

Morphological Adaptations to Migration in Birds

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Abstract Migratory flight performance has direct or carry-over effects on fitness. Therefore, selection is expected to act on minimizing the costs of migratory flight, which increases with the distance covered. Aerodynamic theory predicts how morphological adaptations improve flight performance. These predictions have rarely been tested in comparative analyses that account for scaling and phylogenetic effects. We amassed a unique dataset of 149 European bird species and 10 morphological traits. Mass-adjusted aspect ratio increased, while mass-adjusted heart weight and wing loading decreased with increasing migration distance. These results were robust to whether the analyses were based on the entire species pool or limited to passerines or migrants. Our findings indicate that selection due to migration acts on wing traits that reduce the energetic cost of transportation to increase the flight range. Consequently, the demands for high ‘exercise organ’

performance might be low, and hence such energetically expensive tissues are not associated (pectoral muscle) or are inversely associated (heart) with migration distance.

Keywords Aerodynamics · Functional morphology · ‘Migratory syndrome’ · Organ size · Phylogenetic comparative analysis · Wing morphology

Introduction

Flight capacity constitutes complex adaptations in homeothermic vertebrates: animals get airborne to migrate, forage, display, hunt or escape from predators. Extraordinary locomotion during migratory journeys is the one that fascinated scientists for a long time due to impressive distances covered (e.g. 64,000 km a year by sooty shearwaters *Puffinus griseus*; Shaffer et al. 2006) and high relevance for ecological, evolutionary, conservation and health considerations (e.g. Webster et al. 2002; Alerstam et al. 2003; Møller et al. 2008; Bowlin et al. 2010; Altizer et al. 2011; Bauer and Hoye 2014).

Birds exhibit a large number of morphological (e.g. body mass, bones, feathered wings, wing-powering muscles, streamlined shape) and physiological and visceral organic (e.g. respiration, cardiovascular system, metabolic rate) adaptations that are thought to enhance flight capacity (Piersma et al. 2005; Videler 2005). However, besides these ‘general flight adaptations’, Darwinian selection is expected to add further ‘adaptive layers’ that particularly optimize the net pay-off of migratory flight. This expectation is reasonable considering (1) the energetic and antioxidant expenses that migratory flight entails, mainly when covering long distances (Costantini et al. 2007; Klaassen 1996; Rayner 1990), (2) the substantial mortality

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rate during migration (Klaassen et al. 2014; Newton 2004), and (3) the huge variation in migration distance among species. Aerodynamic theory predicts how morphological adaptations might maximize performance through either energy-efficiency (i.e. transport cost minimization) or time-efficiency of migratory flight (Hedenström 2008; Norberg 1990, 1994). We apply this functional morphology paradigm for studying morphological adaptations to long-distance migratory flight in birds.

A flying bird should produce lift and thrust that exceed weight (i.e. pull of gravity) and drag, respectively, to maintain a forward momentum. Both lift and thrust are ensured by the feathered wings and their highly complex movement during the stroke cycle. Wing loading (i.e. weight/wing area) and aspect ratio (i.e. wingspan²/wing area) are two wing morphology variables considered to greatly influence flight capacity and economy. Aerodynamic theory predicts higher body mass and/or smaller wing area if time-efficiency (i.e. flight speed maximization) is selected for because flight velocity scales to wing loading to the 0.32 power (Alerstam et al. 2007), while higher aspect ratio and lower wing loading is expected to evolve if optimal flight economy (longest flight range for smallest flight power) is selected (Norberg 1990). Therefore, both temporal and energetic currencies of migratory flight depend on the size and shape of the wing. Long-distance migratory birds were reported to have higher aspect ratio, longer distal wing, pointed wingtips and lower wing-loading than short-distance migrants or residents (Calmaestra and Moreno 2001; Fiedler 2005; Kaboli et al. 2007; Leisler and Winkler 2003; Lockwood et al. 1998; Mönkkönen 1995; Voelker 2001; Winkler and Leisler 1992), which hints toward the importance of energy-efficient flight. However, these studies do not uniformly detect such correlations between migration distance and morphological traits and reached contrasting conclusions (reviewed by Mulvihill and Chandler 1990; Lockwood et al. 1998) about whether migration represents an important selective force that shapes avian external morphology (Leisler and Winkler 2003).

Visceral organs also play an important role in migratory flight because they contribute to body mass and metabolic rate (Piersma and Lindström 1997). Given that the performance of organs increases with their size (Piersma and Lindström 1997), migrants are expected to have well-developed ‘exercise organs’ such as flight muscles (pectoral and supracoracoid), heart and lung (Piersma et al. 2005). This should be favoured owing to (1) higher mechanical power production by larger cross-sectional surface of muscles, (2) better respiration and oxygen supply to sustain mechanical power generation and to compensate for the hypoxic conditions of high altitude flights, and/or (3) steady energy supply by organs providing protein substrate

for catabolism, along with fat, to sustain flight (Battley et al. 2000; Jenni et al. 2000; Klaassen 1996; Pennycuick 1998; Piersma et al. 2005). Besides exercise organs, nutritional organs (gizzard, liver) also contribute to the energy turnover, and hence the physiology of flight, by regulating food processing. While exercise organs are functional during flight, nutritional organs are atrophied during migration to reduce loading and hypertrophied only at stopover refuelling stations. It was shown that migrants have larger bony surfaces for flight muscle attachment (Calmaestra and Moreno 2000), but similar pectoral muscle and heart weights as sedentary species, except that heart size was larger in migrant Charadriiformes based on a non-phylogenetic comparative analysis (Winkler and Leisler 1992). A phylogenetic analysis based on large sample size and data for the size of multiple organs analysed in a unified approach is thus desirable for knowing how organ weights are related to migration demands.

