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

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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

on current infection of individual hosts. We thus analysed whether dispersal covaried with the intensity of infestation by the haematophagous louse fly, *Ornithomya biloba* (Diptera, Hippoboscidae), and chewing lice, which produce characteristic holes in the vanes of wing and tail feathers (Møller, 1994; Vas, Csörgö, Møller, & Rózsa, 2008). Little is known about the fundamental biology, including dispersal, of these parasites (see Methods) and on coevolution with their hosts. However, louse flies are likely to have both much smaller populations and opportunities for dispersal among host colonies compared with chewing lice (see Methods). Because in host–parasite systems the species with the higher migration (dispersal) rate is believed to evolve faster (Gandon, 2002), we expected that local adaptation, and thus a lower level of host infestation in philopatric hosts, was more likely to emerge from the analysis of louse fly than chewing lice abundance.

METHODS

Study Organism

Barn swallows are small (ca. 20 g), long-distance migratory, aerially insectivorous passerines that most often breed in colonies, seldom solitarily, inside rural buildings such as cowsheds, stables and garages (Ambrosini, Bani, Massimino, Fornasari, & Saino, 2011; Cramp, 1998; Møller, 1994, 2001; Turner, 2006). In northern Italy and southern Switzerland, adults arrive from their wintering range in sub-Saharan Africa in March–June and leave in August–October. The breeding season starts in April and may last until August when the last broods fledge. Socially monogamous pairs may have one to three clutches of two to seven eggs per breeding season. Eggs are incubated by the female for ca. 14 days (Turner, 2006). Hatching asynchrony is small, but non-negligible as it has consequences for nestling body mass rank throughout the nestling period and also in adulthood (Saino, Incagli, & Martinelli, 2001). Offspring fledge 18–20 days after hatching. Published estimates of natal dispersal distance (i.e. the distance between the natal colony and the colony of first reproduction, normally at age 1 year) are in the order of 5 km for males and 10 km for females (Turner, 2006). However, natal dispersal distances vary between geographical populations, probably according to availability of suitable breeding sites and also topography (Balbontín et al., 2009). Moreover, estimates of natal dispersal distance are likely to be heavily affected by sampling design. In the same study area in Switzerland in which part of this study was carried out, mean natal dispersal distance has been shown to be as small as 1.8 km for males and 3.3 km for females (Scandolara et al., in press). Overall, local recruitment is relatively rare, with 5% or fewer of the fledglings being recruited locally (Saino et al., 2012). The local recruitment datum, however, incorporates the effect of both mortality and dispersal. Dispersal is much more pronounced in females, as suggested by the five to eight times larger local recruitment rate of males, given an even sex ratio at fledging and similar mortality rates between the sexes. Breeding philopatry is high: fewer than 0.5% of adults breed on different farms in consecutive years, implying that no analysis of breeding dispersal in relation to coloration can be performed in our study population (Møller, 1994; Saino et al., 2012; see van den Brink et al., 2012).

In the same Swiss population in which the present study was partly carried out, natal dispersal of males was positively predicted by their position in the brood size hierarchy, while dispersal of both sexes was less likely to occur from large colonies located on farms with a large number of livestock (Scandolara et al., in press).

Overall, barn swallows have limited sexual dichromatism (Cramp, 1998). However, belly feathers of males tend to be darker than those of females (our unpublished data) and sex differences exist in the concentration of both eumelanin and pheomelanin in the belly feathers (Saino, Romano, Rubolini, Teplitsky, et al., 2013).

Study Areas and Field Procedures

We studied barn swallows in an area covering ca. 240 km² in northern Italy, east of Milan, during 1997–2010 and in an area in southern Switzerland, west of Bellinzona, in 2009–2012 (ca. 40 km²). Barn swallow colonies were always located in rural buildings within farms scattered in intensively cultivated farmland. The distance between individual study farms and the nearest-neighbouring farm potentially hosting swallows was 0.3–1.0 km. The prevailing crops were maize, permanent pastures and hayfields in both study areas.

Every study year we did repeat capture sessions (April–June) of the adults (i.e. ≥1-year-old individuals) by placing mist nets before dawn at all the exits of the buildings in which barn swallows nest and normally spend the night during the breeding period. In this way we could capture the large majority of the members of individual colonies, as shown by observations with binoculars of individually marked (with colour rings and belly feather markings) birds and by the proportion of individuals that, at the last capture session of the season, were found not to have been previously captured during the same breeding season (see Saino et al., 2012). Because of high efficiency in capturing all the individuals in a colony and of high breeding philopatry, we could assume that all the adults that, in any given breeding season, were found not to have been captured in the previous breeding seasons were 1-year-old immigrants (i.e. individuals dispersing from their original colony and immigrating into our study colonies; hereafter 'dispersers'). This is the case because those individuals that had not been captured previously were very unlikely to be locally breeding birds that had escaped capture in the previous breeding season and had dispersed, given the high breeding philopatry in our study populations (see above).

Local recruits (i.e. the philopatric individuals that were recruited as breeding adults in the colony in which they hatched) could be identified based on extensive ringing of nestlings on our study farms. Although it is possible that some local recruits went undetected because in some years we did not ring all the offspring on a farm, this is very unlikely to have confounded our analyses because local recruitment is very low (see above). In addition, in our analyses only one dispersing individual was matched to any given local recruit (see also below), so that the chances of including in the analyses a local recruit that was misclassified as an immigrant were reduced with respect to a design in which all the putative immigrants were included. Moreover, any inadvertent misclassification of a local recruit as an immigrant should have resulted in conservative results with respect to any phenotypic difference between immigrants and local recruits. We therefore regard this potential effect as negligible and, in any case, as a source of random noise rather than bias.

For the purposes of this study, among the morphological variables we measured upon first capture of adults, we considered the length of both of the outermost tail feathers (averaged for statistical analysis and expressed in mm), which is a sexually selected trait (Møller, 1994), the length of the innermost tail feather, the length of the right wing chord and keel length (expressed in mm × 100), which is as a proxy of body size. In Italy only, one feather was plucked from the white-brownish ventral plumage region for analysis of belly coloration by spectrophotometry (see below). Upon first capture, we also recorded the number of ectoparasitic louse flies that could be detected by carefully inspecting the plumage during ringing and measurement procedures (see also Saino, Calza, & Møller, 1998). As a proxy for the intensity of infestation by chewing lice we recorded the number of characteristic holes that amblyceran and ischnoceran lice make on tail (rectrices) and wing (remiges) feathers (see Vas et al., 2008).

