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

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

Animal movements can affect many important ecological processes such as gene flow (Bohonak 1999) and metapopulation dynamics (Hastings & Harrison 1994). Natal dispersal, defined as the net movement between the natal area and the site of first breeding (Howard 1960), is characterized by long-distance movements which, for nonmigratory species, are usually the longest performed during an individual's lifetime. Not all individuals within a given population disperse (Bowler & Benton 2005; Ronce 2007), but the factors that influence this decision at the individual level are poorly understood, despite the fact that natal dispersal decisions can have profound consequences for population dynamics (Clobert et al. 2001). Dispersal is a complex process, and a variety of factors can affect the decision to leave the natal area (e.g. sex, developmental stage, body size, density, etc.; i.e. condition-dependent dispersal sensu Bowler & Benton 2005). Investigating the behavioural ontogeny of this decision could help us understand why some individuals disperse while others do not. In particular, exploratory movements (i.e. movements outside an individual's home range) performed prior to true dispersal may play a role in the dispersal decision (Selonen & Hanski 2006). Indeed, such movements can provide information on the surrounding environment which can be used by individuals to decide (1) whether or not to disperse and (2) for dispersers, how far and in which direction to disperse during the transition phase (Stamps & Krishnan 1999). Despite this, very few studies have investigated between-individual differences in exploration behaviour and its impact on the dispersal decision.

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

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

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

In this study, we used an especially detailed GPS monitoring of juvenile roe deer, *Capreolus capreolus*, to investigate the influence of exploratory movements on dispersal behaviour in this species. More precisely, we looked for evidence of exploration behaviour and contrasted the exploration frequency and features (distance and duration) of philopatric individuals with those of individuals that subsequently dispersed. Van Moorter et al. (2008) previously showed that juvenile roe deer are more mobile than adults, but these authors did not compare the behaviour of future dispersers with future philopatric animals. Based on this observation, together with the fact that outside the juvenile dispersal phase, roe deer are generally highly sedentary (Hewison et al. 1998), this species thus provides a pertinent study system for exploring the link between predispersal exploration behaviour and dispersal outcomes, thus contributing to a better understanding of the behavioural ontogeny of the dispersal decision.

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

METHODS

Study Area

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