Journal of Animal Ecology

British Ecological Society

*Journal of Animal Ecology* 2009, **78**, 388–395 doi: 10.1111/j.1365-2656.2008.01504.x

# Ecomorphological predictors of natal dispersal distances in birds

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## Summary

**1.** Dispersal is one of the key ecological parameters but it is very difficult to quantify directly. As a consequence, empirical studies often ignore dispersal or use indirect measures.
**2.** Ringing data have previously been used to estimate the natal dispersal distances of 47 British passerine bird species. This provides an excellent opportunity to examine the potential of various indirect measures to predict natal dispersal distances in British birds.
**3.** We use a phylogenetic comparative framework and single- and multipredictor models including ecomorphological, behavioural or ecological traits to predict natal dispersal distance.
**4.** A multipredictor model that includes Kipp's distance (a measure of wing tip length), bill depth and tail graduation explains 45% of the interspecific variation in natal dispersal distance. These morphological characters all relate to aerodynamics with stronger flyers dispersing further.
**5.** However, an index of migration is a strong (but less informative) correlate of dispersal distance and Kipp's distance and bill depth are strong correlates of migration. Thus, we cannot disentangle whether these ecomorphological traits influence dispersal distance directly or whether the relationship between ecomorphology and dispersal is mediated through migratory behaviour.
**6.** Notwithstanding uncertainties regarding the causal links between dispersal distance and wing morphology, we suggest that two ecomorphological traits, Kipp's distance and bill depth, may provide a useful surrogate.

**Key-words:** bill morphology, flight, Kipp's distance, phylogenetic comparative

## Introduction

Dispersal of individuals after birth but before breeding (natal dispersal) or of individuals between breeding attempts (breeding dispersal) is among the most important parameters in ecology and evolution (Clobert *et al.* 2001; Nathan 2001). For instance, dispersal is fundamental to our understanding of the structure and dynamics of metapopulations (Gilpin & Hanski 1991; Hanski 1998), range shifts and expansions (Lester *et al.* 2007), neutral genetic divergence (Wright 1943), local adaptation (Slatkin 1987) and speciation (Gavrilets 2004; Price 2008). Moreover, dispersal should be one of the most important parameters in models used to predict species' responses to climate change, in terms of both a species' ability to track optimal conditions and its ability to adapt *in situ* (Davis & Shaw 2001; Davis, Shaw & Etterson 2005; Brooker *et al.* 2007).

Unfortunately, dispersal is an extremely challenging parameter to quantify directly (Turchin 1998). One possible approach is to track individual organisms using radiotelemetry or satellite tracking (e.g. Martin *et al.* 2008). However, this has only been carried out for a very limited number of larger animals. A second approach is mark–recapture studies of animals, but these studies are typically conducted on a relatively small spatial scale, with the consequence that the tail of the dispersal kernel will not be quantified appropriately (van Noordwijk 1984). A study by Paradis *et al.* (1998) on British ringing data over the period 1909 to 1994 is unusual in that it was conducted on a much larger spatial scale than is the norm and yielded estimates of dispersal for multiple species.

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Indeed, after filtering the data, in order to minimize spatial biases in ringer/observer effort, Paradis and colleagues were able to obtain estimates of natal dispersal distance for 75 bird species. The estimates derived by this study have been used in macroecological (e.g. Gaston & Blackburn 2003) and macroevolutionary (e.g. Belliure *et al.* 2000) studies but, unfortunately, are limited to British birds. A promising approach for indirect quantifying dispersal is to use a population genetic data to quantify gene flow (Lester *et al.* 2007). However, such approaches are time-consuming both in terms of obtaining appropriate samples and characterizing genetic loci.

As a consequence of the challenges of quantifying dispersal distances, many researchers use simple indices to quantify dispersal ability (Owens, Bennett & Harvey 1999; Mayr & Diamond 2001; Bennett & Owens 2002). For example, Owens, Bennett & Harvey (1999) and Phillimore *et al.* (2006) used the migratory behaviour of birds as a proxy for dispersal ability and found that bird families that contained migratory species possessed significantly more species than those that were made up of mainly sedentary species. Interestingly, a correlation between migratory behaviour and dispersal has been shown across some bird species (Paradis *et al.* 1998; Sutherland *et al.* 2000), although it is not known whether this is a global phenomenon.

Ecomorphological traits may potentially be able to provide a means of estimating dispersal ability in birds or other animals (Leisler & Winkler 1985, 1991; Losos & Miles 1994, Ricklefs & Miles 1994). Morphological traits such as wing, bill, and tarsus length are shaped by, and thus provide evidence of, the behaviour and ecological niche of a species (Leisler & Winkler 1991; Wainwright & Reilly 1994). Empirical support for this comes from both intraspecific and interspecific studies, which report positive correlations between wing length and dispersal distance (Paradis *et al.* 1998; Skjelseth *et al.* 2007). Moreover, Böhning-Gaese *et al.* (2006) found a significant relationship between range size and ecomorphological traits that relate to flight ability among *Sylvia* warblers; a result they interpreted as evidence for a role of dispersal in determining range size.

Migratory behaviour may be the causal link between ecomorphology and dispersal distance in birds (Winkler 2005). In several genera migrant species have been found to have longer and more pointed wings than resident species (e.g. Leisler & Winkler 1985, 2003; Winkler & Leisler 1992; Mönkkönen 1995; Lockwood, Swaddle & Rayner 1998). As discussed above, migration and dispersal have been found to correlate by some studies (Paradis *et al.* 1998; Sutherland *et al.* 2000). Nonetheless, other functional links between ecomorphology and dispersal distance also appear possible, for example, via habitat choice (Paradis *et al.* 1998; Sutherland *et al.* 2000).