Little is known about the dispersal ecology and biology of these ectoparasites. Louse flies may enter a pupal diapause after

barn swallows leave the colonies in summer and adult parasites may emerge from puparia when swallows return from migration (Kennedy, Smith, & Smyth, 1975). Indeed, no louse flies were found on a sample of more than 100 swallows captured during spring migration in southern Italy (our personal observation) and more than 300 individuals captured in the Nigerian winter quarters of the same barn swallow population we studied here (Saino, Romano, Caprioli, et al., 2013), indicating that infestation occurs during spring. Mean intensity of infestation is in the order of a few parasites per adult host (range 0−5; present study). Including adult louse flies that are found in active nests, the average number of flies in a swallow colony per adult host is around three (S. Calza & N. Saino, unpublished data). Hence, counts of louse flies per host colony presumably range between a few and a few hundreds (see Ambrosini et al., 2012; Saino, Romano, Rubolini, Caprioli, et al., 2013 for colony sizes). Because louse flies are not found on barn swallows outside the breeding season, and breeding adults do not switch between different colonies during the same (or consecutive) breeding seasons, louse fly dispersal among swallow colonies may be rare and dependent on infested fledglings visiting other breeding colonies before leaving for autumn migration.

Chewing lice are probably much more numerous than louse flies and infest the host throughout the year, as indicated by observation of damage (holes) on newly grown feathers during moult in Africa, by direct observation of the parasites on the host's body, and by the increase in the extent of feather damage during the breeding season (Vas et al., 2008).

For each local recruit (i.e. a 1-year-old individual breeding in the same colony as it hatched) we a posteriori identified one dispersing individual (i.e. an individual that dispersed from its original colony and immigrated into one of our study colonies) for comparison. The disperser that was matched to any given recruit was a 1-year-old individual of the same sex that was captured on the same farm and on the same day as the focal local recruit. When more than one disperser fulfilled these criteria, the choice was randomized. Overall, the individuals included in the study were recruited in 25 colonies, each studied over 1−7 years. The number of recruits per farm ranged between 1 and 57.

The morphological and parasitological variables of both members of each local recruit−disperser pair of matched individuals were measured by the same observer (N.S. in Italy; C.S. in Switzerland). The morphological measurements we used in this study are known to have very high within-observer repeatability (e.g. Møller 1994; Saino, Romano, Rubolini, Teplitsky, et al., 2013).

Ethical Note

The study was carried out under ringing permit 0665 released by the Istituto Nazionale per la Fauna Selvatica, which issues all the relevant permissions required for this kind of work in Italy, and under the auspices of the 'Programma di cooperazione trans-frontaliera Italia-Svizzera 2007−2013 − Indagine naturalistica e variabilità ambientale' (INTERREG project ID 15 7624065 − Misura 1.2). No approval from an ethics committee is currently required for this kind of study according to the existing legislation.

Spectrophotometric Colour Measurements

We measured reflectance of one plucked belly feather using an Avantes DH-2000 spectrometer, equipped with a combined deuterium−tungsten halogen light source, in a dark chamber (see Saino, Romano, Rubolini, Teplitsky, et al., 2013). Feather reflectance was always measured in duplicate and referred to white and black

standards. The illuminated area was ca. 2.5 mm^2 and was centred 2.5 mm from the distal end of the feather, in a white to brownish region depending on the individual. Quantification of colour from the reflectance spectra was performed using the tetrachromatic colour space model by means of the TetraColorSpace program version 1a (Stoddard & Prum, 2008). This approach was preferred over alternative methods because it allows incorporation of information on both plumage reflectance and bird cone sensitivity to obtain biologically realistic colour metrics (see Antonov et al., 2010; Saino, Romano, Rubolini, Teplitsky, et al., 2013; Stoddard & Prum, 2008). In the analyses we assumed a UVS cone type retina and used spectral sensitivity of the blue tit, *Cyanistes caeruleus*, because the blue tit is the species most closely phylogenetically related to the barn swallow for which information on cone spectral sensitivity is implemented by TetraColorSpace. Idealized stimulation of the four cones of passerine birds were normalized to a sum of 1, so that tetrahedral coloration was described by a vector of {uv, s, m, l} values which represents stimulation of the cones sensitive to ultraviolet, short wavelengths, medium wavelengths and long wavelengths, respectively. Tetrahedral colour space vectors were then transformed into the spherical coordinates θ, φ and r (see Antonov et al., 2010; Stoddard & Prum, 2008). θ and φ roughly represent the red−green−blue (θ) and the ultraviolet (φ) components of hue, while r reflects colour saturation (or chroma). For barn swallow belly feathers, increasing θ values indicate paler, whitish coloration and a lower concentration of melanins, while decreasing θ indicates darker, brownish coloration and a higher concentration of melanins. Because the tetrahedral colour space is not a sphere, different hues vary in maximum potential chroma (r_{max}). In the analyses we therefore used 'achieved chroma', computed as $rA = r/r_{max}$.

Because the θ, φ and rA colour components are correlated, besides running the analyses on each colour component separately, we also ran a principal components analysis (PCA) to summarize the colour information, and used the individual scores on the first principal component that was extracted by the PCA.

Repeatability (Lessells & Boag, 1987) of the coloration variables estimated by measuring the same feather twice and measuring two feathers from the same individual exceeded 0.73 in all cases (Saino, Romano, Rubolini, Teplitsky, et al., 2013).

Statistical Analyses

The data set consisted of pairs of individuals: one local recruit and one disperser. Phenotypic variables were used as predictors of dispersal behaviour. Dispersal was coded as a dichotomous variable: local recruitment (code 0) and dispersal (code 1). The data were thus amenable to conditional logistic regression analysis (Breslow & Day, 1980; Hosmer & Lemeshow, 1989), where we modelled the odds of dispersal with pairs of matched individuals ('stratum') to account for the paired nature of the data. Conditional logistic regression models are equivalent to logistic regression models with a constant response, where the model contains no intercept and each predictor is expressed as the difference between the value of the case and the control for each case−control pair (Breslow & Day, 1980; Hosmer & Lemeshow, 1989). Positive values of the coefficients associated with the phenotypic predictors of dispersal indicate that the odds of leaving the original colony increased with the phenotypic values of the focal variable. Whenever possible, exact conditional inference was based on generating conditional distributions of the parameters of interest (see Allison, 2010). When this was not feasible because of computational constraints, we relied on maximum likelihood estimation. The fact that no exact test could be performed in these cases is unlikely to have altered the results, as the univariate analyses (see Table 1) gave consistent results with either estimation method, meaning that all

the significant effects remained such whichever method we used (see Allison, 2010).

