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Original Investigation

Natal dispersal of European hare in a high-density population

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ABSTRACT

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