Here, we test whether 11 morphological traits can predict natal dispersal distance across 47 passerine bird species. In addition, we explore several behavioural and ecological traits that might help explain a relationship between ecomorphology and dispersal. Finally, we evaluate whether one or a combination of the ecomorphological traits could be used as a simple proxy for dispersal distances in future studies.

## Methods

### TAXA AND STUDY REGION

We studied 47 passerine bird species (representing 17 families), for which natal dispersal distance has been estimated from ringing recoveries in Great Britain and Ireland (Paradis *et al.* 1998). We restricted the analyses to passerines because they share a similar body plan and flight style (Rayner 1988).

Ecomorphological analyses were conducted on British specimens, as it is known that there is intraspecific geographical variation in the morphology and migration behaviour of birds (Fiedler 2005). Morphological measurements were conducted on skins of birds housed at the Natural History Museum in Tring. We only selected undamaged skins of adult, nonmoulting birds. For migratory species, we took care that specimens had been collected in the breeding season. For each species, measurement were taken from approximately four male and four female individuals [mean number of males per trait = 3·98 (range = 1–5), median number of females per trait = 3·93 (range = 1–5), Appendix S1, Supporting information], so as to minimize bias associated due to differences between the sexes in either morphology or dispersal (Greenwood 1980).

### MEASUREMENTS

We selected morphological traits that are thought to best reflect flight ability and general ecology of species, following Leisler & Winkler (1991, 1997). We took 11 external morphological measurements of three functional complexes as described by Leisler & Winkler (1991), with the primaries and secondaries numbered in ascendance starting with the most distal, flight apparatus: wing length (bow to wing tip, measure on a flattened wing), Kipp's distance (distance between tip of the first secondary and tip of the longest primary/wing tip with the wing folded), notch length (from the middle of the notch curve of the inner web of second primary to tip of this feather), tail length (from emergence of central rectrix pair to tip of longest tail feather of tail in natural shape) and tail graduation (distance between tip of T1 and T6, giving a positive value for a rounded or wedge shaped tail and negative value for a forked tail); feeding apparatus: bill length (bill tip to skull at nasal-frontal hinge), bill depth (measured at the proximate edge of the nostrils), bill width (measured at the proximate edge of the nostrils) and the length of the longest rictal bristle; hind limb: tarsus length (distance between intertarsal joint and insertion of hind toe) and tarsus depth (big diameter of the tarsus in the middle of the tarsus). B.D. took all measurements. For each morphological trait, we calculated the mean per species (Appendix S1). We estimated the proportion of total variance for each trait that was distributed between species using a mixed effect model with species and sex as nested random effects. In all cases the majority of the variance was distributed among rather than within species, with tail length returning the lowest repeatability (0·946). All ecomorphological traits, except for tail graduation, were normalized before analysis using $\ln(x)$ or $\ln(x + 1)$ transformation. We did not transform tail graduation, as this trait possessed both positive and negative values. In addition, we obtained information on mean body mass for each species (Robinson 2005), but we excluded body mass from multipredictor analyses due to the very high correlation between it and tarsus depth ($r = 0{\cdot}971$, $n = 47$).

### SPECIES TRAITS

Dispersal data were taken from Paradis *et al.* (1998). We restricted the analyses to natal dispersal, as these distances tend to be considerably larger than breeding dispersal distances, especially in passerines (Greenwood & Harvey 1982; Paradis *et al.* 1998; Hansson *et al.* 2002; Winkler 2005), and are hence expected to have a stronger effect on metapopulation dynamics, gene flow and range expansion. We used a $\ln[\ln(x + 1) + 1]$ transformation to normalize the geometric means of natal dispersal distances. Data on migration distance were taken from Wernham *et al.* (2002). We classified the migration behaviour of birds in three classes, primarily resident birds, short-distance migrants wintering mostly in the Mediterranean and long-distance migrants wintering mostly south of the Sahara (or east of the Indian–Pakistan border). We classified diet using data from Ehrlich *et al.* (1994), distinguishing between granivorous [diet during summer and/or winter includes seeds (omnivores are included in this group)] and nongranivorous birds (diet only includes arthropods, aquatic invertebrates and/or fruit). We followed Paradis *et al.* (1998) in classifying birds as occupying open versus closed and dry versus wet summer habitats.

### STATISTICAL ANALYSES

We considered all possible multiple predictor models that possessed four terms or fewer and used AICc to assess the information content of each model (Burnham & Anderson 2004). As the ecomorphological traits will be correlated due to allometry, we assessed the degree to which colinearity posed a statistical problem for each model by calculating the variance inflation factor for each pair of terms in each model (following Fox & Monette 1992). As a rule of thumb, a variance inflation factor exceeding 10 is typically interpreted as evidence for colinearity (Myers 1990). To check for violation of standard statistical assumptions, we visually examined residual and Q-Q plots for all reported models.

We also tested migration, habitat type and food type as predictors of dispersal distance first singly, then by adding these terms to the multipredictor model with lowest AICc. The aim of this latter series of tests was to establish whether (i) a correlation between ecomorphological traits and dispersal had arisen indirectly via correlations between these variables and a third behavioural or ecological variable, or (ii) a correlation between a behavioural or ecological trait and dispersal was independent of any correlations between ecomorphology and dispersal. As an additional test of hypothesis (i) we repeated the ecomorphological trait versus dispersal analyses after excluding nonresidents.

