Natal dispersal of European hare in France

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Abstract

Dispersal is a fundamental process with wide-ranging evolutionary and management consequences. To date, natal dispersal has never been described for the polygynous-promiscuous European hare *Lepus europaeus*. Using telemetry, we investigated the natal dispersal pattern in two zones that differed in hunting pressure and hare density. We quantified both the natal dispersal rates and distances using 84 juvenile hares. We tested for the influence of several factors (age, sex, density and period of the year) on these two variables. Overall, the mean dispersal rate was 43% and the median natal dispersal distances were 209 m for philopatric hares and 1615 m for dispersers. The maximum distance moved was 17.35 km. Natal dispersal rates were higher in the hunting zone with less density for both males and females, but males dispersed more frequently than females in the two zones although females moved over longer distances. Natal dispersal occurred preferentially between 4 and 6 months of age. This very fine description of the natal dispersal pattern allowed us to make inferences about both the evolutionary and proximate causes of natal dispersal. We also advocate that more attention should be paid to dispersal in studies on hare dynamics and on the conception of hare management, because dispersal seems to be more common than previously thought.

Introduction

Natal dispersal, defined as the movements made by the immature animal from its birthplace to the place of its first reproduction or where it would have reproduced if it had survived and found a mate (Howard, 1960), has important consequences for the genetic structure, demography and social evolution of animal species (for reviews, see Chepko-Sade & Halpin, 1987; Johnson & Gaines, 1990; Stenseth & Lidicker, 1992; Clobert *et al.*, 2001). Hence, it is a key behavioural and demographic process that also has major implications for wildlife management and conservation (Macdonald & Johnson, 2001).

Natal dispersal is a common process in birds and mammals (Greenwood, 1980) and kin interactions due to intra-specific local competition for environmental (e.g. food and shelters) and social resources (e.g. mating, Dobson, 1982), as well as inbreeding avoidance (Greenwood, 1980; Wolff, 1993, 1994) have all been invoked as major evolutionary forces driving the evolution of natal dispersal. Identifying evolutionary and proximate factors of dispersal remains a difficult task because evolutionary factors are not exclusive (Dobson & Jones, 1985) and potential proximate factors are numerous (e.g. social subordination hypothesis, Christian, 1970; social cohesion hypothesis, Bekoff, 1977; ontogenic switch hypoth-

esis, Holekamp, 1986). In addition, because the costs–benefits ratio of natal dispersal is often gender-dependent, both the evolutionary and proximate determinism of natal dispersal might differ between the sexes of the same species, leading to a sex bias in both natal dispersal rate and distance (Dobson, 1982; Sutherland *et al.*, 2000). For example, natal dispersal is strongly linked to the mating system and males disperse more than females in polygynous-promiscuous mammals (Greenwood, 1980; Dobson, 1982; Perrin & Mazalov, 2000) because the two genders do not defend the same resources (mates vs. food and shelters, respectively). Thus, only a detailed description of the dispersal pattern of a given species (dispersal rates and distances, age and phenotype of dispersers) in different socio-ecological conditions allows us to infer about its determinism.

Natal dispersal is now well documented in mammals but the dispersal patterns of only a few species of hares (*Lagomorpha*, genus *Lepus*) have been investigated (snowshoe hares *Lepus americanus*; Windberg & Keith, 1976; Boutin *et al.*, 1985; O'Donoghue & Bergman, 1992; Gillis & Krebs, 1999; mountain hare *Lepus timidus*, Dahl & Willebrand, 2005). In contrast, very little is known about the natal dispersal of European hare *Lepus europaeus* (Douglas, 1970; Pielowski, 1972; Broekhuizen & Maaskamp, 1982).

These previous studies have suggested that most hares are philopatric despite the fact that some juvenile dispersal movements have been observed, especially in males.