Besides the size of specific organs, total body mass also matters in optimal migration. Body mass is the most important life-history trait, which can adaptively evolve to meet certain demands or it might constrain the realization of optimal strategies. Migration is not an exception. Body mass or drag due to mass are integral parts of functions about flight economy (Hedenström 2008; Norberg 1994; Pennycuick 2008). Therefore, body mass is expected to evolve with migration distance, although whether an increase or decrease in body mass is advantageous for long-distance migrants is still not established (Hedenström 2008). Previous studies found that body mass either decreases (Jones and Witt 2014; Kaboli et al. 2007; Sol et al. 2005) or increases (Mönkkönen 1992; Winkler and Leisler 1992) with longer migration. Furthermore, morphological adaptation to migration might be constrained by mass due to scaling laws (see e.g. Alerstam et al. 2007), and hence correction for allometry is recommended. However, several comparative studies either did not control for allometry or computed the scaling power of morphologies without accounting for the similarity due to common descent. If evolution of morphological traits is governed by selection due to migratory performance, the mass-independent scatter in morphology is expected to be functional and hence explain variation in migration distance.

Modern phylogenetic analyses of the correlates of migration distance are scarce (Bennett and Owens 2002; Leisler and Winkler 2003), in particular those based on large sample sizes, despite a long history of the topic (Fredericus 1240 cited in Lockwood et al. 1998). Whether external morphology is adapted to meet migratory demands is still questioned, while internal morphological adaptations are poorly understood because only a handful of studies addressed this question at the interspecific level.

Furthermore, although morphological adaptation to migration was subject of scientific enquiry (see references above), most of the previous comparative studies have one or more of the following limitations: (1) lack of phylogenetic control or comparison of highly contrasting sister taxa, (2) small sample sizes or narrow taxonomic ranges (few species or single families studied), (3) migration distance either scored on a two- or four-level scale with subjective thresholds or quantified by manual measurements of distribution maps, and (4) morphological traits tested in isolation instead of being tested concurrently in multiple regression models.

Everything else being equal, migration distance increases both energetic and time costs of flight (Hedenström 1993). Aerodynamic theory predicts that long-distance migrants should have high aspect ratio wings to minimize energy costs (Rayner 1988). High aspect ratio is predicted to be accompanied by either low wing loading (i.e. long wingspan) or higher wing loading (i.e. average or short wingspan) depending on whether low cost of transport (slow and economic flight) or time-efficient travel (faster, but still economic) is the currency under selection, respectively (Norberg 1990). Given that flight power is a function of pectoral muscle weight and flight aerobic capacity is enhanced by larger heart size (Bishop 1997; Rayner 1988), we predicted that exercise organ weights relative to unit mass will be positively associated with migration distance. To test these predictions rooted in aerodynamic theory, we compiled an unprecedented dataset in terms of number of species (149 European bird species), taxonomic span (50 families and 20 orders) and number of morphological traits (size of five organs, four wing size and shape parameters and body mass), which allows for generalisation. We analysed migration distance as a function of morphology by means of phylogenetic models, which constitute a powerful tool for revealing adaptations, and they are claimed suitable for revealing functional adaptations in morphology (Wainwright and Reilly 1994; Piersma et al. 2005). Passerine birds might differ from non-passerines in terms of optimal aerodynamics, which arise from the difference in basal metabolic rate between the two groups (Hedenström 1993). This is also mirrored in morphological adaptations to flight expenses (Rayner 1988). For instance, passerines have a relatively uniform and characteristic flight mode that differs from other avian taxa (Bruderer et al. 2010), and flight type might be related to the morphology of the flight apparatus (Pap et al. 2015; Wang et al. 2011). To assess whether passerines evolved a different set of functional morphology than non-passerines, we also tested our models of migration distance by restricting the analyses to the order of Passeriformes.

Materials and Methods

Specimens

Birds were either captured in the field or collected as fresh carcasses. Captures took place across Romania by using mist nets (Ecotone, Poland) or rarely traps during the breeding seasons 2009–2013. Only adult birds were considered because wing morphologies are predicted to maximize fitness in an age-specific manner (Fiedler 2005). Each bird was banded with a unique metal ring and measured for standard biometry. We took digital pictures (Nikon D80) of the left wing and the body; the wing was fully unfolded and flattened such that the leading edge was held perpendicular to the body axis. The camera was held perpendicular to the wing surface and a ruler was used as metric template. Carcasses from natural deaths (e.g. road kill, building collision, electrocution, starvation) were collected in Romania and Denmark for taxidermy. Those collected in Romania were photographed for wing architecture, while those brought to JE in Denmark contributed to the organ size data. Only carcasses in good condition were considered. Although there is spatial discrepancy in the source of wing architecture and organ weight data, we are confident that these do not affect our analyses for the following reasons. First, APM has also measured wing architecture from wing outline drawings of birds captured in Northern Europe (98 species overlap with the Romanian dataset). Those measures are strongly positively correlated with those in the present study (phylogenetic generalized least squares regression, aspect ratio: $F_{1,95} = 878.10$, $R^2 = 0.90$, $P < 0.0001$; wing loading: $F_{1,94} = 2458.00$, $R^2 = 0.96$, $P < 0.0001$). Second, in the dataset presented here, within species variance was much smaller than the among species variance (see “Results” for intraspecific repeatabilities). Third, similarly to wing morphology, it was previously shown that organ sizes are species-specific and similar between localities within the same species (Garamszegi et al. 2002; Møller et al. 2005). These findings together suggest that external and internal morphological traits are species-specific and thus suitable for multispecies comparison.