There is a tendency for male birds to be more philopatric than females (Greenwood 1980). Therefore, we tested whether the ecomorphological traits we identified as predictors of interspecific variation in natal dispersal were also able to explain intraspecific intersexual differences in natal dispersal. To do this we used a binomial test across species to examine if females tend to have larger mean values than males (for the suite of ecomorphological traits identified in the interspecific analysis).

Finally, we constructed single predictor and multiple predictor models of migration using the ecomorphological and ecological variables, following a similar approach as that which is outlined above for the dispersal models.

The $R^2$ values reported are non-adjusted except where we specify that we are reporting adjusted $R^2$ values.

### PHYLOGENETIC COMPARATIVE APPROACH

All comparative analyses were conducted using the generalized least squares (GLS) phylogenetic comparative method described in Freckleton, Harvey & Pagel (2002). This approach incorporates the maximum likelihood estimation of a power transformation of internal branch lengths (λ) (Pagel 1999) and means that the expected phylogenetic covariance between closely related species is reduced if traits are more labile than expected under a strict Brownian model. $\lambda = 1$ corresponds to the Brownian model, $\lambda = 0$ corresponds to all species being independent and $1 > \lambda > 0$ corresponds to a degree of trait lability. We preferred this approach to independent contrasts (Felsenstein 1985) (which is equivalent to $\lambda = 1$) because behavioural traits in general, and dispersal in particular, have been shown to be quite labile, as compared to morphological traits (Blomberg, Garland & Ives 2003; Phillimore *et al.* 2006). All phylogenetic comparative analyses were conducted in R (R Development Core Team 2008) using the Ape library (Paradis 2006) and code kindly provided by R. P. Freckleton. We used the maximum clade credibility mtDNA phylogeny of British breeding birds (Thomas 2008) as our phylogenetic hypothesis for comparative analyses.

## Results

### ECOMORPHOLOGY AND DISPERSAL

None of the 11 ecomorphological traits or body mass was a significant predictor of dispersal distance (Table 1a). The only term that was close to statistical significance was Kipp's distance, which showed a positive correlation with natal dispersal ($b = 0{\cdot}119 \pm 0{\cdot}065$). In all cases $0{\cdot}5 > \lambda > 0{\cdot}3$, indicating weak phylogenetic signal in the residuals.

The best two-predictor model included Kipp's distance as a positive correlate ($b = 0{\cdot}368 \pm 0{\cdot}070$) and bill depth as a negative correlate ($b = -0{\cdot}402 \pm 0{\cdot}082$). This model had an $R^2_{\text{adj}} = 0{\cdot}385$ and AICc = 12·278, meaning that it explained substantially more information than the best single predictor model. Colinearity did not appear to be a problem in this case (variance inflation factor = 1·618). No other two-predictor model was within 2ΔAICc of the Kipp's distance and bill depth model. This suggests that birds with larger Kipp's distance and shallower bills tend to disperse further (Fig. 1). However, this ratio does not simply reflect Kipp's distance relative to body size, as a model including Kipp's distance and tarsus depth performs substantially worse (AICc = 24·162, note that this is still an improvement on the best single predictor model ΔAICc = 2·674 – see Table 1a).

The best three-predictor model again included Kipp's distance ($b = 0{\cdot}406 \pm 0{\cdot}068$) and bill depth ($b = -0{\cdot}499 \pm 0{\cdot}087$), but also included tail graduation as a positive correlate ($b = 0{\cdot}004 \pm 0{\cdot}002$), suggesting that birds with rounded or wedge-shaped tails dispersed farther than birds with forked tails. A plot of leverage values suggests that the relationship between tail graduation and dispersal distance may not be very robust (Fig. 2c). None of the trait correlations in this model had a variance inflation factor exceeding 2·2. The

**Table 1.** Summary statistics obtained from phylogenetic comparative single predictor analyses of natal dispersal distance for (a) 11 ecomorphological traits and body mass and (b) behavioural and ecological variables

| | Predictor | Slope (± SE) | $R^2$ | Pval | λ | AICc |
|---|---|---|---|---|---|---|
| (a) | Wing length | 0·064 (0·096) | 0·001 | 0·505 | 0·384 | 29·627 |
| | Kipp's distance | 0·119 (0·065) | 0·068 | 0·076 | 0·446 | 26·836 |
| | Notch length | –0·063 (0·042) | 0·048 | 0·140 | 0·427 | 27·831 |
| | Tail length | 0·054 (0·105) | 0·001 | 0·611 | 0·361 | 29·821 |
| | Tail graduation | 0·000 (0·002) | 0·000 | 0·951 | 0·371 | 30·090 |
| | Bill length | 0·031 (0·093) | 0·002 | 0·740 | 0·369 | 29·978 |
| | Bill depth | –0·121 (0·079) | 0·050 | 0·131 | 0·335 | 27·698 |
| | Bill width | –0·067 (0·104) | 0·009 | 0·523 | 0·352 | 29·666 |
| | Bristle length | –0·021 (0·083) | 0·001 | 0·803 | 0·385 | 30·031 |
| | Tarsus length | –0·061 (0·112) | 0·007 | 0·590 | 0·392 | 29·792 |
| | Tarsus depth | –0·029 (0·093) | 0·002 | 0·760 | 0·370 | 29·995 |
| | Mass | –0·015 (0·038) | 0·003 | 0·704 | 0·363 | 29·942 |
| (b) | Migration score | 0·189 (0·042) | 0·294 | < 0·001 | 0·304 | 13·786 |
| | Habitat – open/closed* | –0·139 (0·087) | 0·033 | 0·115 | 0·419 | 27·493 |
| | Habitat – dry/wet* | 0·168 (0·122) | 0·020 | 0·173 | 0·258 | 28·267 |
| | Granivory (1/0)* | –0·264 (0·088) | 0·149 | < 0·01 | 0·474 | 21·569 |

*These binary variables were treated as dummy variables (with open habitat = 0 and closed habitat = 1, dry habitat = 0 and wet habitat = 1 and nongranivorous = 0 and granivorous = 1).

