Brownish, small and lousy barn swallows have greater natal dispersal propensity

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Natal dispersal contributes to population dynamics and genetic structure. Individuals differ in whether or not they disperse and in the distance they travel from their natal site before settling to breed. Differences in natal dispersal are often associated with variation in other traits. These associations may arise because suites of morphological and behavioural traits are ultimately controlled by the same set of genes. The genes that control melanogenesis in vertebrates pleiotropically influence physiology and behaviour, including boldness and exploration. Because these personality traits predict dispersal, we tested the hypothesis that in the barn swallow, Hirundo rustica, melanic coloration predicts natal dispersal, using a solid matched case–control sampling design and a large sample. We found that males but not females with colour traits that reflect relatively more pheomelanic feather pigmentation were more likely to disperse, consistently with observations on the only other species for which dispersal in relation to plumage melanic coloration has so far been studied. To control for any confounding effects, we also analysed the association of dispersal with morphological traits and parasite infestation. Philopatric individuals were larger than dispersers, whereas dispersal strategy did not differ according to tail length, which is a sexually selected trait. Finally, philopatric females had a smaller infestation of a haematophagous louse fly. The present findings corroborate previous evidence that melanic coloration covaries with a suite of traits. In particular, they show that melanin-based plumage coloration predicts natal dispersal, independently of other factors also influencing dispersal. In addition, our results show that philopatric individuals were larger than dispersers possibly because individuals return to a benign natal place or because large body size confers an advantage in competitive interactions. Finally, they are compatible with the idea of host adaptation to local strains of a parasite with presumably small population size and low dispersing capacity.

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Dispersing from the natal area to settle and breed in a different place is a prevailing life history strategy in vagile organisms, with major consequences for population dynamics and genetic structure (Clobert, Danchin, Dhondt, & Nichols, 2001; Greenwood, 1980; Greenwood & Harvey, 1982). Natal dispersal can serve diverse, nonalternative functions such as inbreeding avoidance or increasing the personal and indirect components of inclusive fitness by reducing competition among kin for limiting resources (Bowler & Benton, 2005; Dieckmann, O'Hara, & Weisser, 1999; Hamilton & May, 1977; Johnson & Gaines, 1990). However, dispersal entails costs in terms of time and energy, as well as increased risks and missed opportunities, as is the case when dispersers are more likely to incur predation or to lose the advantage of being adapted to local conditions (Bonte et al., 2012; but see Altwegg, Ringsby, & Sæther, 2000; Arcese, 1989). Variation in natal dispersal is often associated with differences in fitness traits (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009), but disentangling the direction of any causal effect between dispersal and realized fitness has proven difficult.

Owing to its association with life history traits and the costs it entails, natal dispersal is believed to be directly targeted by intense natural selection. Empirical and theoretical studies suggest that variation in natal dispersal may be maintained by differences between individuals in the payoff of any specific dispersal strategy according to habitat quality and density of competitors, individual phenotype and sex (Altwegg et al., 2000; Barbraud, Johnson, & Bertault, 2003; Bowler & Benton, 2005; Greenwood, 1980; Massot, Clobert, Lorenzon, & Rossi, 2002; Nicolaus et al., 2012; Perrin & Mazalov, 1999). The extent of genetic variation in natal

dispersal remains to be elucidated: environmental and early epigenetic effects appear to have been considered as predominating over genetic components (Clobert et al., 2001; Ims & Hjermann, 2001; Tschirren, Fitze, & Richner, 2007), but evidence is accumulating for heritability in dispersal distances (Clobert, 2000; Hansson, Bensch, & Hasselquist, 2003; Pasinelli, Schiegg, & Walters, 2004). In addition, variation in dispersal may be contributed by natural selection on linked traits that are relevant in other functional contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). For example, it has been suggested that behavioural syndromes such as boldness and being explorative, which may be important in sociosexual or resource-finding contexts, are positively related to dispersal (Chapman et al., 2011; Fraser, Gilliam, Daley, Le, & Skalski, 2001; Jokela, Elovainio, Kivimaki, & Keltikangas-Jarvinen, 2008).

In turn, boldness and exploration behaviour have been found to be associated with melanin-based coloration (Mafli, Wakamatsu, & Roulin, 2011; Mateos-Gonzalez & Senar, 2012), thus adding to the large body of evidence for an association between melanin-based coloration and suites of functionally diverse behavioural and physiological traits (Ducrest, Keller, & Roulin, 2008; Roulin & Ducrest, 2011). The relationship between coloration and behaviour may have evolved to serve a signalling function (Andersson, 1994) or simply be a coincidental outcome of physiological constraints. Independently of any signalling function, however, the association of boldness/exploration with dispersal on the one hand and with coloration on the other leads us to expect an association between dispersal and coloration. Extensive within-population variation in melanin-based coloration that is commonly observed in birds and other vertebrates (Cramp, 1998; Hill & McGraw, 2006; Majerus, 1998) may thus partly reflect underlying variation in dispersal. Despite such premises, to the best of our knowledge the covariation between plumage coloration and dispersal has only been investigated in a single species, the barn owl, *Tyto alba*, in which individuals with darker, more pheomelanic plumage disperse over larger distances than less pheomelanic ones (van den Brink, Dreiss, & Roulin, 2012; Roulin, 2013).