Migration Distance

Distribution maps (shape files) were retrieved from <http://www.birdlife.org/datazone/info/spcdownload> (BirdLife International and NatureServe 2012). Maps were usually restricted to longitudes between W20° and E60° (Western Palearctic), but for certain species map boundaries had to be modified according to our knowledge of the migratory behaviour of the subspecies or populations from which

morphological data were gathered (see Electronic Supplementary Material, ESM, Table S1 for modifications). Using the distribution map shape files, we calculated the centroids of the spatial polygons of breeding and wintering ranges using the ‘gCentroid’ function of the R package ‘rgeos’ (Bivand and Rundel 2013). Migration distance was then calculated as the geographic distance between the breeding and wintering centroids using a custom function written in R 3.1 (R Core Team 2015) (see Methodological details in ESM). The latitudinal centroid of the breeding range (LCB) was used as a potential ecological confounder in the analyses since northerly-breeding birds have a higher tendency to be more migratory. The species pool we study captures a great deal of variation in migration distance (range 0–8526 km).

Wing Architecture

Wing architecture comprises four traits: wingspan (m), wing area (m²), wing loading (Nm⁻²) and aspect ratio (dimensionless). These were measured based on wing pictures (see Methodological details in ESM). Wing loading (weight/wing area) gives the relative size of the wings, and aspect ratio (wingspan²/wing area) describes both the size and shape of the wing (high values indicate a narrow wing relative to its length). Our dataset covers a huge variation in body mass (range 5.6–4263.5 g, 760-fold) and wing parameters (wingspan: 0.13–1.83 m, 14-fold; wing area: 0.0042–0.61 m², 145-fold; aspect ratio: 3.72–9.14, 2.5-fold; wing loading: 10.61–195.84 Nm⁻², 18.5-fold; see ESM Table S1).

Organ Size

Numerous bird specimens were brought frozen to JE, more than 95 % of them being found dead and the remaining were shot by hunters. Danish taxidermists are required by law to record the cause of death of all specimens in a log-book. Various visceral organs, labelled as exercise (left pectoralis major muscle [subsequently pectoral muscle], left supracoracoid muscle, heart) or nutritional organs (liver and gizzard) were removed during post-mortem examination and weighed by JE on a precision balance to the nearest 1 mg. Only birds with undamaged organs were considered, while storage caused negligible noise in organ masses (Møller et al. 2005). Data were recorded blindly with respect to the tested hypothesis. Our dataset covers a huge variation in organ mass (gizzard: 0.15–57.22 g, 381-fold; liver: 0.28–68.18 g, 243-fold; pectoral muscle: 0.35–182.79 g, 522-fold; supracoracoid muscle: 0.03–15.15 g, 505-fold; heart: 0.08–27.42 g, 343-fold; see ESM Table S1).

Statistical Analyses

All statistical analyses were conducted as implemented in R 3.1 (R Core Team 2015). To assess whether morphological traits are species-specific and thus suitable for multispecies comparison (Møller and Birkhead 1994), we tested the repeatability of these traits by assessing the importance of among-species compared to within-species variance (function ‘ICCest’ from R package ‘ICC’; Wolak et al. 2011). Since variance is dependent on sample size, the estimation of repeatability in comparative studies with unbalanced sample sizes across species is not equivocal. To cope with this problem, as a first step, species with only one individual sampled were excluded. Subsequently, we randomly picked two values out of the total number of measurements per species for the remaining species and partitioned variance to within- and among-group components. This was iterated 1000 times, so repeatabilities are the average of the 1000 repeatability estimates. Repeatability was tested using raw, non-transformed values.

Subsequently, we investigated by means of regression analyses how avian external and internal morphological traits (1) covary with each other, (2) scale to body mass and (3) explain migration distance. However, in regressions across multiple species the error terms of different species are correlated such that covariance is higher among closely related species due to longer shared phylogenetic history. Therefore, we developed phylogenetically informed models that account for the dependence of species by incorporating a matrix of covariances among species based on their phylogenetic relationships (Martins and Hansen 1997; Pagel 1997, 1999), and we estimated the importance of phylogenetic corrections (Freckleton et al. 2002). These analyses were based on the dated phylogeny published by Thuiller et al. (2011). Because five of our species were missing from this tree, our original sample size of 154 species dropped to 149. We used phylogenetic generalized least squares (PGLS) models as implemented in the ‘pgls’ function of the R package ‘caper’ (Orme et al. 2011). The phylogenetic signal Pagel’s λ (Pagel 1997, 1999) was estimated by maximum likelihood in each model. Strong and weak signal (i.e. λ approaches 1 and 0, respectively) indicates that evolution conforms to or deviates from the Brownian motion model, respectively. Three transformations were adopted prior to the analyses: (1) body mass and all morphological traits were log₁₀-transformed (LCB and migration distance were unaltered because raw values provided better fit to the distribution requirement of model residuals), (2) all morphological trait values were adjusted to unit body mass to rule out a scaling effect, and (3) all fixed effects were standardized to a mean of zero and a SD of one in order to avoid the large difference between the

intervals covered by different traits (cf. wing loading with body mass in ESM Table S1).