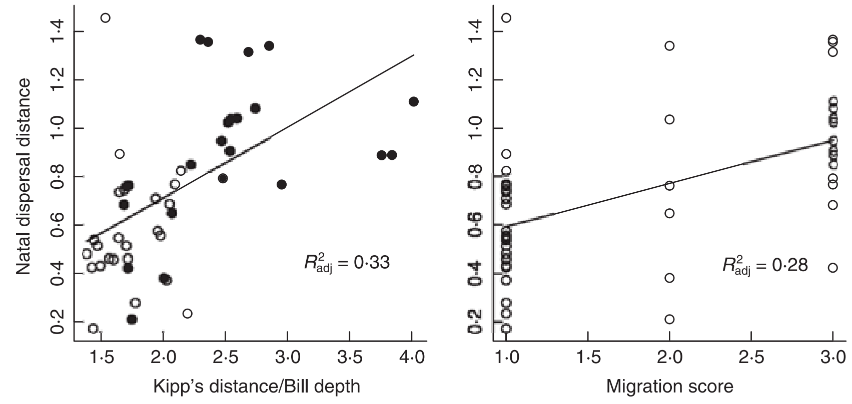

**Fig. 1.** The relationship between natal dispersal distance and the ratio of Kipp's distance:bill depth (left) and migration (right). In the left plot species classed as empty circles represent resident species and filled circles represent short- or long-distance migrants. $R^2_{adj}$ values and predicted relationships were obtained from a GLS model correcting for phylogeny (Pagel 1999; Freckleton *et al.* 2002). Kipp's distance and bill depth are both ln-transformed and the geometric mean of natal dispersal distance was ln(ln($x$ + 1) + 1) transformed.

three predictor model had an $R^2_{adj}$ = 0·449 and AICc = 9·842, making it an improvement on the best two-predictor model (ΔAICc = 2·436). No other three- or four-predictor models were found within 2ΔAICc of the best three-predictor model. The key finding that Kipp's distance was positive correlate and bill depth was a negative correlate was also obtained using an alternative approach where all ecomorphological variables were first divided by the cube root of body mass (B. A. Dawideit, master's thesis).

### BEHAVIOURAL AND ECOLOGICAL INFLUENCES ON DISPERSAL

Migration index showed a strong positive correlation with dispersal distance (Table 1b, Fig. 1b). However, migration explained less variation in dispersal distance ($R^2$ = 0·304) than the best three-predictor ecomorphological model ($R^2_{adj}$ = 0·449). When we added migration to the best three-predictor model, the model AICc increased to 11·300 (ΔAICc = 1·458), from which we infer that the migratory index does not add any extra information to this model. Further evidence that migration score was a less good predictor of dispersal distance than the three ecomorphological terms in the model comes from the fact that migration was nonsignificant ($P$ = 0·115) in this model, while the coefficients and significance of the three ecomorphological terms changed very little.

Habitat (scored along two axes, dry – wet and open – closed) did not predict dispersal, either in single predictor models (Table 1b) or when added to the three ecomorphological predictors (ΔAICc > 2 in both cases). In the latter model, the additional term was nonsignificant while the ecomorphological trait's coefficients and statistical significance remained qualitatively unchanged.

Species that feed on seeds in summer and/or winter (including omnivores) tend to have significantly shorter dispersal distances (Table 1b). However, food type does not capture any predictive information beyond that which is

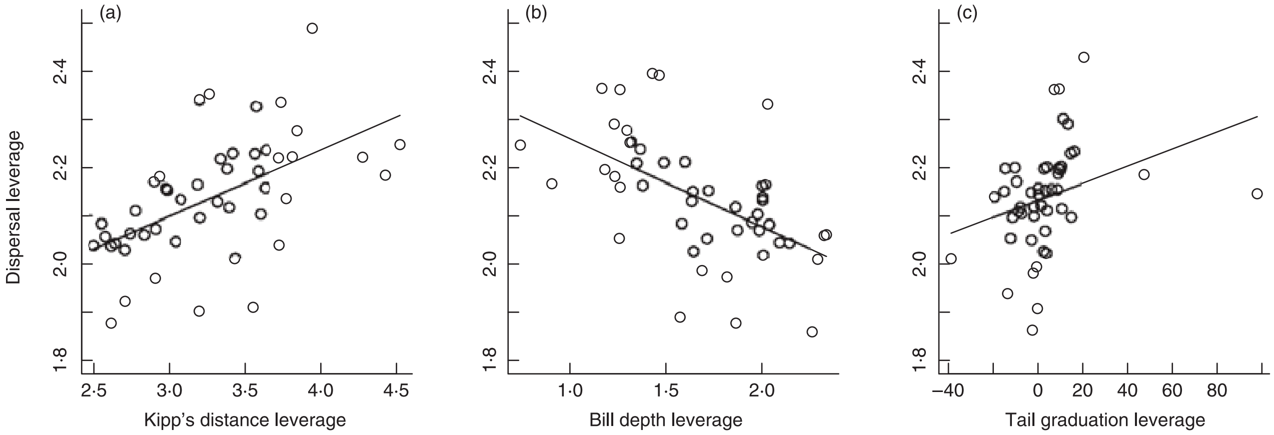

**Fig. 2.** Leverage plots for the best three-predictor model of natal dispersal distance, which included (a) Kipp's distance, (b) bill depth and (c) tail graduation. Kipp's distance and bill depth are both ln-transformed and the geometric mean of natal dispersal distance was $\ln(\ln(x + 1) + 1)$ transformed.

captured by Kipp's distance, bill depth and tail graduation in the three-predictor model (ΔAICc > 2).