In exploratory analyses, we tested for a differential effect of morphological and parasitological variables (colour was measured only in Italy) on the odds of dispersal in either study area in conditional logistic regression models including the effect of the interaction between population and the focal variable of interest. In both sexes, the interaction effect was nonsignificant for all morphological and parasitological predictors of dispersal ($\chi^2_1 < 2.19$, $P > 0.138$), implying that any relationship between dispersal and phenotypic traits did not differ between the Italian and the Swiss study populations. We therefore pooled the data from the two populations in all subsequent analyses. Further details on model selection are reported in the Results section.

When univariate conditional logistic regressions on either sex disclosed significant effects on dispersal, we also subjected colour variables to PCA to try to reduce the dimensionality of the data. The decision on the number of principal components to be considered was based on the Kaiser–Guttman criterion (i.e. interpreting only the PCs with an eigenvalue larger than the mean eigenvalue for all PCs) and confirmed on the basis of the broken-stick criterion (see Borcard, Gillet, & Legendre, 2011).

Because multiple tests were run on the same sets of individuals, the risk of wrongly rejecting null hypotheses was inflated. 'Traditional' Bonferroni-like methods of correction for multiple tests may be too conservative, leading to considerable loss of statistical power. We thus relied on a less conservative false discovery rate (FDR) approach (see Pike, 2011) while adopting the two-stage sharpened algorithm for controlling FDRs (see Pike, 2011). Because the sets of individuals (males or females) for which information on morphology and parasitism was available were considerably larger than the sets for which information on colour was available, the FDR procedure was applied to either set of individuals of each sex separately. The significance threshold for FDR-corrected P values was set at 0.05.

All analyses were performed using SAS 9.2 (SAS Institute Inc., Cary, NC, U.S.A.) and SPSS13 (SPSS Inc., Upper Saddle River, NJ, U.S.A.).

RESULTS

We had information on the phenotype of 118–156 (depending on the trait) male and 20–28 female local recruits and their dispersing counterparts from the two study areas combined (see Table 1 for variable- and population-specific sample sizes).

Dispersal and Plumage Colour

Conditional logistic regression analyses of dispersal revealed partly different patterns of association with phenotypic traits in the two sexes. Melanin-based belly colour saturation significantly and positively predicted dispersal of males but not of females (Table 1, Fig. 1). In fact, for females the relationship was negative, although far from statistical significance. The relationship between dispersal and saturation did not differ significantly between the sexes (sex*saturation effect: $\chi^2_1 = 3.00$, $P = 0.083$). The lack of a sex*saturation effect on the odds of dispersal was due to the extremely large error associated with the coefficient for females (Table 1). However, the relationships between dispersal and colour saturation for the two sexes were opposite in sign and the strength of the association differed markedly between the sexes. There were no significant associations between dispersal of either sex and the θ or ϕ belly feather colour components (Table 1, Fig. 1). Because in males the three colour components were strongly correlated (correlation coefficient between θ and $\phi = -0.64$; θ and $rA = -0.47$; ϕ and $rA = 0.208$; $N = 236$, $P < 0.002$ in all cases) we also ran a PCA on colour components (see Statistical Analyses). Based on the Kaiser–Guttman and 'broken-stick' criterion only the first principal component (PC1), which accounted for 64% of the variance in colour variables, was considered. PC1 was most strongly correlated with θ (loading $= -0.91$) and was also correlated with ϕ and rA (loadings $= 0.80$ and 0.66, respectively). Thus, increasing PC1 scores were associated with increasing pheomelanic darkness and saturation. Conditional regression analysis showed a significant effect of PC1 scores on the odds of dispersing (score statistic $= 5.32$, $P = 0.021$, coefficient $= 0.349 \pm 0.155$). The positive sign of the coefficient implies that the odds of dispersing increased with relative pheomelanization and colour saturation.

Dispersal and Morphological Traits

The odds of being recruited into the natal colony rather than being a disperser were positively predicted by body size in both sexes (Table 1, Fig. 2). A conditional logistic regression model including the interaction between keel length and sex showed that the slope of the association of dispersal with body size differed significantly between the two sexes ($\chi^2_1 = 4.40$, $P = 0.036$): the change in the odds of dispersal per unit change in body mass was larger among females than among males. No significant association between dispersal and tail length was observed in either sex (Table 1).

Dispersal and Ectoparasite Load

The odds of dispersal of males were negatively predicted by the intensity of infestation by chewing lice, implying that local recruits harboured more chewing lice than dispersing individuals, whereas dispersal of males was not predicted by infestation by louse flies (Table 1, Fig. 3). Conversely, dispersal of females was positively predicted by louse fly infestation (i.e. local recruits harboured fewer flies) but was not predicted by chewing lice infestation (Table 1, Fig. 3). Conditional exact tests provided statistically significant

Table 1
Univariate conditional logistic regression models of dispersal in relation to phenotype and parasitism

Predictor	Males				Females			
	N (IT, CH)	Score	Exact P	Coefficient (SE)	N (IT, CH)	Score	Exact P	Coefficient (SE)
θ colour component	236	1.79	0.182	−3.84 (2.897)	40	1.18	0.286	5.559 (5.235)
ϕ colour component	236	2.52	0.113	2.645 (1.693)	40	0.00	0.999	0.003 (3.266)
Colour saturation (rA)	236	8.16	**0.004**	6.315 (2.279)	40	0.86	0.371	−6.199 (6.856)
Tail length	312 (236, 76)	2.82	0.094	0.032 (0.019)	56 (40, 16)	0.730	0.409	−0.047 (0.055)
Keel length	300 (236, 64)	8.64	**0.003**	−0.005 (0.002)	52 (38, 14)	12.43	**<0.001**	−0.036 (0.015)
Chewing lice infestation	300 (236, 64)	6.94	**0.008**	−0.020 (0.008)	54 (40, 14)	0.10	0.773	−0.004 (0.014)
Louse fly infestation	300 (236, 64)	0.33	0.620	−0.082 (0.144)	54 (40, 14)	4.47	**0.019**	1.428 (0.719)

