





Wing morphology covaries with migration distance in a highly aerial insectivorous songbird

Piotr Matyjasiak^{a,f,*}, Cosme López-Calderón^{b,g}, Roberto Ambrosini^{c, }, Javier Balbontín^b,
Alessandra Costanzo^{c, }, Yosef Kiat^{d, }, Andrea Romano^c, Diego Rubolini^{c,e, }

^aMuseum and Institute of Zoology Polish Academy of Sciences, Wilcza 64, PL-00-679 Warsaw, Poland

^bDepartamento de Zoología, Facultad de Biología, Edificio Verde, Avda. de Reina Mercedes s/n, E-41012 Sevilla, Spain

^cDipartimento di Scienze e Politiche Ambientali, Università degli Studi di Milano, via Celoria 26, I-20133 Milan, Italy

^dIsraeli Bird Ringing Center (IBRC), Israel Ornithological Center, Society for the Protection of Nature in Israel, Hanegev 2, Tel-Aviv, Israel

^eIstituto di Ricerca sulle Acque, IRSA-CNR, Via del Mulino 19, I-20861 Brugherio (MB), Italy

^f(present address) Institute of Biological Sciences, Cardinal Stefan Wyszyński University in Warsaw, Wóycickiego 1/3, PL-01-815 Warsaw, Poland

^g(present address) Department of Wetland Ecology, Estación Biológica de Doñana CSIC, Americo Vespucio s/n, E-41092 Seville, Spain

*Address corresponding to Piotr Matyjasiak. E-mail: pmatyjasiak@wp.pl

Handling editor: Zhiy-Yun Jia

Abstract

According to classical prediction of aerodynamic theory, birds and other powered fliers that migrate over long distances should have longer and more pointed wings than those that migrate less. However, the association between wing morphology and migratory behavior can be masked by contrasting selective pressures related to foraging behavior, habitat selection and predator avoidance, possibly at the cost of lower flight energetic efficiency. We studied the handwing morphology of Eurasian barn swallows *Hirundo rustica* from four populations representing a migration distance gradient. This species is an aerial insectivore, so it flies extensively while foraging, and may migrate during the day using a 'fly-and-forage' migration strategy. Prolonged foraging flights may reinforce the effects of migration distance on flight morphology. We found that two wings' aerodynamic properties—*isometric handwing length and pointedness*, both favoring energetically efficient flight, were more pronounced in barn swallows from populations undertaking longer seasonal migrations compared to less migratory populations. Our result contrast with two recent interspecific comparative studies that either reported no relationship or reported a negative relationship between pointedness and the degree of migratory behavior in hirundines. Our results may thus contribute to confirming the universality of the rule that longer migrations are associated with more pointed wings.

Key words: flight morphology, geographical differences, *Hirundo rustica*, migration syndrome, population, wing shape.

The wings of powered fliers, such as birds and bats, are shaped by selection pressures for an optimal structure and shape to increase aerodynamic and mechanical performance, while minimizing flight costs (Pennycuik 1975; Norberg 1990). At the same time, flying organisms show enormous variation in wing shape and size, which can be observed between lineages, as well as at the species level and between populations (Rayner 1988). Aerodynamic and ecomorphological studies have identified a number of pressures that select for divergence in flight morphology and, importantly, have the potential to interact with or oppose each other (Norberg and Rayner 1987; Rayner 1988). Long high aspect ratio (length to breadth ratio) wings with pointed tips are favored by the demands of continuous flight for long periods of time, as in long aerial foraging trips or commuting flights (Norberg and Rayner 1987; Lockwood et al. 1998), dispersal ability (Sheard et al. 2020; Claramunt 2021) and especially seasonal migrations (Bowlin and Wikelski 2008). Long pointed wings (i.e., a wingtip feather shifted towards the leading edge) give the greatest lift in relation to induced drag and

thus reduce the power required to fly and cost of transport (Norberg 1990; Thomas 1996). Co-evolutionary interactions with predators and prey also shape wing morphology, particularly in species that forage on the wing, as wing morphology can affect the efficiency of both foraging (Marchetti et al. 1995; Forstmeier and Kessler 2001; Keast 1996) and predator avoidance (Alatalo et al. 1984; Swaddle and Lockwood 1998; Fernández-Juricic et al. 2006). For instance, broad wings with low wing loading (ratio of body weight to wing area) and relatively short and rounded handwings appear to be associated with the foraging strategy involving catching airborne insects in highly maneuverable flight (Norberg and Rayner 1987; Rayner 1988). This applies both to coursing aerial insectivores (species specializing in continuous aerial insectivory) using insect hawking strategy or hunting in lower air layers where the air can be turbulent, and to species sallying out from a perch to snatch flying insects (Norberg and Rayner 1987; Warrick 1998). The broad and rounded wings produce high power (and more thrust) at low speeds, which has a positive effect on maneuverability and allows for greater acceleration,

Received 2 March 2022; accepted 26 May 2022

© The Author(s) 2022. Published by Oxford University Press on behalf of Editorial Office, Current Zoology.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact journals.permissions@oup.com

but at the cost of lower energetic efficiency in cruising flight (Norberg 1990; Thomas 1996). On the other hand, coursing aerial insectivores can benefit from long, pointed wings that allow for high agility in fast flight maneuvers (measured as the time it takes to initiate and complete a turn; Thomas 1996; Warrick 1998). Finally, sexual selection can influence wing design. By generating more lift, the large or long wings help perform energy-expensive aerial displays (Hedenström and Møller 1992; Voelker 2001; Carvalho Provinciato et al. 2018) or compensate for the aerodynamic drag of long tail ornaments (Balmford et al. 1994; Møller et al. 1995b), leading to sexual dimorphism in wing size and shape.

