



Melanin-based coloration predicts natal dispersal in the barn owl, *Tyto alba*

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Searching for a suitable breeding site is an important decision in the life of most animals. The decisions where to settle and how far to travel before doing so depend on many factors. Individual differences in dispersal distance could result from different strategies (e.g. specialists versus generalists), which might result in similar reproductive success in different habitats, or different competitive abilities to acquire a territory close to the natal site. The barn owl is polymorphic in melanic coloration, which is associated with many physiological and behavioural traits such as habitat choice, stress response and docility, raising the possibility that the coloration is also related to dispersal. We studied natal dispersal (from rearing site to site of first breeding attempt) and breeding dispersal (from one breeding site to the next) in barn owls using a long-term data set. Darker reddish individuals moved further than paler individuals during natal dispersal, but not during breeding dispersal. A cross-fostering experiment showed that the colour of the biological and foster parents had no influence on dispersal distance. The distance dispersed by parents and same-sex offspring was correlated, whereas natal and breeding dispersal were not repeatable within individuals, indicating that they are two different processes. Given that the distance travelled in natal dispersal appears to be heritable, the underlying genes might be coupled to those related to coloration. We discuss hypotheses to explain the potential adaptive function of the link between coloration and natal dispersal.

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Dispersal is an important aspect of population dynamics. The choice of a territory can, to a large extent, determine breeding success (Cody 1981), making it an important event in the life of an individual. The movements in the period preceding a breeding attempt are usually divided into two categories: natal dispersal, which is defined as the movements from the site where an individual was born to the site where it first breeds; and breeding dispersal, which is the distance between the two locations of successive breeding events (Greenwood & Harvey 1982). The distances covered in natal dispersal are usually greater than those in breeding dispersal.

How individuals decide where to settle and how great a distance they will travel before settling depends on many factors. Individual strategies and environmental factors can explain interindividual variation in dispersal distances. Intraspecific competition for mates or other resources contribute greatly to dispersal (Johnson & Gaines 1990; Perrin & Mazalov 2000), so that individuals that are out-competed have to move more. Body condition might also be of importance (Bowler & Benton 2005; Clobert et al. 2009), although it

is not clear whether individuals in better condition are more or less likely to disperse than individuals in worse condition (Belthoff & Dufty 1998; Meylan et al. 2002; Bonte & De la Pena 2009). Local adaptation sometimes also plays an important role in the decision where and when to settle down (Edelaar et al. 2008). Some traits are better suited for different local environments and this would greatly influence the decisions individuals have to make when searching for a breeding location. Local adaptation can also impact the direction or the distance moved to a new nest site. For example, in response to predators or as a predator, individuals with different skin or plumage coloration might be better camouflaged in different habitats (Bortolotti 2006 cited in Hill & McGraw 2006).

Another possibility that might lead to observed differences in dispersal behaviour is that the searching and moving behaviour is influenced by innate individual differences. Dispersal is a risky undertaking, with the possibility of predation during dispersal (Yoder et al. 2004) or of not being able to find a suitable breeding site in the unknown destination area. It is therefore not surprising that dispersers can differ in personality, physiology or morphology from nondispersers (Cote et al. 2010). When individual differences in behaviour are consistent and repeatable, they can be called temperament or animal personalities (Sih et al. 2004a; Reale et al. 2007). Suites of personality traits can also be correlated. For example, explorative and less explorative individuals are often divided into 'bold' and 'shy' categories, although these are extremes

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of a continuum (Reale et al. 2007). An example is the Trinidad killifish, *Rivulus hartii*, in which, when corrected for sex, predation risk and body size, individuals categorized as bold in behavioural tests in the laboratory dispersed further than shy individuals when returned to natural conditions (Fraser et al. 2001). Bold individuals are also more likely to migrate in roach fish, *Rutilus rutilus* (Chapman et al. 2011) and even in humans individuals with increased activity levels (a trait that is associated with boldness/shyness; Reale et al. 2007) migrate more often (Jokela et al. 2008). Thus boldness and dispersal seem related to each other.

On a European scale, barn owls show a gradient in pheomelanin and eumelanin coloration from south to north (Roulin 2003). This gradient might reflect differences in the specific habitat requirements of the different colour morphs (Antoniazza et al. 2010). The females tend to disperse further than males (Taylor 1994) and we have already demonstrated that white nonpheomelanin males have a higher chance of being recruited in our local Swiss population than their darker reddish pheomelanin siblings (Roulin & Altwegg 2007). Reddish individuals eat more voles and grow longer tails than whiter individuals, which eat more mice (Roulin 2004, 2006). Furthermore, it appears that whiter individuals breed more often in wooded habitats than reddish conspecifics (Charter et al. 2012; Dreiss et al. 2012). We also found a relationship between a eumelanin trait (diameter of black spots located at the tip of ventral feathers) and personality traits in our study population of barn owls (Van den Brink et al. 2012). The results already found in associations between colour and habitat choice and between colour and personality traits make this species suitable to investigate a possible relationship between dispersal behaviour and both pheomelanin- and eumelanin-based coloration. Since dispersal is sometimes also associated with personality traits we can assume that both personality and local adaptation might play a role in possible differences in barn owl dispersal distances.