The odds of dispersing (versus being recruited in the colony of origin) are modelled. The column 'N (IT, CH)' shows the total sample size and the sample size for the Italian (IT) and the Swiss (CH) populations. Colour was measured only in Italy. Probability values from exact score tests are presented. Bold values were significant also after controlling for the increase in the risk of wrongly rejecting a null hypothesis by the false discovery rates procedure.
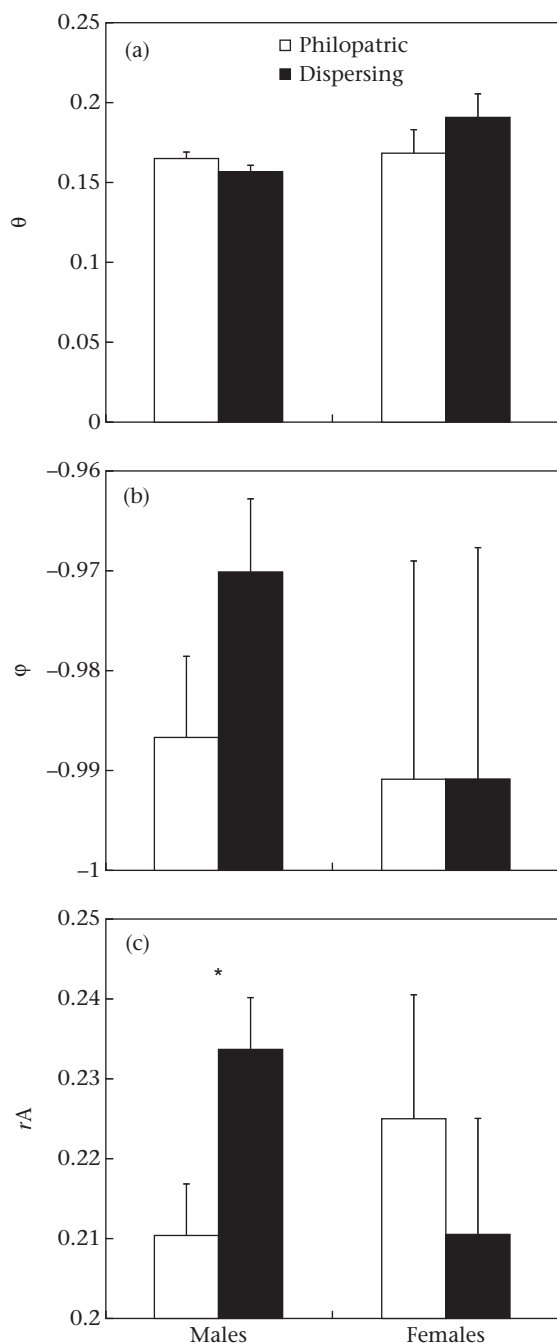
Figure 1. Mean + SE tetrahedral colour component values of philopatric and dispersing male and female barn swallows. (a) The red–green–blue (θ) and (b) the ultraviolet (φ) components of hue, and (c) colour saturation (rA; see also Spectrophotometric Colour Measurements in the Methods). Small θ and large φ or rA values indicate increasing pheomelanin relative to eumelanin concentrations. Sample sizes are reported in Table 1. An asterisk indicates that the odds of dispersing were significantly associated with the focal variable.

evidence for a differential effect of louse fly (score statistic = 5.68, $P = 0.017$) but not of chewing lice infestation on dispersal of the two sexes (score statistic = 1.07, $P = 0.308$).

Dispersal in Relation to Multiple Phenotypic Traits

The main aim of this study was to test for a covariation of dispersal and colour while controlling for potentially confounding phenotypic and parasitological variables. Some phenotypic variables were reciprocally correlated (e.g. colour variables) and we had no a priori expectations on interaction effects among the phenotypic variables on dispersal. To avoid multicollinearity and model overparametrization problems particularly for females, which had the smaller sample size, we refrained from applying complex multivariate models that included all phenotypic variables with their interactions as predictors of dispersal. We instead applied conditional logistic regressions that included only the variables that significantly predicted dispersal in univariate models on either sex (see Table 1).

There were no significant two-way interaction effects between colour saturation, body size and chewing lice infestation on dispersal of males ($\chi^2_1 < 0.70$, $P > 0.40$). A simplified model excluding any interaction effect confirmed the positive effect of colour saturation ($\chi^2_1 = 10.04, P = 0.002$) and the negative effect of keel length ($\chi^2_1 = 9.40$, $P = 0.002$) and chewing lice infestation ($\chi^2_1 = 9.11, P = 0.003$) on dispersal of males.

Among females, dispersal was not predicted by the interaction between keel length and louse fly infestation ($\chi^2_1 = 0.11$, $P > 0.741$). A simplified model including only the main effects confirmed that the odds of dispersing declined significantly with body size ($\chi^2_1 = 4.64, P = 0.031$), while a marginally nonsignificant positive association between dispersal and louse fly infestation existed ($\chi^2_1 = 3.34$, $P = 0.067$), suggesting consistency with the results of univariate analyses.

DISCUSSION

We analysed natal dispersal in barn swallows and found that philopatric individuals differed from dispersers in a number of phenotypic traits, including melanic plumage coloration, body size and parasite load. The associations between these traits and dispersal were independent of the concomitant association with other traits, but were dependent on sex. In the analyses, by matching philopatric and dispersing individuals for sex, year, date and colony we effectively controlled for a number of potentially confounding temporal and local effects.