In this study, we mainly focused on the covariation between observed natal dispersal decisions, that is, whether individuals were philopatric and were recruited as 1-year-old breeders in their natal colony or dispersed and settled as breeders in a different colony (hereafter 'dispersal'), and melanin-based coloration of adult barn swallows, *Hirundo rustica*. Barn swallows show extensive variation in white-to-brownish ventral plumage coloration both in Palaearctic and in Nearctic populations (McGraw, Safran, & Wakamatsu, 2005; Safran, Neuman, McGraw, & Lovette, 2005; Saino, Romano, Rubolini, Teplitsky, et al., 2013; Vortman, Lotem, Dor, Lovette, & Safran, 2011). Darker individuals have larger concentrations of both pheomelanin and eumelanin in their belly feathers, and the darkness and saturation of belly colour increase with the concentration of pheomelanin relative to eumelanin (Saino, Romano, Rubolini, Teplitsky, et al., 2013). Hence, the coloration of the belly feathers reflects production of pheomelanin relative to eumelanin, which have partly common biosynthetic pathways (Hearing, 1998; Prota, 1992). In the present study we assumed that previous observations on pheo-/eumelanic determinism of coloration from the same population we studied here (Saino, Romano, Rubolini, Teplitsky, et al., 2013) hold also for the present sample of individuals. In addition, in this study we also assumed that observed dispersal at least partly reflects genetically based, underlying dispersal propensity. This assumption is warranted in particular in species such as the barn swallow for which weak or no constraints to natal dispersal (e.g. vagility, limitation of nesting places within dispersal range, social interactions including multipurpose territoriality) seem to operate (see Cramp, 1998; Møller, 1994; Turner, 2006).

Based on previous observations on the association between melanization and natal dispersal in the barn owl (van den Brink et al., 2012), we expected individuals that exhibit more pheomelanic relative to eumelanic coloration to show larger odds of dispersing. To test for a difference in coloration between individuals with different natal dispersal, while controlling for several potentially confounding effects, we adopted a solid sampling design in which we compared any 1-year-old philopatric individual with a dispersing individual of the same sex that immigrated in the same colony and year and was captured on the same date as the philopatric individual. In this way, we could control for both habitat quality at the settling site and temporal effects.

Any association between dispersal and melanin-based coloration, however, may be partly confounded by causal links between other traits and dispersal. Indeed, natal dispersal decisions are believed to depend on a constellation of extrinsic as well as phenotype-dependent factors which may also covary with melanization. In particular, we investigated the concomitant association of dispersal with morphological traits, including the expression of secondary sexual traits particularly in males (Balbontín et al., 2009; Belthoff & Dufty, 1998; Bonte & de la Peña, 2009; Clobert et al., 2009), as well as with the intensity of ectoparasite infestation (Gandon, 2002; Gandon, Capowiez, Dubois, Michalakis, & Olivieri, 1996).

The morphology of the locomotory apparatus may affect dispersal ability (Dawideit, Phillimore, Laube, Leisler, & Böhning-Gaese, 2009; de la Hera, Perez-Tris, & Telleria, 2012; Major, 2012; Roulin, 2006), although any such effect is more likely to occur in species in which dispersal distances are large relative to inherent vagility. In the barn swallow, however, migration distances are considerably larger, by three to four orders of magnitude, than dispersal distances (Turner, 2006). In fact, wing length or other nonsexually selected plumage traits were not found to predict dispersal (Scandolara et al., in press). Length of the outermost tail feathers of males is a sexually selected trait in our study population (Møller, 1994; Møller, Saino, Taramino, Galeotti, & Ferrario, 1998; Saino, Primmer, Ellegren, & Møller, 1997). According to the mate competition hypothesis (Dobson, 1982; Dobson & Jones, 1985), a positive relationship with philopatry might be expected, because long-tailed males should have an advantage in competition for a mate in our male-biased breeding population (Saino, Romano, Rubolini, Caprioli, et al., 2013). Rearing conditions may affect growth trajectories and thus final body size. We therefore expected offspring to use such beneficial effect of rearing conditions ('silver spoon' effect; Grafen, 1988) to assess habitat quality, being more philopatric when reared under benign conditions. We thus tested for a positive relationship between philopatry and skeletal body size.

Finally, parasites may play a major role in generating variation in dispersal strategies (Brown & Brown, 1992; Gandon, 2002; Gandon et al., 1996). This is the case because spatial structure of populations can influence the extent of reciprocal adaptation of the host and the parasite, affecting the relative costs of dispersing or being philopatric (see e.g. Gandon et al., 1996; Kaltz & Shykoff, 1998; Lively & Dybdhal, 2000; Tschirren et al., 2007). It is often assumed that, because of their shorter generation time and large genetically effective population size, parasites are advantaged over their coevolving hosts and are therefore more likely to be adapted to local host strains than vice versa (Gandon, 2002). Although empirical evidence suggests that this may be the most common scenario, results are mixed and no adaptation or even maladaptation to local hosts has been documented (e.g. Ebert, 1994; Dufva, 1996; Oppliger, Vernet, & Baez, 1999; Parker, 1985; and see Gandon, 2002). The outcome of host–parasite coevolutionary processes in terms of optimal host dispersal strategies is therefore likely to depend on the specific host–parasite system, on spatial and temporal variation in infection (Boulinier, McCoy, & Sorci, 2001), and