First, the pairwise relationships between the nine morphological characters as well as body mass was assessed by bivariate PGLS models with one trait as dependent and the rest sequentially set as a single fixed term. Second, to estimate the scaling of morphological characters to body mass, we used phylogenetically informed reduced major axis (PRMA) regressions ('*phyl.RMA*' function from R package '*phytools*'; Revell 2012) because accounting for dependence due to common descent is highly recommended in scaling studies (Harvey 2000). Scaling is expressed as a power function of the form $Y = a \times \text{mass}^b$, where Y is one of the morphological variables. With log-transformation the function becomes $\log(Y) = \log(a) + b \times \log(\text{mass})$, where a is the PRMA regression coefficient and b is the PRMA regression slope. Third, we fitted three sets of PGLS models with migratory flight distance as response variable and the following fixed effect formula: (1) all internal morphological traits + \log_{10} body mass + LCB; (2) all external morphological traits + \log_{10} body mass + LCB; and (3) all internal and external morphological traits + \log_{10} body mass + LCB (hereafter referred to as 'organ size', 'wing morphology' and 'organ and wing' models, respectively). These three sets of multiple regression models were reduced to minimal adequate models by a backward stepwise elimination procedure, discarding the least significant predictor at each step until only significant predictors remained. Using the information-theoretic approach and multi-model averaging yielded qualitatively similar results (not shown). We did not model second-order interactions between morphological traits since (1) this would enormously increase the number of parameters to be estimated leading to undue overfitting, and (2) the correlation between main effects and interaction terms would imply a serious multicollinearity issue.

Because morphological traits intercorrelate even after adjustment for body mass (see "Results"), we verified whether there is a multicollinearity problem in the models by computing the variance inflation factors (VIFs) within each MAM of the three model sets and found that values were all below the more conservative VIF <5 threshold. Therefore, multicollinearity does not bias our results. We also employed two filtering. First, we repeated the above three model sets by only using Passeriformes (84 out of 149 species, 56.4 %) to assess the robustness of the results to difference between passerines and non-passerines. Second, we repeated the above three model sets by excluding resident species with the filtering criterion of migration distance >0 km (127 out of 149 species, 85.2 %) to assess whether the morphological predictors of migration distance could arise due to the disparity between resident and migratory species subsets.

Results

Repeatability and Scaling

Each organ size and wing morphology trait was highly repeatable, and repeatability values, expressed as intra-class correlation coefficient (ICC), had a narrow confidence interval, which together show that these traits are highly species-specific (gizzard: $ICC = 0.93$, 95 % CI 0.90–0.96; liver: $ICC = 0.78$, 95 % CI 0.69–0.84; pectoral muscle: $ICC = 0.76$, 95 % CI 0.64–0.84; supracoracoid muscle: $ICC = 0.75$, 95 % CI 0.64–0.83; heart: $ICC = 0.92$, 95 % CI 0.89–0.95; wingspan: $ICC = 0.99$, 95 % CI 0.99–0.99; wing area: $ICC = 0.98$, 95 % CI 0.97–0.99; aspect ratio: $ICC = 0.91$, 95 % CI 0.88–0.94; note that wing loading has identical repeatability to that of wing area; for organ weights see also Garamszegi et al. 2002; Møller et al. 2005). Hence, species are confidently characterised in our dataset even if they are represented by only two individuals. Therefore, we included species irrespective of samples size per morphological trait in the analyses.

The scaling exponents of the nine morphological traits are shown in Table 1. We derived the mass-adjusted morphological trait values using the equation mass-adjusted trait = original trait/mass^{*b*}, where b is the scaling exponent (i.e. PRMA slope). These mass-independent morphological trait values were used in the subsequent analyses.

Covariation of Morphological Traits

External and internal morphological traits were significantly associated (all traits \log_{10} -transformed but not corrected for body mass, all $P \leq 0.02$; not shown). These associations probably stem from the body mass-dependence of morphological traits. However, a large number of

Table 1 Scaling of organ size and wing morphology traits estimated by phylogenetic reduced major axis (PRMA) regression

Morphological trait	<i>n</i>	<i>a</i>	<i>b</i>	R^2	Pagel's λ
Gizzard	107	−1.65	1.02	0.79	0.96
Liver	112	−1.45	0.94	0.85	0.91
Pectoral muscle	90	−1.24	1.01	0.89	0.92
Supracoracoid muscle	88	−2.06	0.98	0.85	1.00
Heart	112	−1.97	0.95	0.92	0.94
Wingspan	149	0.87	0.36	0.84	0.97
Wing area	149	1.04	0.69	0.85	0.96
Aspect ratio	149	0.43	0.14	0.04	0.96
Wing loading	149	0.59	0.45	0.65	0.96

PRMA coefficient, a , and slope, b , are reported together with the coefficient of determination, R^2 , and phylogenetic signal, Pagel's λ . For details, see "Materials and Methods"

relationships remained significant after traits were adjusted to unit body mass (ESM Table S2).

Migration Distance

The MAMs of each of the three multiple regression PGLS model sets contain LCB as a positive predictor of distance between breeding and wintering grounds with northerly-breeding species migrating longer distances for all species or passerines only (Tables 2, 3, 4). Body mass was a significant negative predictor of migration distance in the ‘organ size’ model set and when the analysis was based on the entire species pool, while in other models it was dropped during model reduction to MAMs (Tables 2, 3, 4).

In the ‘organ size’ model set (Table 2), mass-adjusted heart weight was significantly inversely related to migration distance in the full models based on both the entire species pool and on passerines only. However, it was dropped during model simplification to MAMs with other organ size traits. Therefore, none of the MAMs included the size of any organ to explain variation in migration distance among species (Table 2). Similarly, the size of

neither organ was retained when only the passerines were considered (Table 2). The MAM of the entire species pool fitted significantly better the data than the null model, which modelled only the intercept and did not include any organ size trait (AIC = 683.48 and 670.97 for null model and MAM, respectively; likelihood ratio test, LRT, of null model vs. MAM: LR = 16.51, df = 3, 5, P = 0.0003). The MAM based on only migratory species is the null model, since all morphological traits and the confounding LCB were rejected during model reduction.