Dispersal and Plumage Colour

The association between colour and natal dispersal was the main focus of our study because a theoretical background exists to interpret any covariation between melanic coloration and dispersal (Ducrest et al., 2008; Roulin & Ducrest, 2011), but little empirical information on this association exists. Indeed, we are aware of only one species for which natal dispersal has been analysed in relation to plumage melanization: in the barn owl, darker reddish, more pheomelanic individuals moved further from their natal site than paler, less pheomelanic ones (van den Brink et al., 2012; Roulin, 2013). In male barn swallows, the pattern of natal dispersal was consistent with that observed in the barn owl, as individuals with darker, more saturated colour were more likely to disperse. Darker reddish, more saturated belly feather colour is associated with increasing ratios of pheomelanin to eumelanin (Saino, Romano, Rubolini, Teplitsky, et al., 2013). This implies that individuals with more pheomelanic relative to eumelanic coloration were more likely to disperse. Our findings suggest that variation in dispersal is consistently associated with melanism in phylogenetically distant species with broadly different life histories. In the barn owl, pheomelanization rather than eumelanization predicted dispersal, suggesting that the association between dispersal and coloration in the barn swallow might be ultimately driven by pheomelanization per se, rather than by relative investment in pheomelanization compared to eumelanization.
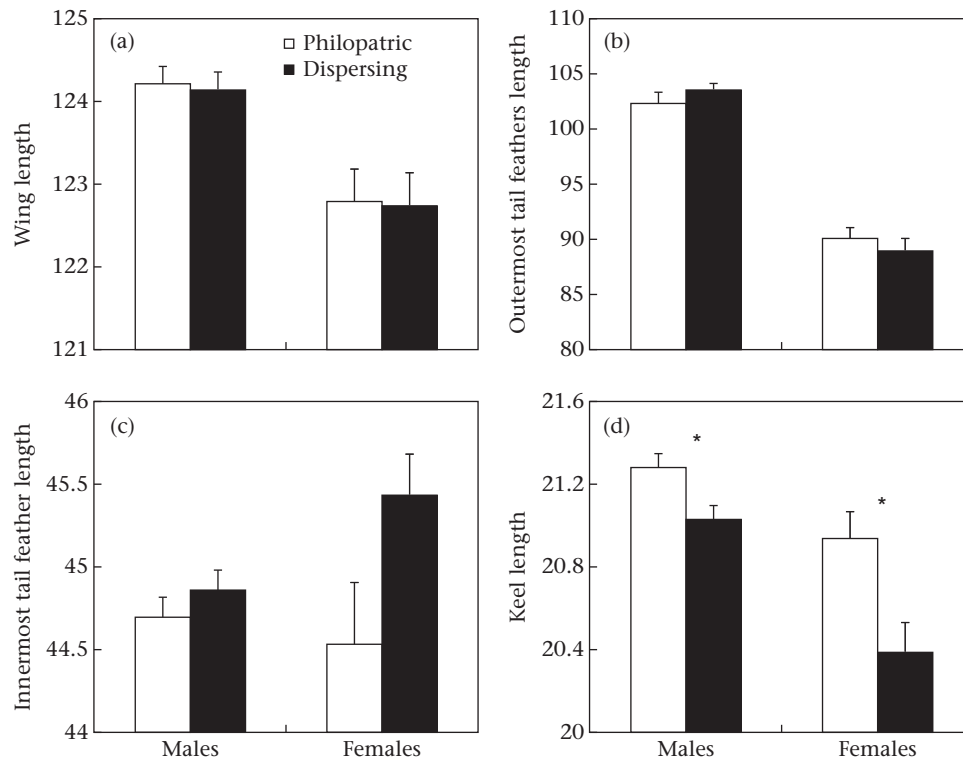
Figure 2. Mean + SE morphological trait values (in mm) of philopatric and dispersing male and female barn swallows. (a) Wing length, (b) outermost tail feather length, (c) innermost tail feather length and (d) keel length. Sample sizes are reported in Table 1. An asterisk indicates that the odds of dispersing were significantly associated with the focal variable.

In the present study, the slopes of the relationships between dispersal and coloration did not differ between the sexes, although they were opposite in sign. This was mainly due to the large error associated with the parameter estimate for females. However, the relationship was considerably stronger, being highly significant, in males than in females, for which it was far from statistical significance. This difference may suggest a role of sexual selection in the evolution of this relationship. In the present sample of males, infestation by chewing lice was larger among relatively less pheomelanic individuals (Spearman's ρ with $\theta = 0.131$ and with $\varphi = -0.167, P < 0.05$ and $N = 236$ in both cases). In addition, darker, presumably relatively more pheomelanic individuals have been shown to have greater success in sperm competition in other barn swallow populations (Vortman et al., 2011), although information on sexual selection from our study population is not yet available. These pieces of evidence combined may suggest that dispersal and coloration are linked traits under sexual selection, with dispersing individuals harbouring fewer parasites and having greater success in sperm competition.

At a proximate level, the association between dispersal and melanization in barn swallow males may be mediated by exploration. Dispersal covaries with boldness and exploration (Budaev, 1997; Dingemanse, Both, Van Noordwijk, Rutten, & Drent, 2003; see van den Brink et al., 2012). Darker, more melanic siskin, *Carduelis spinus*, males have been found to be more active at exploration (Mateos-Gonzalez & Senar, 2012). Hence, dispersal of more pheomelanic male barn swallows may be mediated by their exploration tendencies.

Dispersal behaviour is generally considered to be under strong selection (Clobert et al., 2001). Dispersing individuals may face diverse costs at all stages of the dispersal process (Bonte et al., 2012). On the other hand, philopatry may also entail costs in terms of both local competition with kin for limiting resources and

inbreeding (Bowler & Benton, 2005; Hamilton & May, 1977; Johnson & Gaines, 1990). The mechanisms that maintain variation in dispersal in relation to melanization of male barn swallows are open to speculation. It has been hypothesized that because of antagonistically pleiotropic effects that some of the genes that control melanization have on major life history traits (Ducrest et al., 2008), between-individual variation in melanin-based coloration may reflect underlying variation in life history strategies that are associated with a minor or no net difference in fitness. Philopatric males have been shown to be more viable at least among barn swallows breeding in Spain (Balbontín et al., 2009; but see Saino et al., 2012 for different results based on a small sample). In addition, in our study population, darker, relatively more pheomelanic males (but not females) are less viable (Saino, Romano, Rubolini, Ambrosini, et al., 2013). The present findings are thus consistent with the expectation from previous studies of barn swallows because they show that philopatric individuals have relatively less pheomelanic coloration. Overall, available data from barn swallows thus suggest that philopatric, paler and relatively less pheomelanic males may accrue a viability advantage over dispersing, darker and more pheomelanic males, which may in turn be more successful in sperm competition. This is consistent with the general idea that the evolution of behavioural syndromes can maintain polymorphism in coping strategies (Wolf, Sander van Doorn, Leimar, & Weissing, 2007) and, specifically, that colour variation is associated with variation in life history strategies with similar fitness payoffs.

Several additional functional interpretations can be devised for the difference we observed in dispersal in relation to melanization (see van den Brink et al., 2012). Colour-related susceptibility to the consequences of inbreeding, which has been hypothesized for barn owls, may not be important in causing differential dispersal because close inbreeding is likely to be rare in barn swallows, given large population sizes within the normal natal dispersal range,
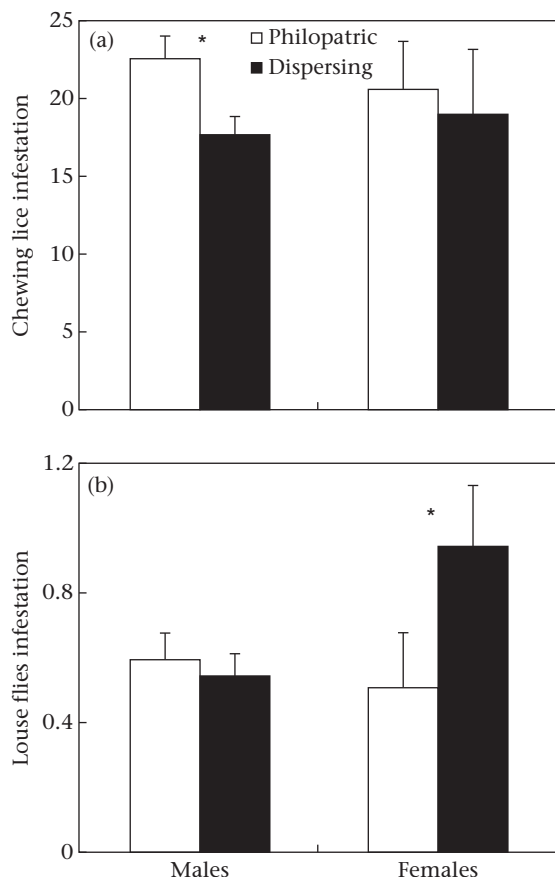
Figure 3. Mean + SE parasite infestation (counts; see Study Areas and Field Procedures in the Methods) of philopatric and dispersing male and female barn swallows. (a) Chewing lice and (b) louse flies. Sample sizes are reported in Table 1. An asterisk indicates that the odds of dispersing were significantly associated with the focal variable.