Using radio-telemetry, the purpose of our study was to investigate the natal dispersal pattern of juveniles in a wild population of European hares. After ensuring that weaned juveniles had not yet dispersed by describing their neonatal movements before weaning (see Supplementary Material Appendix S1), we identified dispersing and philopatric juvenile hares based on successive telemetry locations using the classification of McShea & Madison (1992). Secondly, taking advantage of an intensive fieldwork in a high-density non-hunting reserve and in the low-density hunting surrounding area, we described and quantified both the natal dispersal rates and distances in the two zones. We then tested for the influence of several endogenous (age, sex) and exogenous (density, period of the year) factors on the individual dispersal probability and distance, thereby allowing us to make inferences on the sex-specific determinism of natal dispersal. More specifically, we tested the following predictions: (1) a male bias in the probability of dispersal and in natal dispersal distance (NDD) should exist, given the polygynous-promiscuous mating system of European hare (Greenwood, 1980; Dobson, 1982; Wolff, 1993); (2) Hares born in the zone with the highest density should disperse more in response to a higher level of local resource competition (Dobson, 1982; Favre *et al.*, 1997); and (3) a preferential age at dispersal should exist if hares have to reach a threshold body mass before dispersal (Holekamp, 1986).

Material and methods

Study area and species

The study was conducted during 1994–1996 in Chareil–Montord (centre of France, 46°18′N, 3°17′E), a mixed cropping-livestock farming area. Details of the study area can be found in Bray & Léonard (2000). The Chareil–Montord European hare research protocol was allowed by the local authorities of Allier (France) in full conformity with the French law. Within the study area, we delimited two zones with different hunting pressures: the hunting zone (HZ, 12.3 km^2) and the non-hunting zone (NHZ, 4.3 km^2). The two zones showed different hare densities at the beginning of the reproductive season in early March. Hare densities were estimated in each zone using night counts and distance sampling (Péroux *et al.*, 1997; Langbein *et al.*, 1999). The mean density was 14 hares km^{-2} in the HZ and 49 hares km^{-2} in the NHZ over the study period. The average field size (1.9 ha) and density of roads and paths (5 km km^{-2}) were similar in the two zones, contrary to the density of hays and ditches (2.86 vs. 4.41 km km^{-2}, respectively, in HZ and NHZ).

The European hare is a medium-sized mammal (2.5–6 kg). Mostly solitary, they do not live in stable structured social groups but form some non-territorial and temporary feeding groups characterized by a dominance hierarchy for the acquisition of food and mate resources (Broekhuizen & Maaskamp, 1982; Cowan & Bell, 1986; Holley, 1986). The mating system is promiscuous-polygynous but males do not monopolize the females (for a review see Cowan & Bell, 1986).

Capture and monitoring of juvenile hares

Juveniles (from weaning to first reproduction) from litter of different ranks were trapped from May to October each year. A total of 109 juveniles were captured using unbaited box traps (Bray & Léonard, 2000). They were equipped with eartags ('TIP-TAG' type) and radio transmitters (TXP2, 50 g, 3000 m range, battery life 16 months, Televilt, Lindesberg, Sweden). For each first capture, trap location, sex, body mass and skull length were recorded. Age (in days) of juveniles at first capture was then estimated using different methods depending on their skull length (see Supplementary Material Appendix S2). At the time of first capture, 53 juveniles were 31–60 days old and 56 were 61–90 days old.

Telemetry locations were recorded weekly (one diurnal and one nocturnal location on the same day) by triangulation using a hand-held five-element Yagi antenna or visually located (at night).

To analyse the dispersal pattern, we selected only the 87 juveniles (45 females and 42 males; 33 in the HZ and 54 in the NHZ) that were radio-tracked until they were 90 days old, and at least during 1 month (to avoid potential biases in mortality and dispersal following capture, respectively). The monitoring duration and number of locations per individual ranged from 45 to 650 days (mean = 193 days), and from 17 to 167 locations (mean = 55 locations).