In the ‘wing morphology’ model set (Table 3), wing loading was the only significant predictor of migration distance in the full model involving all studied species, where species making longer journeys having lower loadings. After model simplification to MAMs, however, aspect ratio was also retained besides wing loading when the analysis was based on the entire species pool. Species that migrate farther have significantly higher aspect ratio. When the analysis was restricted to passerines, both wing loading and aspect ratio were rejected, and wingspan and wing area became significant explanatory variables. Passerines that migrate farther have longer wingspan and smaller wing

Table 2 ‘Organ size’ model set: multiple regression PGLS model of migration distance in relation to log₁₀ body mass, latitudinal centroid of the breeding range (LCB) and all the organ size traits adjusted for body mass

Full model				MAM			
Predictors	β (SE)	t	P	Predictors	β (SE)	t	P
<i>(a) All species</i>				<i>(a) All species</i>			
<i>n</i> = 83, Pagel’s λ = 0.98				<i>n</i> = 149, Pagel’s λ = 0.80			
Intercept	3.39 (1.41)	2.41	0.019	Intercept	3.75 (1.10)	3.39	<0.001
Log ₁₀ body mass	−0.84 (0.49)	1.73	0.088	Log ₁₀ body mass	−1.26 (0.37)	3.39	<0.001
LCB	0.43 (0.22)	1.94	0.056	LCB	0.45 (0.17)	2.67	0.009
Gizzard	−0.32 (0.31)	1.02	0.313				
Liver	0.50 (0.36)	1.38	0.173				
Pectoral muscle	0.55 (0.35)	1.59	0.115				
Supracoracoid muscle	−0.61 (0.45)	1.36	0.179				
Heart	−0.77 (0.35)	2.22	0.03				
<i>(b) Only passerine species</i>				<i>(b) Only passerine species</i>			
<i>n</i> = 55, Pagel’s λ = 0.99				<i>n</i> = 84, Pagel’s λ = 0.86			
Intercept	1.80 (0.93)	1.92	0.06	Intercept	2.11 (0.92)	2.31	0.024
Log ₁₀ body mass	−0.47 (0.38)	1.22	0.229	LCB	0.61 (0.19)	3.17	0.002
LCB	0.34 (0.25)	1.36	0.182				
Gizzard	−0.59 (0.39)	1.52	0.135				
Liver	0.82 (0.43)	1.92	0.062				
Pectoral muscle	0.75 (0.41)	1.83	0.074				
Supracoracoid muscle	−0.33 (0.46)	0.73	0.468				
Heart	−0.59 (0.29)	2.02	0.049				

Both the full model and the derived minimal adequate model (MAM) are shown for analyses based on either (a) the entire species pool or (b) restricted to passerines. Significant relationships are highlighted in bold

Table 3 ‘Wing morphology’ model set: multiple regression PGLS model of migration distance in relation to \log_{10} body mass, latitudinal centroid of the breeding range (LCB) and all wing morphology traits adjusted for body mass

Full model				MAM			
Predictors	β (SE)	t	P	Predictors	β (SE)	t	P
(a) <i>All species</i>				$n = 149$, Pagel’s $\lambda = 0.76$			
Intercept	3.47 (0.92)	3.76	<0.001	Intercept	3.20 (0.87)	3.67	<0.001
\log_{10} body mass	−0.92 (0.66)	1.39	0.167	LCB	0.42 (0.15)	2.71	0.008
LCB	0.44 (0.15)	2.90	0.004	Aspect ratio	1.67 (0.22)	7.67	< 0.001
Wingspan	0.91 (1.75)	0.52	0.605	Wing loading	−0.69 (0.24)	2.88	0.005
Wing area	−1.46 (1.28)	1.14	0.257				
Aspect ratio	1.15 (0.90)	1.27	0.206				
Wing loading	−1.34 (0.60)	2.23	0.028				
(b) <i>Only passerine species</i>				$n = 84$, Pagel’s $\lambda = 0.86$			
Intercept	2.57 (0.76)	3.37	0.001	Intercept	2.49 (0.78)	3.20	0.002
\log_{10} body mass	−0.98 (0.91)	1.08	0.286	LCB	0.59 (0.17)	3.57	< 0.001
LCB	0.58 (0.17)	3.32	0.001	Wingspan	2.74 (0.51)	5.33	< 0.001
Wingspan	2.84 (3.35)	0.85	0.398	Wing area	−1.67 (0.48)	3.51	< 0.001
Wing area	−2.87 (2.01)	1.43	0.157				
Aspect ratio	−0.16 (2.23)	0.07	0.943				
Wing loading	−1.24 (1.20)	1.04	0.303				

Both the full model and the derived minimal adequate model (MAM) are shown for analyses based on either (a) the entire species pool or (b) restricted to passerines. Significant relationships are highlighted in bold

area (Table 3). The MAM of the entire species pool fitted significantly better the data than the null model, which modelled only the intercept and did not include any wing morphology trait (AIC = 683.48 and 634.86 for null model and MAM, respectively; LRT of null model vs. MAM: LR = 54.62, $df = 3, 6$, $P < 0.0001$). The MAM based on only migratory species contained the same significant predictors as the MAM without restriction to migrants (n species = 127, Pagel’s $\lambda = 0.74$; LCB: $\beta \pm SE = 0.45 \pm 0.17$, $t = 2.63$, $P = 0.01$; mass-adjusted aspect ratio: $\beta \pm SE = 1.58 \pm 0.26$, $t = 6.14$, $P < 0.0001$; mass-adjusted wing loading: $\beta \pm SE = -0.76 \pm 0.26$, $t = 2.86$, $P = 0.005$).