partial temporal segregation among generations and partial spatial segregation between opposite-sex siblings owing to females being less philopatric and dispersing further. Adaptation of colour variants to local conditions at the colony/natal area level could also be invoked (Dreiss et al., 2012). This idea has not yet been tested formally. However, our study colonies were scattered over a large area and much of the variation in ecological conditions, in terms of nesting or foraging habitat, occurs over much shorter distances than those encompassed by the study area itself (our unpublished data). Hence, the possibility that our study farms were systematically located in habitats that favoured immigration of more pheomelanic individuals seems remote. It has also been suggested that melanization could be at linkage disequilibrium with traits that are functionally related to dispersal by, for example, affecting locomotion. Dispersal distances of barn swallows are three to four orders of magnitude smaller than migration distances and it therefore seems unlikely that ability to disperse is restricted by morphology of, for example, the flight apparatus (see also above).

Dispersal and Morphological Traits

Tail length, which is a sexually selected trait in males from our study population (Saino et al., 1997), did not predict dispersal significantly, lending no support to the competition for mates hypothesis, which posits that less attractive males should disperse to avoid competition for mates (Balbontín et al., 2009; Dobson, 1982;

Dobson & Jones, 1985). Yet, there was a strong, negative effect of body size on dispersal in both sexes, this effect being significantly larger among females. Dispersal declines with hatching date and significantly so only in females (Scandolara et al., in press). However, in the present sample of philopatric individuals for which hatching date was known, there was no association with keel length (ANOVA controlling for population: effect of hatching date: $F_{1,147} = 1.21$, $P = 0.273$), implying that the association between philopatry and body size was not the spurious result of dispersal depending on seasonal effects that concomitantly affected body size. Yet, large body size may result from favourable rearing conditions, and large offspring may cue onto such conditions or onto their own phenotype to decide not to disperse from a favourable habitat. This effect could be more pronounced among females, which may be more sensitive to habitat quality given their larger reproductive investment.

Dispersal and Ectoparasitism

We also identified differential variation in dispersal according to host sex and parasite species. Males that were more heavily infested by feather lice were less likely to disperse, whereas larger counts of louse flies were recorded among dispersing than philopatric females. Louse flies probably infest their host upon arrival to the breeding colony. Because of extremely high breeding philopatry of the host and of the life cycle of louse flies (see Study Areas and Field Procedures), dispersal of louse flies and thus gene flow among host colonies can be expected to be small. Greater infestation among immigrants may therefore suggest that female hosts are more resistant to parasite strains from their original colony. This is in agreement with our expectation that any local host adaptation was more likely to emerge for louse flies than for chewing lice (Gandon, 2002). Virulence of louse flies to nestlings (Saino et al., 1998) and potentially also to adults may thus be a cost of natal dispersal for female barn swallows.

The dynamics of transmission of feather lice are unknown. Adult hosts harbour the parasite all year round (our personal observation; see also Study Areas and Field Procedures). Because feather holes are normally found also on yearlings during moult in Africa, dispersal and gene flow of this parasite among host colonies must be large, thanks to large host natal dispersal. Hence, the present findings suggest that either philopatric hosts are inherently more susceptible to parasite infestation in the year of hatching (or to reinfestation upon return to the natal colony) or intensity of infestation is itself a determinant of dispersal. The latter could be the case if the parasite has debilitating/aerodynamic effects that hinder prospecting for breeding sites either before or after the first migration to Africa. Alternatively, chewing lice infestation may covary with philopatry as a spurious effect of the association between melanization and both dispersal and parasitism (see above).

In conclusion, we have observed that natal dispersal of barn swallows is related to melanization, as males that allocated relatively more to pheomelanization than eumelanization had greater odds of dispersing. This is consistent with the pattern observed in the only other avian model for which natal dispersal has been analysed in relation to melanization. The association between natal dispersal and melanization corroborates previous evidence from the same or other barn swallow populations for an association of melanization with major life history traits. Extensive variation in plumage melanization within bird populations thus calls for more studies on the covariation with dispersal behaviour. The association between dispersal and colour was independent of any effect of body size, which was found to be larger in philopatric individuals of both sexes, possibly because of fidelity to a natal place with favourable rearing conditions. Finally, the intensity of infestation by

ectoparasites was found to predict natal dispersal. Lower infestation by louse flies in philopatric females, in particular, suggests adaptation to local strains of a parasite with probably little gene flow among hosts' colonies.

Acknowledgments

References

Allison, P. D. (2010). *Survival analysis using SAS: A practical guide* (2nd ed.). Cary, NC: SAS Institute.

Altwegg, R., Ringsby, T. H., & Sæther, B.-H. (2000). Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology, 69*, 762–770.

Ambrosini, R., Bani, L., Massimino, D., Fornasari, L., & Saino, N. (2011). Large scale spatial distribution of breeding barn swallows *Hirundo rustica* in relation to cattle farming. *Bird Study, 58*, 495–505.

Ambrosini, R., Rubolini, D., Trovò, P., Liberini, G., Bandini, M., Romano, A., et al. (2012). Maintenance of livestock farming may buffer population decline of the barn swallow *Hirundo rustica*. *Bird Conservation International, 22*, 411–428.

Andersson, M. A. (1994). *Sexual selection*. Cambridge: Cambridge University Press.

Antonov, A., Stokke, B. G., Vikan, J. R., Fossoy, F., Ranke, P. S., & Røskaft, E. (2010). Egg phenotype differentiation in sympatric cuckoo *Cuculus canorus* gentes. *Journal of Evolutionary Biology, 23*, 1170–1182.

Arcese, P. (1989). Intrasexual competition, mating system and natal dispersal in song sparrows. *Animal Behaviour, 38*, 958–979.

Balbontín, J., Møller, A. P., Hermosell, I. G., Marzal, A., Reviriego, M., & de Lope, F. (2009). Geographic patterns of natal dispersal in barn swallows *Hirundo rustica* from Denmark and Spain. *Behavioral Ecology and Sociobiology, 63*, 1197–1205.