Typology and dispersal rate

Using McShea & Madison's trackogram classification (1992), four dispersal categories can be distinguished according to schematic patterns of successive home-range positions and overlaps (Fig. 1). A hare was considered to be philopatric if classified as stationary (Fig. 1a) or explorer (Fig. 1b), or as a disperser if classified either as a 'shift' disperser (Fig. 1c) or 'one-way' disperser (Fig. 1d). Dispersal rate was estimated as the proportion of dispersers among the individuals taken into account.

Determinism of dispersal probability

We tested for the effects of year (3 years), sex, zone (HZ vs. NHZ), age and period of the year on the probability for a hare to disperse. Before the age of 4 months, juveniles would not have reached the adult size yet and would not be sexually mature. At 4 months of age, nearly all juveniles would have gained adult body weight (Caillol *et al.*, 1992), although most of them are still reproductively inactive. By the age of 6 months, nearly all reach sexual maturity (Raczynski, 1964; Pépin, 1977; Broekhuizen & Maaskamp, 1981). Age was thus modelled as a three-modality factor (<4, 4–6, ≥6 months old). We divided the year into three different periods to investigate the potential influence of the
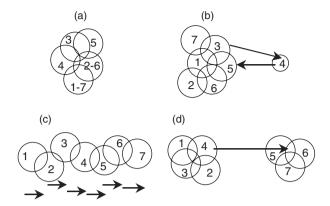
Figure 1 Patterns of home-range positions and overlaps seen in European hare *Lepus europaeus* (from McShea & Madison, 1992). Four schematic patterns were observed: (a) type 'stationary': each home-range perimeter overlaps previous estimates; (b) type 'explorer': idem (a) but the hare makes short-term excursion outside its natal home range before returning to it (the excursion distance is higher and unusual); (c) type 'shift' disperser: hare gradually changes its home range; (d) type 'one-way' disperser: hare suddenly changes its home range by making a one-way and permanent movement to establish in a new home range disjunctive from the previous one.

reproductive activity, hunting and the change in vegetal cover. The first period (May–August) is characterized by reproductive activity and a high proportion of fields with a dense vegetal cover until wheat harvesting in mid-summer. The second period (September–November) is the hunting season within the HZ, and the habitat is wholly open at the end of this period (after corn harvesting during November). The third period (December–February) is characterized by the beginning of the reproductive season (essentially mating activity), and social interactions between hares are thus enhanced.

We were not able to estimate either an age or a period of dispersal for 'shift' dispersers due to their particular continuous pattern of dispersal. Consequently, we first analysed the dispersal probability as a function of sex, zone and year. Secondly, we analysed the probability of a hare making a 'one-way' dispersal (excluding the 'shift' dispersers), adding the age and period factors to the previous factors. A hare might thus appear from one to five times within different age and period classes in this second analysis.

We used the 'bias-reduced logistic regression' methodology of Heinze & Schemper (2002) to assess patterns in dispersal probability (see Supplementary Material Appendix S3). Indeed, given the relatively low occurrence of dispersal events in hares (10% in average, but equal to zero in given classes: e.g. third age class in the HZ), standard logistic regression might give biased results due to convergence problems (McCullagh & Nelder, 1989) by underestimating the probabilities of dispersal events (King & Zeng, 2001). A way to overcome such biases is to modify the maximum likelihood estimator (Firth, 1993; Heinze & Schemper, 2002), which bears the consequence that one could not compute the Akaike information criterion (AIC;

Akaike, 1974) required for the model selection using the theoretical information approach. As recommended for the modelling of rare events such as dispersal, penalized profile likelihoods could then be used to test the effect of year, age, period, zone and sex on dispersal event occurrence (Venables & Ripley, 1999; Heinze & Schemper, 2002).