In the ‘organ and wing’ model set (Table 4), mass-adjusted heart mass was negatively related to migration distance in the full models of all species and passerines only, while mass-adjusted aspect ratio was positively related to migration distance in the full model involving all species. After minimization to MAMs, these two traits remained significantly associated with migration distance; species that cover longer distances have smaller relative heart weight and higher aspect ratio (Table 4; Fig. 1). The MAM of the entire species pool fitted significantly better the data than the null model, which modelled only the intercept and did not include any organ size or wing morphology trait (AIC = 502.65 and 464.13 for null model and MAM, respectively; LRT of null model vs. MAM: LR = 44.52,

$df = 3, 6$, $P < 0.0001$). The MAM based on only migratory species contained the same significant predictors as the MAM without restriction to migrants (n species = 92, Pagel’s $\lambda = 0.88$; LCB: $\beta \pm SE = 0.44 \pm 0.19$, $t = 2.35$, $P = 0.02$; mass-adjusted heart weight: $\beta \pm SE = -0.62 \pm 0.27$, $t = 2.30$, $P = 0.02$; mass-adjusted aspect ratio: $\beta \pm SE = 1.88 \pm 0.31$, $t = 5.99$, $P < 0.0001$).

To verify the robustness of our results, we conducted two sets of sensitivity analyses. First, because flapping or soaring flight style might favour different morphological traits in long-distance migrants, we tested whether exclusion of soaring birds (9 species; flight style label ‘2a’ in Bruderer et al. 2010) altered the results, but found qualitatively similar results (see ESM Tables S3–S5). Second, because organ sizes can considerably change as a function of migratory stage, we excluded all individuals with unknown collection date or collected during spring or fall migratory periods and once again we found qualitatively unchanged results (see ESM Tables S6 and S7).

Discussion

The prevailing view on the evolution of the flight apparatus suggests that flight-related morphology is evolutionarily labile (Piersma et al. 2005) and mirrors better the habitat-

Table 4 ‘Organ and wing’ model set: multiple regression PGLS model of migration distance in relation to \log_{10} body mass, latitudinal centroid of the breeding range (LCB) and all organ size and wing morphology traits adjusted for body mass

Full model				MAM			
Predictors	β (SE)	<i>t</i>	<i>P</i>	Predictors	β (SE)	<i>t</i>	<i>P</i>
(a) <i>All species</i> <i>n</i> = 83, Pagel’s λ = 0.96				<i>n</i> = 112, Pagel’s λ = 0.87			
Intercept	2.51 (1.16)	2.16	0.034	Intercept	2.84 (0.96)	2.96	0.004
Log ₁₀ body mass	0.90 (0.95)	0.95	0.346	LCB	0.39 (0.17)	2.33	0.021
LCB	0.30 (0.20)	1.52	0.133	Heart	−0.54 (0.23)	2.34	0.021
Gizzard	−0.17 (0.27)	0.64	0.521	Aspect ratio	1.83 (0.26)	7.14	<0.001
Liver	0.44 (0.32)	1.36	0.179				
Pectoral muscle	0.10 (0.35)	0.30	0.768				
Supracoracoid muscle	0.06 (0.41)	0.15	0.883				
Heart	−0.85 (0.33)	2.58	0.012				
Wingspan	−2.50 (2.35)	1.06	0.292				
Wing area	1.55 (1.90)	0.82	0.417				
Aspect ratio	3.20 (1.28)	2.50	0.015				
Wing loading	−1.07 (0.85)	1.26	0.213				
(b) <i>Only passerine species</i> <i>n</i> = 55, Pagel’s λ = 0.91				<i>n</i> = 67, Pagel’s λ = 0.83			
Intercept	2.38 (0.72)	3.32	0.002	Intercept	2.12 (0.74)	2.84	0.006
Log ₁₀ body mass	0.70 (0.83)	0.84	0.403	LCB	0.56 (0.21)	2.70	0.009
LCB	0.25 (0.24)	1.04	0.306	Heart	−0.63 (0.27)	2.36	0.021
Gizzard	−0.29 (0.34)	0.85	0.40	Aspect ratio	1.74 (0.31)	5.57	<0.001
Liver	0.65 (0.38)	1.69	0.098				
Pectoral muscle	−0.14 (0.42)	0.33	0.74				
Supracoracoid muscle	0.45 (0.42)	1.07	0.292				
Heart	−0.71 (0.30)	2.32	0.025				
Wingspan	−1.19 (3.37)	0.35	0.725				
Wing area	0.82 (1.87)	0.44	0.662				
Aspect ratio	2.63 (2.39)	1.10	0.277				
Wing loading	−0.62 (1.29)	0.48	0.635				

Both the full model and the derived minimal adequate model (MAM) are shown for analyses based on either (a) the entire species pool or (b) restricted to passerines. Significant relationships are highlighted in bold

specific feeding behaviour and related flight style than migratory behaviour (e.g. Rayner 1988; Norberg 1990; Leisler and Winkler 2003). By contrast, we found that such traits are conservative as evidenced by a strong phylogenetic signal. Despite this phylogenetic constraint, a few traits were significant predictors of migration distance across an ecologically diverse array of species studied.