We first studied the relationship between the individual colour and the natal dispersal of recruits: individuals born in the study area that ultimately also breed there. During the study period, cross-fostering experiments were performed, giving us the opportunity to study genetic and environmental influences on dispersal. Second, we followed the movements between consecutive breeding attempts of individuals breeding in our study area during their breeding career, the breeding dispersal. We investigated whether differences in breeding dispersal distance between individuals were related to their melanin colour and several other traits such as habitat characteristics or life history traits such as breeding success, age at first breeding and wing and tail length. Natal and breeding dispersal take place in different life stages and therefore we might see differences in distance travelled and underlying factors causing the two types of dispersal. Finally, we investigated whether dispersal distance and/or coloration are also related to reproductive success. We discuss whether local adaptation, personality or other factors can explain colour-specific dispersal behaviour.

METHODS

Study Species and Study Area

Between 1994 and 2010 we studied a population of barn owls breeding in the Broye plain, a 25 × 15 km area in western Switzerland (46°49'N, 06°56'E). The Veterinary Service of the Canton of Vaud, Switzerland, authorized this study under licence number 1146, allowing us to take blood samples for DNA and to cross-foster nestlings. The Swiss Ornithological station, Sempach, Switzerland, authorized the ringing of individuals. This population breeds mostly in nestboxes placed on farms. The barn owl is

a medium-sized owl with worldwide occurrence. It hunts mainly voles and mice in open agricultural areas (Glutz von Blotzheim 1987). It displays a distinct colour polymorphism ranging from spotless white to dark reddish pheomelanin and heavily marked with eumelanin black spots. Males are generally paler pheomelanin and show fewer and smaller black spots than females, although both sexes can display any phenotype (Roulin et al. 1998). The laying period ranges from February to August and the last fledglings appear as late as November. Clutches consist of two to nine eggs. Hatching occurs asynchronously with 2.5-day intervals, because the mother starts incubation directly after laying the first egg. This can result in an age difference of up to 3 weeks in a nest of nine offspring. After fledging at approximately 55 days of age, juveniles remain in the direct vicinity of their nest site for 1–2 months where they still receive regular feedings from their parents (Glutz von Blotzheim 1987; Taylor 1994). When individuals have become independent they will disperse and try to find their own breeding site. As in most bird species (Clarke et al. 1997), females generally disperse further than males, which might be driven by inbreeding avoidance (Greenwood & Harvey 1982). The average migrating distances vary tremendously between populations, with mean distances ranging from within 10 km for a population in Britain to between 50 and 100 km for German and Dutch populations (Taylor 1994; Kniprath 2010). Dispersal distances appear related to food availability, with increasing distances in years with low vole densities (Taylor 1994). The distances reported here are mostly from recoveries of dead birds, which does not rule out the possibility that dispersal distances are inflated owing to transport between death and recovery (e.g. on the bumper of a car; Taylor 1994).

Cross-fostering

Between 1994 and 2010 we performed cross-fostering experiments, where nestlings from one nest were raised in another nest. Of the 185 studied individuals, 55 were cross-fostered. For more details see Roulin & Dijkstra (2003) and Roulin (2006). Pairs of nests were matched by hatching date and some or all of the nestlings were swapped between them. We did this by immediately transporting nestlings by car from the nest of origin to the nest of rearing. During this procedure they were placed in a cloth bag, which was kept close to the body of one of the researchers to ensure the nestlings did not get cold during the time it took to drive between nest sites. The transport was always completed within 1 h. This allowed us to study whether the dispersal behaviour was heritable by comparing dispersal distances between cross-fostered nestlings with those of their biological and foster parents. If local adaptation plays a large role in natal dispersal, we can expect cross-fostered individuals not to be optimally adapted to the habitat where they were raised. This might then lead them to disperse further than noncross-fostered individuals.

Assessment of Coloration

At the age of fledging at about 55 days old, A.R. measured colour traits (pheomelanin coloration, number of eumelanin spots and eumelanin spot diameter) and biometric measurements for all nestlings. Adult individuals were measured each year during the breeding season with females being distinguished from males by the presence of a brood patch. For our analyses we used the measurements of an individual made in the same year as the year under investigation. The methods of measuring and the exact measurements taken are described in more detail in Roulin (1999). Colour traits are heritable, both spot diameter ($h^2 = 0.82$; Roulin et al. 2010) and pheomelanin coloration ($h^2 = 0.81$; Roulin &

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