We used the logistf package (Heinze & Ploner, 2004) for R software (R Development Core Team, 2004) to perform a penalized likelihood ratio test on some or all selected factors, and conduct a backward stepwise selection procedure. The model year × zone × sex was used as the starting model in the analysis of the dispersal probability. The model including the simple effects of the factors year, sex, age and zone, as well as all their interaction terms, excluding the four-way interaction due to the sparseness of the data, was used as the starting model in the analysis of the 'one-way' dispersal probability. The period effect was tested in a specific way. Because hunting occurs only in the HZ, one might expect the period effect to interact with the zone. Starting from the previous best-selected model, we specifically tested for this zone × period interaction and for the simple effect of period.

Dispersal distance

We defined the NDD as the linear distance between birthplace and 'breeding' spot for a given individual. The birthplace was approximated by the place of first capture (Supplementary Material Appendix S1). We called 'breeding' spot the arithmetic centre of the home range calculated over 10 locations in February ($t + 1$, i.e. next year after the birthyear). We chose this month because all reproducing hares are expected to have bred at least once at this time (Marboutin *et al.*, 2003). For juveniles that died before February ($t + 1$), we used the last 10 locations before death to obtain an approximation of the 'breeding' spot. If a 'one-way' disperser established for < 1 month within its new home range before dying, we used all locations after its 'one-way' dispersal to estimate its 'breeding' spot.

We tested for the effects of year, zone (HZ vs. NHZ) and sex on NDD using a general linear model (GLM). Before analysis, NDD were log10-transformed, because the distribution of original values was highly skewed. Because the distribution of dispersal distances is clearly split with no overlap between philopatric and disperser hares (see 'Results'), we analysed these two datasets separately. For each one, we started the model selection from the three-way interaction model year × sex × zone, down to the simple effects of the factors using traditional χ^2-tests and R software (R Development Core Team, 2004).

Results

Pattern of natal dispersal: dispersal status and NDD

Eighty-four out of 87 juveniles could be classified according to the schematic dispersal pattern (Fig. 1). Two of the

remaining died 1 day after they had left their natal home ranges, which precluded us from disentangling excursion and dispersal. The last juvenile showed an erratic movement pattern that did not allow us to classify it into any category.

Forty-six individuals displayed only restricted movements around their birthplace and were thus defined as 'stationary' hares (1a-type). Two juveniles made an excursion outside their home ranges but returned permanently after a short period (<1 month) (1b-type). Eight juveniles left gradually their birthplace and were thus classified as 'shift' dispersers (1c-type). Finally, 28 juveniles made a very quick (about 1 week) 'one-way' movement to leave their natal home range and settle in a disjunctive home range ('one-way' dispersers, 1d-type).
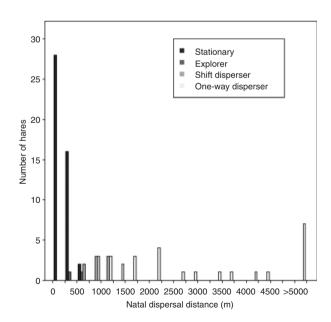
The NDD increased according to the schematic dispersal pattern (Fig. 2). Forty-four out of the 46 'stationary' juveniles had an NDD of <500 m (median = 202.5 m). The two remaining 'stationary' showed an NDD, respectively, equal to 608 and 564 m. The NDDs of the two explorers were 460 and 680 m but their 'breeding' spot still encompassed their birthplace. Overall, NDD for philopatric hares was always <700 m. The median NDD was 967 m (range 742–1071 m) and 2057 m (range 762–17 353 m), respectively, for 'shift' and 'one-way' dispersers. Overall, NDD for disperser hares was always over 700 m, and the distribution of dispersers' NDD did not overlap with the distribution of philopatric hares' NDD (Fig. 2). We thus analysed the determinism of NDD separately for each of these two groups.

For the philopatric hares, neither the year nor the sex nor the zone had any effect on NDD (all P-values >0.25 whatever the simple, the two- or the three-way interaction terms). For disperser hares, the three- and the two-way interaction terms were not significant either, as well as the

single effects of year and zone (all P-values >0.53). However, female dispersers showed a greater NDD than male dispersers (P-value = 0.05, median: 2743 m in females, 1523 m in males, Fig. 3). This difference is mainly due to an excess of long-distance female dispersers: six out of seven hares that had dispersed over 5000 m were females (Fig. 3).