Body mass was not a consistent predictor of migration distance being retained only in the organ size model set based on the entire species pool. Our findings thus suggest that the aerodynamic advantages of neither small nor large body mass drive the evolution of body mass to meet the challenges imposed by long-distance migratory flights. The weak association between body mass and migration distance is probably the mere consequence of several selective forces governing the evolution of body size (Winkler and

Leisler 1992), which is evidenced by the wide scatter of body masses even among long-distance migrants (from swallows to large raptors). Because the weight of visceral organs has a considerable contribution to body mass, and because we measured them mostly outside the migratory period, future studies analysing organ sizes measured on migratory birds could clarify this question.

Aspect ratio was proposed by many as a key adaptation to migration (see “Introduction”; but see Rayner 1990). The single stringent test of this hypothesis was conducted by Lockwood et al. (1998), who used 27 species pairs to control for phylogenetic effects and showed that birds categorised as migrants had higher aspect ratio than residents. We extended this analysis by using 149 species, modelling migration distance as a continuous variable and using multiple regression by considering many

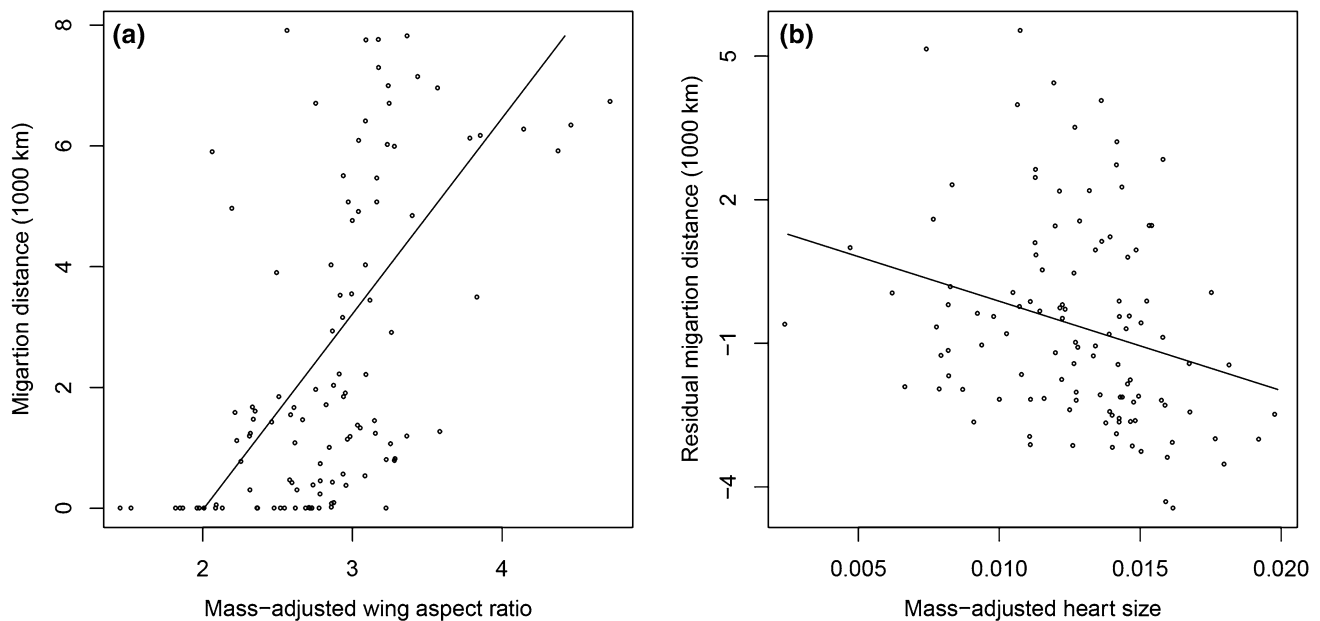


Fig. 1 Migration distance as a function of **a** mass-adjusted wing aspect ratio and **b** mass-adjusted heart mass. The graphs are drawn based on the MAM in Table 4a. On panel (b), residual migration distance reflects migration distance corrected for LCB and aspect ratio

morphological traits in addition to aspect ratio. Our findings corroborate that of Lockwood et al. (1998). Previous comparative studies did not find a correlation between wing loading and migration distance (Marchetti et al. 1995; Winkler and Leisler 1992), but we did when considering only external morphological traits and the entire species pool. This study is the first (1) to show a strong relationship between migration distance and heart weight and (2) to simultaneously analyse many morphological traits by taking phylogenetic and scaling effects into account.

The amount of work done to maintain level flight is a function of the magnitude of the net lift (i.e. lift-to-drag ratio), and the size and shape of the wing is decisive in this respect (Norberg 1990; Pennycuick 2008). Selection might not only minimize workload (i.e. energy or power per unit distance, also coined energy-efficiency or cost of transportation), but time per unit distance flown as well (i.e. time-efficiency). The two currencies are related to each other via flight velocity and because long travels assimilate more energy (Hedenström 1993). It is still unresolved which currency is more important for migrants (for energy, see Rayner 1988; Norberg 1994; for time, see Hedenström 1993, 2008). Lindhe Norberg (2002) argued that high aspect ratio combined with short wings (i.e. high wing loading) is favourable for long commuting flight because it ensures fast but still economic flight. Rayner (1988) used principal component analysis to obtain axes that correspond to size, wing loading and aspect ratio, and found that maximum range power (i.e. power needed to fly maximum range with unit energy) increases with larger size and

higher wing loading and decreases with higher aspect ratio, and migrants have high aspect ratio and low to medium wing loading. We reconsidered these associations by controlling for scaling and phylogenetic effects and found that long-distance migrants might reduce the maximum range power via higher aspect ratio, while wing loading has limited effects. In the model restricted to passerines, aspect ratio was discarded from the model, while wingspan was longer and wing area smaller with increasing migration distance. Note however, that long wingspan in combination with small wing area is characteristic for high aspect ratio wings. Therefore, high aspect ratio seems to be a general adaptation to long-distance migration in birds.