When short- and long-distance migrants were excluded from comparative analyses of natal dispersal, a model with Kipp's distance, bill depth and tail graduation as predictors had considerably lower explanatory power than the model that included all species ($R^2_{\mathrm{adj}}$ = 0·246, AICc = 5·25, Kipp's distance $b$ = 0·261 ± 0·134, bill depth $b$ = −0·165 ± 0·189, tail graduation $b$ = 0·002 ± 0·002, see also Fig. 1a). Single predictor models explained a greater proportion of the variation than the aforementioned multi-predictor model, with Kipp's distance (AICc = −0·80), bow length (AICc = −0·59), wing length (AICc = −1·17), notch length (AICc = −2·22) and tarsus depth (AICc = −1·24) all being significant positive correlates of dispersal and all possessing an $R^2_{\mathrm{adj}}$ > 0·25.

There was no tendency for female birds to exceed males in their Kipp's distance to bill depth ratios (female value > male value in 22/47 species, $P$ = 0·779).

### ECOMORPHOLOGY AND MIGRATION

The best single ecomorphological predictor of migration was notch length, which explained 28% of the variance ($b$ = −0·456 ± 0·109, λ = 0·00, AICc = 114·749). In addition, tarsus length ($b$ = −0·822 ± 0·307, $R^2$ = 0·138), tarsus depth ($b$ = −0·771 ± 0·254, $R^2$ = 0·170), bill length ($b$ = −0·550 ± 0·269, $R^2$ = 0·085), bill depth ($b$ = −0·87 ± 0·208, $R^2$ = 0·282), bill width ($b$ = −0·842 ± 0·295, $R^2$ = 0·153) and tail graduation ($b$ = −0·014 ± 0·006, $R^2$ = 0·104) were all significant at $P < 0·05$.

The best multiple-predictor model (out of all models with four additive terms or less) was similar to the dispersal models, in that Kipp's distance ($b$ = 1·837 ± 0·411) and bill depth ($b$ = −1·045 ± 0·293) were both highly significant terms. In addition, wing length ($b$ = −2·239 ± 0·770) and rictal bristle length ($b$ = 0·585 ± 0·216) were included in this model ($R^2_{\mathrm{adj}}$ = 0·563, AICc = 97·485). The only model that was within 2ΔAICc of the best model shared three of the same terms with the best one, Kipp's distance, bill depth and wing length, and only differed in that bow length was a positive correlate in the place of bristle length ($R^2_{\mathrm{adj}}$ = 0·557, AICc = 99·169). Both of these models possessed variance inflation factors > 10, which suggests colinearity may be a problem. However, we found that a two term model that included just Kipp's distance and bill depth ($R^2_{\mathrm{adj}}$ = 0·468, AICc = 101·829) possessed very similar coefficients and had a variance inflation factor < 2.

## Discussion

### ECOMORPHOLOGICAL TRAITS AND DISPERSAL DISTANCE

The best predictors of natal dispersal distance proved to be Kipp's distance, bill depth and tail graduation, which together explained approximately 45% of the variation in dispersal distance. These three predictors were substantially better than an index of migration at predicting natal dispersal. However, in a multiple-predictor model, Kipp's distance and bill depth also showed strong correlations with migration distance. Kipp's distance was close to statistical significance when considered in a single predictor model, although predictive power increased greatly when bill depth was added to the model, suggesting dispersal is predicted by Kipp's distance relative to bill depth, rather than Kipp's distance per se. The four species with the highest Kipp's distance to bill depth ratio are the three Hirundines (*Riparia riparia*, *Hirundo rustica* and *Delichon urbicum*) and *Phylloscopus trochilus* (the willow warbler), all of which have above average dispersal distances and are also long-distance migrants.

Kipp's distance measures the length of the wing tip and is an important component of aspect ratio. A larger Kipp's distance relative to size describes a more pointed wing; typically thought to be important in forward flight (Leisler & Winkler 2003) as a higher aspect ratio permits more efficient and faster flight (Rayner 1988; Norberg 1989). A second route whereby a correlation between relative Kipp's distance and dispersal might arise is habitat use. Species that inhabit closed habitats, such as forests, tend to have more rounded wing tips, which increases maneuverability, whereas species inhabiting open habitat often have more pointed wing tips (Leisler & Winkler 1985, 1991). We might thus expect species of closed habitats to disperse less than species inhabiting open habitats. If there is a difference between the habitat types in terms of their patchiness, then this may lead to longer dispersal distances and thus, indirectly, generate an association between wing morphology and dispersal distance. Paradis *et al.* (1998) found that birds (passerine and nonpasserine) inhabiting wet habitats dispersed further than those living in dry habitats, which they explained by the greater patchiness of wet habitats in space and/or time. However, we found no support for these indirect routes of causation, as both habitat predictors were nonsignificant predictors of dispersal in the subset of 47 passerine species that we considered.