Determinism of dispersal

We first analysed the effect of the main factors (sex, zone and year) on the dispersal probability (either 'shift' or 'one-way' dispersal). Starting from the model year × zone × sex, the three-way interaction term and all the two-way interaction terms were not significant (all P-values >0.21). The effect of year was not significant (P-value = 0.14), contrary to both the effects of zone (P-value = 0.008) and sex (P-value = 0.01). Natal dispersal rates were higher in the HZ for both males and females, but males dispersed more frequently than females in the two zones (Table 1).

Secondly, modelling the 'one-way' dispersal probability (excluding the 'shift' dispersers; see 'Material and methods'), all three- and two-way interactions terms were not significant (all P-values >0.22, Table 2). The age effect was highly significant (P-value = 0.0005, Table 2), with a greater propensity to disperse in 4–5-month-old hares (18/28 'one-way' dispersers). The effect of the zone remained significant (P-value = 0.016, Table 2). Contrary to our first analysis on the probability to disperse, the sex and the year effects became barely significant (respectively, P-value = 0.09 and 0.06 vs. P-value = 0.01 and 0.14 in the first analysis, Table 2). These two contrasted results can be attributed to the restricted dataset used in the second analysis. Indeed, excluding the 'shift' dispersers led to underestimate both the number of dispersers in the second year, because six out of
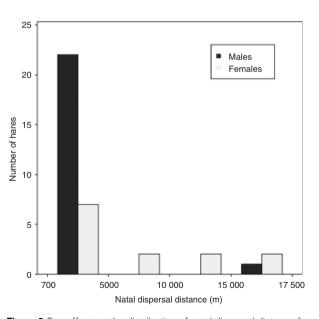

Figure 2 Distribution of natal dispersal distances for each dispersal status (stationary, explorer, 'shift' disperser and 'one-way' disperser).

Figure 3 Sex effect on the distribution of natal dispersal distance for dispersers (either 'shift' or 'one-way' dispersers).

Table 1 Dispersal rates of juvenile hares Lepus europaeus according to birth zone (hunting zone HZ vs. non-hunting zone NHZ) and sex

	HZ	NHZ
Males	0.857 (n=14)	0.407 (n=27)
Females	0.375 (n=16)	0.259 (n=27)

Dispersing hares were either 'shift' or 'one-way' dispersers.

eight 'shift' dispersals occurred in 1995, and the number of male dispersers, because seven out of eight 'shift' dispersers were males. There was no significant effect of the period on the 'one-way' dispersal probability (Table 2), either in interaction with the zone ($P = 0.27$) or in simple effect ($P = 0.41$). Overall, the natal dispersal probability of a juvenile hare therefore depended on sex, age and on the zone of first capture. All these effects were only additive.

Discussion

Evaluation of hare dispersal rate and distance

In our population of European hare, natal dispersal was common and males dispersed more than females whereas females dispersed farther than males. In addition to this gender effect on natal dispersal, we also showed that both juvenile males and females dispersed preferentially between 4 and 6 months of age, and that the mean dispersal rates were higher in the low-density HZ for both sexes. We have to discuss two potential biases before interpreting these results. Firstly, dispersal rates might be underestimated in our study because some juvenile hares died before the age of 6 months, and what these individuals would have done if they had survived is unknown. This classical bias when studying dispersal (Johannesen & Andreassen, 1998) might be evaluated with a reduced dataset composed only of the 32 juveniles that were still alive on the 1st March of the year after their birth: the overall dispersal rate was nearly equal (41%) (Bray, 1998) to the one estimated from the full dataset (43%). Secondly, the NDD for disperser juvenile hares were always over 700 m. As the mean home-range size in adult hares was 0.37 km^2 (Y. Bray, unpubl. data) and assuming circular home ranges, NDD for disperser juveniles was always more than twice the home-range radius of adults (e.g. the median NDD for 'one-way' dispersers was 2.8-fold the mean radius). This result may suggest that the individuals assigned in the disperser class by our typology were real dispersers with regard to their NDD: they indeed probably left their birthplace as a result of their dispersal movements. The impact of these two potential biases, therefore, was minimal, and we could confidently interpret our results.