High aspect ratio is acknowledged for reducing the cost of transportation (i.e. maximization of flight range per unit energy) because it decreases the induced and profile drag (at low-to-medium and high airspeed, respectively), better shedding of wingtip vortices, and better glide ratio (sinking per horizontal speed) (Norberg 1990, 1994; Pennycuick 2008; Rayner 1988; Shyy et al. 2008; Withers 1981). Note that high aspect ratio might increase wing loading owing to the narrow wing mean chord (Norberg 1990; Alerstam et al. 2007; this study) and ultimately flight energetics (Rayner 1988), inasmuch as wingspan does not change. Depending on model set, wing loading either decreased or was not related to migration distance indicating that wingspan increased in parallel with aspect ratio, which prevented an elevated wing loading. The positive correlation of aspect ratio with wingspan, but lack of correlation with wing area, and the only subtle decrease of wing area

with migration distance lend support to this assertion (ESM Table S2). The combination of high aspect ratio with low-to-moderate wing loading is thought to be highly energy-efficient (Norberg 1990). Taken together, our results suggest that flight economy has selective priority over time-efficiency.

Contrary to our predictions, migration distance was not associated with flight muscle sizes and has a strong inverse relationship with heart weight. The supracoracoid muscle may function more in wing strokes related to diverse flight modes and in turn not being shaped by selection due to migratory flight. In contrast, pectoral muscle and heart weight directly determine the power available for flight (Bishop 1997; Rayner 1988). Further tests are required to clarify this questions, for instance, by collecting flight muscle size data from individuals belonging to several bird species that are prior to take on wings (exhibit zugunruhe and associated hypertrophied muscles) or are en route (exhibit either hypertrophied or atrophied muscles depending on how long they migrated before or on refuelling state).

Alternatively, organ weight of long-distance migrants might mirror the energetic exigencies that these birds face. Evidence from avian comparative studies (e.g. Wiersma et al. 2012) and mammalian artificial selection lines (Konarzewski and Diamond 1995) show that heart tissue is energetically expensive. Furthermore, both pectoral muscle and heart weight are considered indicators of aerobic costs during extensive locomotion (Bishop 1997; Klaassen 1996), which is supported by species with energetically expensive flight mode possessing larger relative flight muscle and heart weight in order to produce more power and to meet the aerobic scope (Bishop 1997; Norberg 1990). The average-sized flight muscles of long-distance migrants do not demand a large heart because heart size is optimized to satisfy the oxygen demand of exercise tissues (Bishop and Butler 1995). On the other hand, accepting the higher aspect ratio coupled with moderate wing loading as energy-saving adaptations in long-distance migrants, this might permit the evolutionary shrinkage of energetically costly exercise organs. A similar case has been reported for swordtail fish; species with longer sexually selected sword had higher swimming velocity and smaller heart mass (Oufiero et al. 2014). It should be noted, however, that the organ sizes presented here reflect the baseline levels and are not related to the size adjustments in the pre- or post-migratory periods. Great knots *Calidris tenuirostris* substantially reduce their organ sizes, except brain and lung, during a 5400 km flight (Battley et al. 2000). Therefore, the energetic hypothesis proposed above should be tested with comparative data for the relationship between migration distance and the magnitude of change in organ sizes between pre- and post-migratory periods.

Given the high demands of long-distance migration and a vast array of external and internal morphological traits expected to be related to these demands, it was proposed that a ‘migratory syndrome’ should exist (Dingle 2006; Piersma et al. 2005). The existence of syndromes implies that the traits that integrate into a syndrome are correlated by being either synergistic or antagonistic (Dingle 2006). However, the covariance of internal and external morphological traits thought to be part of the flight apparatus was not scrutinized by accounting for scaling and phylogenetic effects. Two recent reviews concluded that an integrated migratory syndrome is unlikely to exist because there are multiple solutions to the same migratory problem, and, therefore, only a subset of the allegedly migratory trait requirements are found per species (Dingle 2006; Piersma et al. 2005). Our results agree with this viewpoint, since only a few traits were strong predictors of migration distance despite the fact that several morphological traits correlate with each other.

To summarize, we showed that some morphological traits are likely adaptations to long-distance migration and related flight costs. Moreover, small-sized passerines seemingly are not exempt from this selection pressure. Therefore, we disagree with others (see also Voelker 2001), who suggested that migratory flight performance is negligible particularly in small birds and at best leads to subtle differences in morphology (Leisler and Winkler 2003; Rayner 1988; Winkler and Leisler 1992). Combining the results about the predictors of migration distance and covariance of morphological traits suggests that selection primarily optimizes the preservation of energy assets during long travels in order to increase flight range per unit energy. By virtue of their high aspect ratio that conserves energy and moderate wing loading that generates sufficient lift, migrants might not be subject to strong selection for large flight muscle and aerobic capacity. We encourage the collection of a considerable amount of new morphological data from several other bird species because questions like how flight style affects functional morphology of migrants and the scaling rules of these traits, and how organ sizes are adjusted during the migratory season deserve future comparative studies.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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