The influence of bill depth on natal dispersal distances is more difficult to interpret than Kipp's distance, because bill shape is expected to be subject to strong natural selection for feeding (e.g. Grant 1985; Grant & Grant 2007) and also covaries with interspecific variation in preening behaviour (Clayton & Cotgreave 1994). Of the species studied here, all those with a shallow bill depth and long natal dispersal distance are also insectivorous and migratory, meaning that we cannot exclude the possibility of an indirect relationship between feeding and dispersal via migration. Peach, Hammer & Oatley (2001) found that insectivorous (and nectivorous) birds in Malawi disperse significantly farther than granivorous birds (excluding members of the Ploceinae), implying that there may be some generality to this association.

The third ecomorphological variable in the model, tail graduation, has also been linked to flight ability. Species that migrate long distances tend to have more square tails, whereas species that migrate shorter distances or are residents often have more graduated tails (Leisler & Winkler 2003). Thus, our finding that species with more wedge-shape tails disperse further runs counter to the expectation, since high performance fliers/long-distance dispersers should have square or forked tails. However, the reliability of this ecomorphological trait as a correlate of dispersal distance is somewhat dubious on statistical grounds (Fig. 2c), so we do not discuss it further.

### ECOMORPHOLOGICAL TRAITS AND MIGRATORY BEHAVIOUR

Two out of the three ecomorphological traits that best predicted interspecific variation in dispersal distances, Kipp's distance and bill depth, were also strong predictors of migratory behaviour, explaining more than 45% of the variance in this trait. This is in agreement with a large number of studies, which report a positive relationship between wing-tip length and migration distances (e.g. Kipp 1942; Mönkkönen 1995; Lockwood *et al.* 1998; Leisler & Winkler 2003), but see (Niemi 1985). In a study on *Anthus* pipits, Leisler & Winkler (2003) found that a combination of Kipp's distance, notch length and tail graduation (the latter two entering with a negative sign) explain 64% of the interspecific variation in migration distance. Bill shape also proves to be correlated with migration distance in some passerine groups (Leisler & Winkler 1991), but it remains unclear whether this has arisen due to (i) the costs of flying long distances placing a selection pressure for shallow bills or (ii) a trend for migratory species to be insectivorous (Newton 1995, 2003, 2008) and an insectivorous diet, in turn, influencing bill morphology.

### RELATIONSHIP BETWEEN ECOMORPHOLOGICAL TRAITS, DISPERSAL AND MIGRATION

The observation that the same ecomorphological traits are the best predictors of dispersal distance and migratory behaviour suggests a close link between these two types of mobility (see Paradis *et al.* 1998; Sutherland *et al.* 2000). Moreover, in our analysis migration is a significant (but less informative) predictor of dispersal distance. How then can we explain these correlations? One possibility is that a large Kipp's distance relative to bill depth reflects flight ability (presumably with migration as the selective force) and it is flight ability per se that directly influences dispersal, thus the route of causation might run migratory behaviour > ecomorphology > natal dispersal distance. However, we cannot discount an alternative route of causation whereby migratory behaviour influences both ecomorphology and natal dispersal distance directly. Migratory taxa may be less likely to return to the natal location due to either mistakes in locating their natal territory or due to some behavioural difference. Indeed, Winkler (2005) points out that migration leads to a whole syndrome of physiological and cognitive adaptations in addition to morphological adaptations. For instance, long-distance migrants have evolved hormonal and physiological adaptations (Holbreton & Dufty 2005) and migrants appear to be more exploratory, less neophobic and able to more rapidly process spatial information than resident species (Mettke-Hofmann & Gwinner 2004; Mettke-Hofmann & Greenberg 2005). It is possible that this 'migration syndrome' may also lead to longer natal dispersal distances, perhaps as a consequence of the settling behaviour (Paradis *et al.* 1998). While the observation that the ecomorphological traits predict dispersal better than migration is more consistent with the first explanation, we cannot reject the second explanation, particularly if these ecomorphological traits happen to be better estimators of migratory behaviour than the simple migration index we use. Further support for the latter hypothesis emerged when we excluded migratory species from the analysis and found that the relationship between the Kipp's distance : bill depth ratio and dispersal was much less pronounced (Fig. 1a).

### ECOMORPHOLOGICAL TRAITS, DISPERSAL AND SEX

As interspecific variation in natal dispersal distances are correlated to ecomorphological traits we might expect that intraspecific variation in dispersal should predict variation along the same ecomorphological axes; i.e. because female birds generally disperse further than males, females should tend towards larger Kipp's distance to bill depth ratios. However, we found no evidence for such a trend. Our failure to detect such a trend may reflect (i) the absence of such a trend, (ii) intraspecific variation in dispersal being less pronounced than the interspecific variation or, related to the last point, (iii) very low power to detect such a trend. Support for explanations (ii) and (iii) comes from the observation that most variation in ecomorphological traits lies within rather than between species and thus our sampling of four males and four females is unlikely to be sufficient to accurately capture ecomorphological differences between the sexes.

