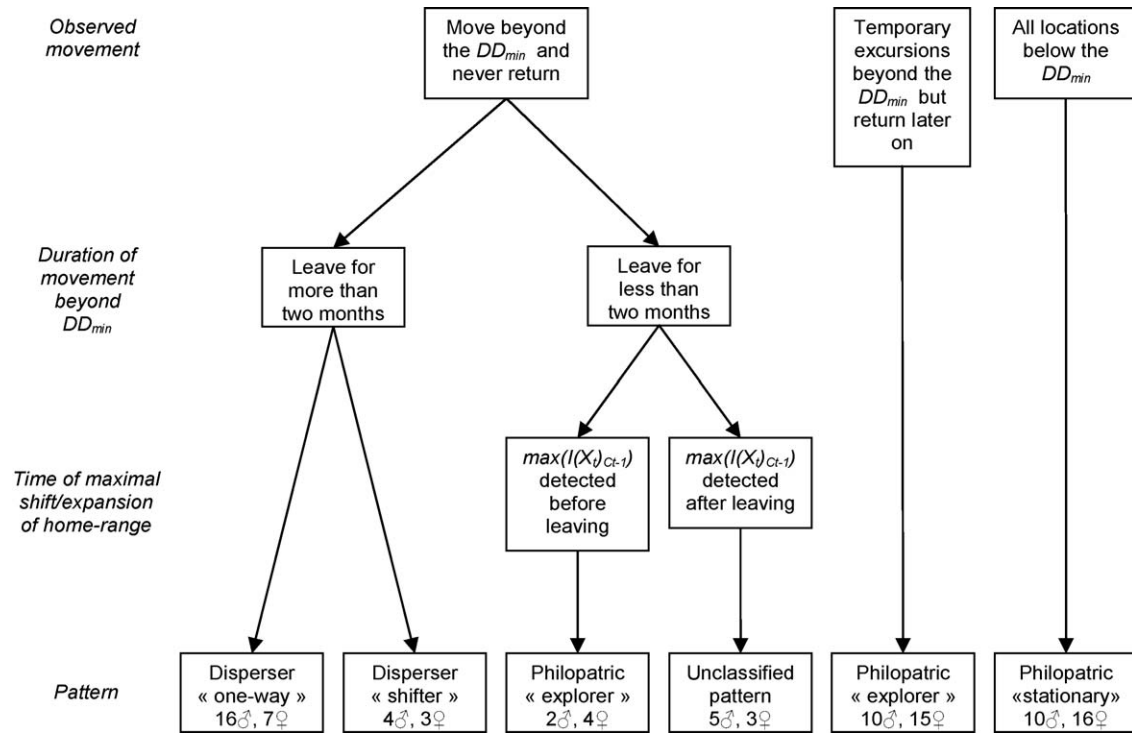
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Fig. 5. Decision rules for classifying the movement patterns into philopatric or dispersal patterns.

et al., 2008). Hence, for each adult hare, the appropriate number of locations k_{opt} for estimating home-range size was selected as the minimum value of k for which the bootstrap estimates remain always at least equal to 95% of the home-range size (95% MCP) estimated with the entire set of locations. Finally, we chose the median value of k_{opt} computed over all adults (*i.e.* 35 locations) as the minimum required number of locations to compute a reliable MCP_{95}, this in turn leading to 15 exploitable individuals.

We used linear models to test for the effect of density on home-range size. We estimated local density with distance sampling for each individual using the seven closest count points around the arithmetic centre of their locations. MCP estimates (95% MCP) were log-transformed before the analysis because the distribution of original values was highly skewed. We used the model $\log(MCP_{95}) \sim Sex + Density$ to test for the effect of local density on the size of adult home-ranges using the 15 retained individuals. We did not find any effect of these two variables (all $P > 0.3$). This result was confirmed using all individuals ($n = 42$) and the 100% MCP with the model $\log(MCP_{100}) \sim nbloc + Sex + Density$ where $nbloc$ was the number of locations (all $P > 0.09$). As a result, we confidently used a common adult home-range radius to assert excursions and possibly dispersal in the subsequent analyses.

Appendix C. Parameter estimates of GEEs and standard logistic regression used to model the departure probability in the second step.

	GEE "unstructured" correlation matrix		GEE "exchangeable" correlation matrix		Standard logistic regression	
	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error
Intercept	−0.97	2.11	−1.05	2.17	−1.05	2.18
Year 2004	−0.72	0.65	−0.73	0.65	−0.73	0.66
Year 2005	0.43	0.59	0.41	0.60	0.41	0.57
Hunt. period	−0.31	0.47	−0.32	0.48	−0.31	0.52
Density	−0.03	0.05	−0.03	0.06	−0.03	0.06
Sex male	−0.17	2.38	−0.07	2.43	−0.07	2.40
Age 2	−1.21	1.29	−1.17	1.26	−1.16	2.99
Density * *Sexe*	0.03	0.06	0.03	0.06	0.03	0.06
Density * *Age* 2	−0.01	0.03	−0.01	0.03	−0.01	0.06

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