The overall dispersal rate (43%) and the maximal NDD (17 353 m) in our study were higher than those previously reported for European hare. Douglas (1970) reported that only 17% (6/36) of juvenile hares were recaptured over 1 km from initial capture sites and the maximum distance moved

Table 2 Effects of zone, age, sex, period (per) and year (y) on the proportion of 'one-way' dispersers (disp)

Fitted model	Specific PLRT for	PLRT (d.f.) and P-value
Logit(disp)=y+zone+age+sex+y×zone+y×age+y×sex+zone×age+zone×sex+age×sex+y×zone×age+y×zone×sex+y×age×sex+zone×age×sex+y×zone×age×sex+y×sex×age +zone×sex×age	zone×sex×age	2.98 (2) P=0.22
Logit(disp)=y+zone+age+sex+y×zone+y×age+y×sex+zone×age+zone×sex+age×sex+y×zone×age+y×zone×sex+y×age×sex+zone×age×sex+y×sex×age	y×sex×age	3.32 (4) P=0.50
Logit(disp)=y+zone+age+sex+y×zone+y×age+y×sex+zone×age+zone×sex+age×sex+y×zone×age+y×zone×sex+y×age×sex+zone×age×sex	y×zone×age	0.64 (4) P=0.96
Logit(disp)=y+zone+age+sex+y×zone+y×age+y×sex+zone×age+zone×sex+age×sex+y×zone×age+y×zone×sex+zone×age×sex	age×sex	0.47 (2) P=0.79
Logit(disp)=y+zone+age+sex+y×zone+y×age+y×sex+zone×age+zone×sex+age×sex+y×zone×age+zone×age×sex	zone×sex	0.33 (1) P=0.56
Logit(disp)=y+zone+age+sex+y×zone+y×age+y×sex+zone×age+zone×sex+age×sex+zone×age×sex	zone×age	2.81 (2) P=0.25
Logit(disp)=y+zone+age+sex+y×zone+y×age+y×sex+zone×age+zone×sex+age×sex	y×sex	0.33 (2) P=0.84
Logit(disp)=y+zone+age+sex+y×zone+y×age+zone×age+zone×sex+age×sex	y×age	4.72 (4) P=0.32
Logit(disp)=y+zone+age+sex+y×zone+age+sex	y×zone	2.13 (2) P=0.35
Logit(disp)=y+zone+age+sex+y×zone+age+sex	sex	2.86 (1) P=0.09
Logit(disp)=y+zone+age+sex	age	**15.14 (2) P=0.0005**
Logit(disp)=y+zone+age+sex	zone	**5.77 (1) P=0.016**
Logit(disp)=y+zone+age+sex	y	5.59 (2) P=0.06
Specific test of the period effect		
Logit(disp)=zone+age+sex+per+per×zone	per×zone	2.58 (2) P=0.27
Logit(disp)=zone+age+sex+per	per	1.78 (2) P=0.41

Models including additive effects (+) or interaction (×) were performed as follows: logit(disp)=$\mu+\beta_i.X_i+\varepsilon$ where μ is the intercept, β_i the slope for the ith term of the model and ε the error term of the fitted model using the 'bias-reduced logistic regression' methodology of Heinze & Schemper (2002). X_i was the simple effect of a given factor, or two- or three-way interactions term. The tests of the effects were performed using the penalized likelihood ratio test (PLRT) as described in Heinze & Ploner (2004). Significant effects ($P<0.05$) are shown in bold. Marginal effects ($0.05 \leq P<0.10$) are shown in italics.