### APPLICATIONS

Although we lack a firm understanding regarding directions of causality in the correlations between ecomorphological traits, migration and dispersal distance, two traits together, Kipp's distance and bill depth, explained nearly 40% of the variation in dispersal distance (a corollary of this is that 60% of the variance in dispersal remains unexplained). The predictive power of these variables makes biological sense in terms of aerodynamics and flying ability. Consequently, we suggest that, in the absence of direct estimates of dispersal distance, these traits (either fitted separately in a model or more simply as a ratio) could be used as a simple surrogate for dispersal in passerines. We found that these two variables predict dispersal distance considerably better than the simple indices of migratory behaviour that have been employed as surrogates of dispersal distance elsewhere (e.g. Owens *et al.* 1999; Phillimore *et al.* 2006). Both of the ecomorphological measures can be taken relatively easily on museum skins or from wild birds, meaning that this approach may prove useful in large-scale comparative, macroevolutionary and macroecological studies. The measure may even work for species where little is known about their biology, e.g. many tropical species. However, we should sound a cautionary note, as the temperate species included in this study are likely to be biased towards better dispersers and more long-distance migrants than would be the case at lower latitudes (Newton 2008). Thus, for studies that extrapolate beyond the taxa and temperate region considered here, we suggest that the role of these two ecomorphological traits as correlates of dispersal needs corroboration.

## Acknowledgements

We are very grateful to Christian Rutz and an anonymous referee for constructive comments that improved the manuscript, Mark Adams and Robert Prys-Jones of the Natural History Museum for access to and assistance using the skins housed at Tring and R. Freckleton for providing R code. Funding was provided by a Virtual Institute of the Helmholtz Association.

## References

Belliure, J., Sorci, G., Møller, A.P. & Clobert, J. (2000) Dispersal distances predict subspecies richness in birds. *Journal of Evolutionary Biology*, **13**, 480–487.

Bennett, P.M. & Owens, I.P.F. (2002) *Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction*. Oxford University Press, Oxford, UK.

Blomberg, S.E., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.

Böhning-Gaese, K., Caprano, T., van Ewijk, K. & Veith, M. (2006) Range size: disentangling current traits, phylogenetic and biogeographic factors. *American Naturalist*, **167**, 555–567.

Brooker, R.W., Travis, J.M.J., Clark, E.J. & Dytham, C. (2007) Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245**, 59–65.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research*, **33**, 261–304.

Clayton, D. & Cotgreave, P. (1994) Relationship of bill morphology to grooming behaviour in birds. *Animal Behaviour*, **47**, 195–201.

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

Davis, M. & Shaw, R. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.

Davis, M., Shaw, R. & Etterson, J. (2005) Evolutionary responses to changing climate. *Ecology*, **86**, 1704–1714.

Ehrlich, P.R., Dobkin, D.S., Wheye, D. & Pimm, S.L. (1994) *The Birdwatcher's Handbook: A Guide to the Natural History of the Birds of Britain and Europe*. Oxford University Press, Oxford, UK.

Felsenstein, J. (1985) Phylogeny and the comparative method. *American Naturalist*, **125**, 1–15.

Fiedler, W. (2005) Ecomorphology of the external flight apparatus of blackcaps (*Sylvia atricapilla*) with different migration behavior. *Bird Hormones and Bird Migrations: Analyzing Hormones in Droppings and Egg Yolks and Assessing Adaptations in Long-distance Migration* (eds W. Goyman, S. Jenni-Eirmann & U. Bauchinger), pp. 253–263. Annals of the New York Academy of Sciences, New York.

Fox, J. & Monette, G. (1992) Generalized collinearity diagnostics. *Journal of the American Statistical Association*, **87**, 178–183.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist*, **160**, 712–726.

Gaston, K.J. & Blackburn, T.M. (2003) Dispersal and the interspecific abundance-occupancy relationship in British birds. *Global Ecology and Biogeography*, **12**, 373–379.

Gavrilets, S. (2004) *Fitness Landscapes and the Origin of a Species*. Princeton University Press, Princeton, New Jersey.

Gilpin, M.E. & Hanski, I. (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigation*. Academic Press, London.

Grant, P.R. (1985) Selection on bill characters in a population of Darwin's finches: *Geospiza conirostris* on Isla Genovesa, Galapagos. *Evolution*, **39**, 523–532.

Grant, P.R. & Grant, B.R. (2007) *How and Why Species Multiply: The Radiation of Darwin's Finches*. Princeton University Press, Princeton, New Jersey.

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.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.

Hansson, B., Bensch, S., Hasselquist, S. & Nielsen, B. (2002) Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. *Oecologia*, **130**, 536–542.

Holbreton, R.L. & Dufty, A.M.J. (2005) Hormones and variation in life history strategies in migratory and nonmigratory birds. *Birds of Two Worlds – the Ecology and Evolution of Migration* (eds R. Greenberg & P.P. Marra), pp. 290–302. John Hopkins University Press, Baltimore, Maryland.

Kipp, F. (1942) Über Flügelbau und Wanderzug der Vögel. *Biologisches Zentralblatt*, **62**, 289–299.

Leisler, B. & Winkler, H. (1985) Ecomorphology. *Current Ornithology*, **2**, 155–186.

Leisler, B. & Winkler, H. (1991) Ergebnisse und Konzepte ökomorphologischer Untersuchungen an Vögeln. *Journal für Ornithologie*, **132**, 373–425.

Leisler, B. & Winkler, H. (1997) Ökomorphologische Untersuchungen am Beispiel der Webervögel (Ploceidae) und Eisvögel (Alcedinidae). Mitteilungen aus dem Zoologischen Museum in Berlin 73 Suppl. *Annalen für Ornithologie*, **21**, 17–43.

Leisler, B. & Winkler, H. (2003) Morphological consequences of migration in passerines. *Avian Migration* (eds P. Berthold, E. Gwinner & E. Sonnenschein), pp. 175–186. Springer, Berlin, Heidelberg, Germany.

Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal and geographic range size. *Ecology Letters*, **10**, 745–758.

Lockwood, R., Swaddle, J.P. & Rayner, J.M.V. (1998) Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology*, **29**, 273–292.

Losos, J.B. & Miles, D.B. (1994) Adaptation, constraint, and the comparative method: phylogenetic issues and methods. *Ecological Morphology: Integrative Organismal Biology* (eds P.C. Wainwright & S.M. Reilly), pp. 60–98. Chicago University Press, Chicago, Illinois.

Martin, C.A., Alonso, J.C., Alonso, J.A., Palacin, C., Magana, M. & Martin, B. (2008) Natal dispersal in great bustards: the effect of sex, local population size and spatial isolation. *Journal of Animal Ecology*, **77**, 326–334.

Mayr, E. & Diamond, J. (2001) *The Birds of Northern Melanesia: Speciation, Ecology and Biogeography*. Oxford University Press, New York.

Mettke-Hofmann, C. & Greenberg, R. (2005) Behavioral and cognitive adaptions to long-distance migration. *Birds of Two Worlds – the Ecology and Evolution of Migration* (eds R. Greenberg & P.P. Marra), pp. 114–123. John Hopkins University Press, Baltimore, Maryland.

Mettke-Hofmann, C. & Gwinner, E. (2004) Differential assessment of environmental information in a migratory and nonmigratory passerine. *Animal Behaviour*, **68**, 1079–1086.

Mönkkönen, M. (1995) Do migrant birds have more pointed wings? A comparative study. *Evolutionary Ecology*, **9**, 520–528.

Myers, R.H. (1990) *Classical and Modern Regression with Applications*. PWS-Kent, Boston, Massachusetts.

Nathan, R. (2001) The challenges of studying dispersal. *Trends in Ecology & Evolution*, **16**, 481–483.

Newton, I. (1995) The contribution of some recent research on birds to ecological understanding. *Journal of Animal Ecology*, **64**, 675–696.

Newton, I. (2003) *Speciation and Biogeography of Birds*. Academic Press, London.

Newton, I. (2008) *The Migration Ecology of Birds*. Academic Press, London.

Niemi, G. (1985) Patterns of morphological evolution in bird genera of New World and Old World peatlands. *Ecology*, **66**, 1215–1228.

Norberg, U.M. (1989) *Vertebrate Flight, Mechanics, Physiology, Morphology, Ecology and Evolution*. Springer-Verlag, Berlin, Germany.

Owens, I.P.F., Bennett, P.M. & Harvey, P.H. (1999) Species richness among birds: body size, life history, sexual selection or ecology? *Proceedings of the Royal Society B: Biological Sciences*, **266**, 933–939.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Paradis, E. (2006) *Analysis of Phylogenetics and Evolution with R*. Springer, New York.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1998) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, **67**, 518–536.

Peach, W., Hanmer, D. & Oatley, T. (2001) Do southern African songbirds live longer than their European counterparts? *Oikos*, **93**, 235–249.

Phillimore, A.B., Freckleton, R.P., Orme, C.D.L. & Owens, I.P.F. (2006) Ecology predicts large-scale patterns of phylogenetic diversification in birds. *American Naturalist*, **168**, 220–229.

Price, T.D. (2008) *Speciation in Birds*. Roberts & Company Publishers, Greenwood Village, Colorado.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rayner, J.M.V. (1988) Form and function in avian flight. *Current Ornithology*, **5**, 1–66.

Ricklefs, R.E. & Miles, D.B. (1994) Ecological and evolutionary influences from morphology: an ecological perspective. *Ecological Morphology: Integrative Organismal Biology* (eds P.C. Wainwright & S.M. Reilly), pp. 13–41. Chicago University Press, Chicago, Illinois.

Robinson, R.A. (2005) *BirdFacts: Species Profiles of Birds Occurring in Britain and Ireland*. BTO, Thetford, UK.

Skjelseth, S., Ringsby, T.H., Tufto, J., Jensen, H. & Saether, B.-E. (2007) Dispersal of introduced house sparrows *Passer domesticus*: an experiment. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1763–1771.

Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science*, **236**, 787–792.

Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P. (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, **4**, 16.

Thomas, G.H. (2008) Phylogenetic distributions of British birds of conservation concern. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2077–2083.

Turchin, P. (1998) *Quantitative Analysis of Movement*. Sinauer & Associates, Sunderland, Massachusetts.

van Noordwijk, A.J. (1984) Problems in the analysis of dispersal and a critique of its 'heritability' in the great tit. *Journal of Animal Ecology*, **53**, 533–544.

Wainwright, P.C. & Reilly, S.M. (1994) Introduction. *Ecological Morphology: Integrative Organismal Biology* (eds P.C. Wainwright & S.M. Reilly), pp. 1–12. Chicago University Press, Chicago, Illinois.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (2002) *The Migration Atlas: Movements of the Birds of Britain and Ireland*. T. & A.D. Poyser, London.

Winkler, D.W. (2005) How do migration and dispersal interact? *Birds of Two Worlds* (eds R. Greenberg & P.P. Marra), pp. 401–413. John Hopkins University Press, Baltimore, Maryland.

Winkler, H. & Leisler, B. (1992) On the ecomorphology of migrants. *Ibis*, **134**, 21–28.

Wright, S. (1943) Isolation by distance. *Genetics*, **28**, 114–138.

*Received 24 June 2008; accepted 24 October 2008*
*Handling Editor: Ben Sheldon*

## Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Mean ecomorphological measurements for the focal taxa