Barbraud, C., Johnson, A. R., & Bertault, G. (2003). Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. *Journal of Animal Ecology, 72*, 246–257.

Belthoff, J. R., & Dufty, A. M. (1998). Corticosterone, body condition and locomotor activity: a model for dispersal in screech-owls. *Animal Behaviour, 55*, 405–415.

Bonte, D., & de la Peña, E. (2009). Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology, 22*, 1242–1251.

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., et al. (2012). Costs of dispersal. *Biological Reviews, 87*, 290–312.

Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology with R*. New York: Springer.

Boulinier, T., McCoy, K. D., & Sorci, G. (2001). Dispersal and parasitism. In J. Clobert, E. Danchin, & A. A. Dhondt (Eds.), *Dispersal* (pp. 169–179). Oxford: Oxford University Press.

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews, 80*, 205–225.

Breslow, N. E., & Day, N. E. (1980). *Statistical methods in cancer research, Vol. I: The analysis of case-control studies*. Lyon: International Agency for Research on Cancer.

van den Brink, V., Dreiss, A. N., & Roulin, A. (2012). Melanin-based coloration predicts natal dispersal in the barn owl, *Tyto alba*. *Animal Behaviour, 84*, 805–812.

Brown, C. R., & Brown, M. B. (1992). Ectoparasitism as a cause of natal dispersal in cliff swallow. *Ecology, 73*, 1718–1723.

Budaev, S. V. (1997). 'Personality' in the guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology, 111*, 399–411.

Chapman, B. B., Hulthen, K., Blomqvist, D. R., Hansson, L. A., Nilsson, J. A., Brodersen, J., et al. (2011). To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters, 14*, 871–876.

Clobert, J. (2000). Processes at the origin of similarities in dispersal behaviour among siblings. *Journal of Evolutionary Biology, 13*, 707–719.

Clobert, J., Danchin, E., Dhondt, A. A., & Nichols, J. D. (2001). *Dispersal*. Oxford: Oxford University Press.

Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters, 12*, 197–209.

Cramp, S. (1998). *The complete birds of the western Palearctic on CD-ROM*. Oxford: Oxford University Press.

Dawideit, B. A., Phillimore, A. B., Laube, I., Leisler, B., & Böhning-Gaese, K. (2009). Ecomorphological predictors of natal dispersal distances in birds. *Journal of Animal Ecology, 78*, 388–395.

Dieckmann, U., O'Hara, B., & Weisser, W. (1999). The evolutionary ecology of dispersal. *Trends in Ecology & Evolution, 14*, 88–90.

Dingemanse, N. J., Both, C., Van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B, 270*, 741–747.

Dobson, F. S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour, 30*, 1183–1192.

Dobson, F. S., & Jones, W. T. (1985). Multiple causes of dispersal. *American Naturalist, 126*, 855–858.

Dreiss, A. N., Antoniazza, S., Butti, R., Fumagalli, L., Sonnay, C., Frey, C., et al. (2012). Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration. *Journal of Evolutionary Biology, 25*, 103–114.

Ducrest, A.-L., Keller, L., & Roulin, A. (2008). Pleiotropy and the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution, 23*, 502–510.

Dufva, R. (1996). Sympatric and allopatric combinations of hen fleas and great tits: a test of local adaptation hypothesis. *Journal of Evolutionary Biology, 9*, 505–510.

Ebert, D. (1994). Virulence and local adaptation of a horizontally transmitted parasite. *Science, 265*, 1084–1086.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist, 158*, 124–135.

Gandon, S. (2002). Local adaptation and the geometry of host-parasite coevolution. *Ecology Letters, 5*, 246–256.

Gandon, S., Capowiez, Y., Dubois, Y., Michalakis, Y., & Olivieri, I. (1996). Local adaptation and gene-for-gene coevolution in a metapopulation model. *Proceedings of the Royal Society B, 263*, 1003–1009.

Grafen, A. (1988). On the uses of data on lifetime reproductive success. In T. H. Clutton-Brock (Ed.), *Reproductive success* (pp. 454–471). Chicago: University of Chicago.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour, 28*, 1140–1162.

Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics, 13*, 1–21.

Hamilton, W. D., & May, R. M. (1977). Dispersal in stable habitats. *Nature, 269*, 578–581.

Hansson, B., Bensch, S., & Hasselquist, D. (2003). Heritability of dispersal in the great reed warbler. *Ecology Letters, 6*, 290–294.

Hearing, V. J. (1998). The regulation of melanin production. In J. J. Nordlund, R. Boissy, V. J. Hearing, R. A. King, & J.-P. Ortonne (Eds.), *The pigmentary system. Physiology and pathophysiology* (pp. 423–438). New York: Oxford University Press.

de la Hera, I., Perez-Tris, J., & Telleria, J. L. (2012). Habitat distribution of migratory and sedentary blackcaps *Sylvia atricapilla* in Southern Iberia: a morphological and biogeochemical approach. *Journal of Avian Biology, 43*, 333–340.

Hill, G. E., & McGraw, K. J. (2006). *Bird coloration: Function and evolution* (Vol. 2). Cambridge, MA: Harvard University Press.

Hosmer, D. W., & Lemeshow, S. (1989). *Applied logistic regression*. New York: J. Wiley.

Ims, R. A., & Hjermann, D.Ø. (2001). Condition-dependent dispersal. In J. Clobert, E. Danchin, A. A. Dhondt, & J. D. Nichols (Eds.), *Dispersal* (pp. 203–216). Oxford: Oxford University Press.

Johnson, M. L., & Gaines, M. S. (1990). Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics, 21*, 449–480.

Jokela, M., Elovainio, M., Kivimaki, M., & Keltikangas-Jarvinen, L. (2008). Temperament and migration patterns in Finland. *Psychological Science, 19*, 831–837.

Kaltz, O., & Shykoff, J. (1998). Local adaptation in host–parasite systems. *Heredity, 81*, 361–370.

Kennedy, J. A., Smith, J. R., & Smyth, M. (1975). Diapause in *Ornithomya biloba* Dufour (Diptera: Hippoboscidae) parasitic on fairy martins in South Australia. *Journal of Parasitology, 3*, 369–372.

Lessells, C. M., & Boag, P. T. (1987). Unrepeatable repeatabilities: a common mistake. *Auk, 104*, 116–121.

Lively, C. M., & Dybdhal, M. F. (2000). Parasite adaptation to locally common host genotypes. *Nature, 405*, 679–681.