was 3150 m. The same dispersal rate was reported by Pielowski (1972) and the dispersal distance of hares in their first year of life ranged from 1 to 3 km. Lastly, from 99 leverets released and 23 recovered, Broekhuizen & Maaskamp (1981) reported only two movements over 1 km. These prior studies relying on trapping may have failed to detect long-distance dispersers and probably underestimated the dispersal rate. More recently, Dahl & Willebrand (2005) revealed the natal dispersal of mountain hare using telemetry, but few ($n = 6$) leverets were radiotracked beyond 180 days. Finally, Gillis & Krebs (1999) reported a dispersal rate of 50% and a dispersal distance of up to 16 km for snowshoe hare, which concurs with our findings. They also suggested that natal dispersal might play a greater role in the population dynamics than previously thought.

Age and sex effects on dispersal rate and distance

As commonly shown in polygynous-promiscuous mammals (Greenwood, 1980; Dobson, 1982), and other lagomorphs in particular (e.g. North American pika *Ochotona princeps*, Smith & Ivins, 1983; European rabbit *Oryctolagus cuniculus*, Künkele & Von Holst, 1996; Plateau Pika *Ochotona curzionidae*, Dobson, Smith & Wang, 1998; snowshoe hare, Gillis & Krebs, 1999), natal dispersal was male-biased (by a two-fold factor), in agreement with our first prediction. However, not all males dispersed and not all females were philopatric. Such an intermediary pattern of natal dispersal suggests both non-exclusive causes of dispersal, and potentially different causes related to the gender of individuals (Dobson & Jones, 1985; Perrin & Goudet, 2001). Females commonly defend non-sexual resources (food and shelters) whereas male compete for their access to females (Clutton-Brock, 1988). In such a system, both local mate competition (Dobson, 1982; Moore & Ali, 1984) and inbreeding avoidance (Greenwood, 1980; Wolff, 1993) have been invoked as major evolutionary factors to explain why males are more prone to disperse than females; the dispersal of females, when it occurs, is more related to local resource competition (Dobson, 1979; Favre *et al.*, 1997). Assessing the relative influence of these evolutionary forces is facilitated by the analysis of proximate determinism of dispersal probability, dispersal mode and NDD.

In European hares, dispersal occurred mainly during the fifth and sixth months of life. This result is consistent with our second prediction on the need for juvenile hares to reach a threshold body mass before dispersal (ontogenetic-switch hypothesis, Holekamp, 1986). Indeed, at the age of 4 months, juvenile hares would have reached the adult size. However, during their fifth and sixth months of life, they would have nearly all gained sexual maturity, and would have also become putative competitors for adults (see for an example in roe deer *Capreolus capreolus*, Wahlstrom, 1994). Without behavioural data, it is impossible to disentangle 'voluntary' dispersal and 'forced' expulsion (Christian, 1970; Bekoff, 1977). However, the distribution of NDD and a particular mode of dispersal in males might help us

to understand the evolutionary and proximate determinisms of natal dispersal in this European hare population. Females dispersed on average farther than males (contrary to our first prediction), but this difference was mainly due to an excess of long-distance dispersing females (Fig. 3) and to an excess of males among the short-distance 'shift' dispersers (7/8). This predominance of males among 'shift' dispersers might indicate that males, once they have dispersed, search for the nearest suitable place to reproduce. It would thus appear that they escape less from their 'ecological' environment than from their 'social' environment (Waser & Jones, 1983; Isbell & Van Vuren, 1996), suggesting that factors such as local mate competition and inbreeding avoidance may predominantly determine dispersal in males. Conversely, females dispersed farther than males, which could suggest that they escape both from their 'social' and 'ecological' natal environments. This is in accordance with the idea that local resource competition for food and shelters is the predominant factor acting on female dispersal in polygynous-promiscuous mammals. This distinction between 'social' dispersal and 'ecological' dispersal (called 'locational' dispersal by Isbell & Van Vuren, 1996) is important to make because variation in the costs of these two kinds of dispersal is likely to influence decisions about whether, when and where to disperse. This last point calls for future behavioural and genetic studies in European hare to assess both the proximate causes of dispersal and the gender-specific costs–benefits ratio of dispersal (survival and reproduction).