Mafli, A., Wakamatsu, K., & Roulin, A. (2011). Melanin-based coloration predicts aggressiveness and boldness in captive eastern Hermann's tortoises. *Animal Behaviour, 81*, 859–863.

Majerus, M. E. N. (1998). *Melanism, evolution in action*. Oxford: Oxford University Press.

Major, R. E. (2012). Latitudinal and insular variation in morphology of a small Australian passerine: consequences for dispersal distance and conservation. *Australian Journal of Zoology, 60*, 210–218.

Massot, M., Clobert, J., Lorenzon, P., & Rossi, J. M. (2002). Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology, 71*, 253–261.

Mateos-Gonzalez, F., & Senar, J. C. (2012). Melanin-based trait predicts individual exploratory behaviour in siskins, *Carduelis spinus*. *Animal Behaviour, 83*, 229–232.

McGraw, K. J., Safran, R. J., & Wakamatsu, K. (2005). How feather colour reflects its melanin content. *Functional Ecology, 19*, 816–821.

Møller, A. P. (1994). *Sexual selection and the barn swallow*. Oxford: Oxford University Press.

Møller, A. P. (2001). The effect of dairy farming on barn swallow *Hirundo rustica* abundance, distribution and reproduction. *Journal of Applied Ecology, 38*, 378–389.

Møller, A. P., Saino, N., Taramino, G., Galeotti, P., & Ferrario, S. (1998). Paternity and multiple signaling: effects of a secondary sexual character and song on paternity in the barn swallow. *American Naturalist, 151*, 236–242.

Nicolaus, M., Michler, S. P. M., Jalvingh, K. M., Ubels, R., van der Velde, M., Komdeur, J., et al. (2012). Social environment affects juvenile dispersal in great tits (*Parus major*). *Journal of Animal Ecology, 81*, 827–837.

Oppliger, A., Vernet, R., & Baez, M. (1999). Parasite local maladaptation in the Canarian lizard *Gallotia galloti* (Reptilia: Lacertidae) parasitized by haemogregarian blood parasite. *Journal of Evolutionary Biology, 12*, 951–955.

Parker, M. A. (1985). Local population differentiation for compatibility in an annual legume and its host-specific pathogen. *Evolution, 39*, 713–723.

Pasinelli, G., Schiegg, K., & Walters, J. R. (2004). Genetic and environmental influences on natal dispersal distance in a resident bird species. *American Naturalist, 164*, 660–669.

Perrin, N., & Mazalov, V. (1999). Dispersal and inbreeding avoidance. *American Naturalist, 154*, 282–292.

Pike, N. (2011). Using false discovery rates for multiple comparisons in ecology and evolution. *Methods in Ecology and Evolution, 2*, 278–282.

Prota, G. (1992). *Melanins and melanogenesis*. New York: Academic Press.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*, 291–318.

Roulin, A. (2006). Linkage disequilibrium between a melanin-based colour polymorphism and tail length in the barn owl. *Biological Journal of the Linnean Society, 88*, 475–488.

Roulin, A. (2013). Ring recoveries of dead birds confirm that darker pheomelanic barn owls disperse longer distances. *Journal of Ornithology, 154*, 871–874.

Roulin, A., & Ducrest, A. L. (2011). Association between melanism, physiology and behaviour: a role for the melanocortin system. *European Journal of Pharmacology, 660*, 226–233.

Safran, R. J., Neuman, C. R., McGraw, K. J., & Lovette, I. J. (2005). Dynamic paternity allocation as a function of plumage color in barn swallows. *Science, 309*, 2210–2212.

Saino, N., Calza, S., & Møller, A. P. (1998). Effects of a dipteran ectoparasite on immune response and growth trade-offs in barn swallows, *Hirundo rustica*, nestlings. *Oikos, 81*, 217–228.

Saino, N., Incagli, M., & Martinelli, R. (2001). Immunity, growth and begging behaviour of nestling barn swallows *Hirundo rustica* in relation to hatching order. *Journal of Avian Biology, 32*, 263–270.

Saino, N., Primmer, C. R., Ellegren, H., & Møller, A. P. (1997). An experimental study of paternity and tail ornamentation in the barn swallow (*Hirundo rustica*). *Evolution, 51*, 562–570.

Saino, N., Romano, M., Ambrosini, R., Rubolini, D., Boncoraglio, G., Caprioli, M., et al. (2012). Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching date and phenotypic quality. *Journal of Animal Ecology, 81*, 1004–1012.

Saino, N., Romano, M., Caprioli, M., Fasola, M., Lardelli, R., Micheloni, P., et al. (2013). Timing of molt of barn swallows is delayed in a rare *Clock* genotype. *PeerJ, 1*, e17.

Saino, N., Romano, M., Rubolini, D., Ambrosini, R., Caprioli, M., Milzani, A., et al. (2013). Viability is associated with melanin-based coloration in the barn swallow (*Hirundo rustica*). *PLoS One, 8*, e60426.

Saino, N., Romano, M., Rubolini, D., Caprioli, M., Ambrosini, R., Boncoraglio, G., et al. (2013). Population and colony-level determinants of tertiary sex ratio in the declining barn swallow. *PLoS One, 8*, e56493.

Saino, N., Romano, M., Rubolini, D., Teplitsky, C., Ambrosini, R., Caprioli, M., et al. (2013). Sexual dimorphism in melanin pigmentation, feather coloration and its heritability in the barn swallow (*Hirundo rustica*). *PLoS One, 6*, e58024.

Scandolara, C., Lardelli, R., Sgarbi, G., Caprioli, M., Ambrosini, R., Rubolini, D., et al. (in press). Context-, phenotype-, and kin-dependent natal dispersal of barn swallows (*Hirundo rustica*). *Behavioral Ecology*.

Stoddard, M. S., & Prum, R. O. (2008). Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *American Naturalist, 171*, 755–776.

Tschirren, B., Fitze, P. S., & Richner, H. (2007). Maternal modulation of natal dispersal in a passerine bird: an adaptive strategy to cope with parasitism? *American Naturalist, 169*, 87–93.

Turner, A. (2006). *The barn swallow*. London: T. & A. D. Poyser.

Vas, Z., Csörgö, T., Møller, A. P., & Rózsa, L. (2008). The feather holes of the barn swallow *Hirundo rustica* and other small passerines are probably caused by *Brueelia* spp. lice. *Journal of Parasitology, 94*, 1438–1440.

Vortman, Y., Lotem, A., Dor, R., Lovette, I. J., & Safran, R. J. (2011). The sexual signals of the East-Mediterranean barn swallow: a different swallow tale. *Behavioral Ecology, 22*, 1344–1352.

Wolf, M., Sander van Doorn, G., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature, 447*, 581–584.