Inverse density dependence of dispersal rate

The gender difference in the dispersal rate and distance, and the mean dispersal distance in both sexes were unaffected by the birth zone (HZ vs. NHZ) of the hares. However, dispersal rates were higher in the HZ than in the NHZ, the difference being more pronounced in males (Table 1). Because hunting had no effect on the probability to disperse in the HZ (for similar results, see Reitz & Léonard, 1994), we can argue that the higher density in the NHZ might be associated with the lower dispersal rates in this zone, which was not expected from our second prediction. The density dependence of dispersal rates has been one of the most discussed topics in the 'dispersal' framework these last 25 years (for a review, see Matthysen, 2005). Inverse density dependence of dispersal is not rare (Matthysen, 2005; Støen *et al.*, 2006 for a good example in brown bears *Ursus arctos*) and our results might be explained by two different factors.

The first factor might be an underestimation of the dispersal rates in the NHZ. Hence, the mean adult home range sizes were smaller in the highest density NHZ than in the HZ (0.37 vs. 0.39 km^2 in females, 0.23 vs. 0.64 km^2 in males (Y. Bray, unpubl. data); see Rühe & Hohmann, 2004 for similar results). Thus, escaping from an unsuitable social environment in a high-density zone might be carried out through shorter and continuous fine-scaled shifting rather than a long and one-way movement (especially for males, which showed large differences both in dispersal rate and

home-range size between zones). Such a bias would especially underestimate the male dispersal rate in the NHZ (by missing some dispersal events) whereas this bias should be less in females, which are expected to escape their ecological environment to a greater extent than their social one in our population. Missing some short-distance dispersers in the high-density NHZ would also explain the lack of inverse density dependence of NDD in our study.

Secondly, this negative density dependence of dispersal rate in our population might also be explained by the 'social fence' hypothesis (Hestbeck, 1982). This hypothesis states that limited movements of juveniles in a high-density zone may indicate social stress and avoidance of confrontations with conspecifics. Because the local environment is saturated, juveniles should 'prefer' to remain philopatric to escape the very high cost of dispersal. Again, only behavioural data on social interactions between juvenile and adult hares would help us to better understand the proximate factors that influence dispersal.

Management implications and conclusion

Natal dispersal in European hares thus seems common, and some individuals made long-distance dispersal movements in our population. Such a pattern might explain the pioneer ability of this species (Péroux, 1995) and may have some consequences in terms of conservation and management. Indeed, natal dispersal impacts both the local population size through the balance between local emigration and immigration, and the meta-population dynamics through the colonization of new areas (Hanski, 2001). The European hare populations are well known to show some large heterogeneities in density at a fine spatial scale (about 1 km, Kovacs & Heltay, 1981), and the inverse density-dependent dispersal found in our population might explain such a pattern if local emigration is not balanced by immigration. Our results highlight the necessity to manage larger areas than is usually done to encompass all the dispersal process, and thus meta-population dynamics. In addition, because dispersal is partly dependent on the habitat quality (both social and environmental factors, Wiens, 2001), future studies should consider the availability and the distribution of both resources (food, shelters) and dispersal routes (corridors, fragmentation) for a better understanding of the natal dispersal determination, and its consequences for meta-population dynamics.

Acknowledgements

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Supplementary material

The following material is available for this article online:

Appendix S1 Neonatal movements of leverets until weaning: does the capture site a proxy of the birth site?

Appendix S2 Age determination for juveniles at first capture.

Appendix S3 Why we do not use GLM or GEE models?

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