It has long been predicted that bird or bat species that undertake longer seasonal migrations have longer and pointier wings compared to sedentary species (Winkler and Leisler 1992, 2005; Mönkkönen 1995; Lockwood et al. 1998; Leisler and Winkler 2003; and earlier work cited therein). In recent years, the existence of this relationship has been confirmed by a number of comparative (Outlaw 2011; Wang and Clarke 2015; Vágási et al. 2016; Phillips et al. 2018; MacPherson et al. 2022) or individual-based studies (Fiedler 2005; Milá et al. 2008; Baldwin et al. 2010; Förschler and Bairlein 2011; Neto et al. 2013; but see Fudickar and Partecke 2012; Corman et al. 2014; and below). However, few studies to date have focused on diurnal migratory species that hunt on the wing and therefore fly extensively when foraging, such as swallows and swifts (aerial insectivores), falcons (bird or airborne insect hunters) and terns (fish or aquatic insect hunters). These species are of particular interest for two reasons. First, sustained foraging flights might reinforce the effects of seasonal migration demands on flight morphology (Norberg and Rayner 1987; Rayner 1988). Second, these birds can reduce their cost of migratory flight by utilizing the ‘fly-and-forage’ migration strategy, whereby they combine foraging with covering migration distance (Alerstam 2009). The results of recent comparative studies involving hirundines (swallows and martins, Hirundinidae) contradict the general rule that migratory species have pointier wings compared to more sedentary species (Philips et al. 2018). Even the opposite relationship has been shown—that migratory hirundines possess more rounded handwings than sedentary ones (Huber et al. 2017). However, the results of other studies suggest that in the barn swallow *Hirundo rustica* wing pointedness is favored by selection because birds with pointier wings arrive earlier from spring migration (Matyjasiak et al. 2013) and breed earlier (Saino et al. 2017), thus achieving greater seasonal reproductive success.

We investigated the relationship between wingtip morphology and migratory distance in Eurasian barn swallows. This species breeds in a wide band throughout Eurasia and North America, as well as locally in northern Africa and South America, spending the winter in the tropics and across the southern hemisphere. There are at least six subspecies characterized by differences in seasonal migration distance (Turner 2006; Liechti et al. 2015; Briedis et al. 2018; Brown and Brown 2020; López-Calderón et al. 2021). The West Eurasian nominate *H. r. rustica* is a long-distance migrant, wintering in sub-Saharan Africa and the Indian subcontinent. Individuals from northern parts of Europe are the farthest migrants, wintering in Africa south of the equator, whereas those from southern Europe winter in west-central Africa (Ambrosini et al. 2009). The East-Mediterranean *H. r. transitiva* is partly sedentary and partly a short-distance migrant,

while the Egyptian *H. r. savignii* is sedentary. West Eurasian barn swallows are characterized by elongated outermost tail feathers, males having significantly longer tail than females. The function of this sexually dimorphic trait has been hotly debated (Evans and Thomas 1997; Møller et al. 1998). In males, the proximal part of these feathers apparently aids in flight maneuverability (Evans 1998; Rowe et al. 2001; Matyjasiak et al. 2004), while the distal part is aerodynamically costly and purely ornamental (Møller 1994; Møller et al. 1995a; Matyjasiak et al. 2009). The length of the outermost tail feathers increases with latitude and thus with migration distance (Møller 1995; Møller et al. 2006). Furthermore, it covaries positively with the length and size of the wings, which is considered an adaptation that compensates for the aerodynamic cost of ornamental tail (Møller et al. 1995b).

We tested whether migration distance in barn swallows is related to wingtip length, wingtip pointedness and wingtip trailing edge concavity, which are known morphological variables important to determine the aerodynamic cost of flight (Rayner 1988; Norberg 1990; Lockwood et al. 1998). We predicted that (1) wingtip length (relative to body size) would increase with migration distance and (2) that long-distance migrating populations would have pointier wingtips compared to less migratory or sedentary ones. In concave wings, the intermediate primary feathers are short relative to the outer and inner primaries; hence more concave handwings translate into higher aspect ratio wings (Lockwood et al. 1998). We therefore predicted that (3) longer migrating populations would have more concave wingtips.

Materials and Methods

Study species

Barn swallows are small (body mass: *ca.* 18 g, wing span: *ca.* 0.34 m), strong flying, aerially insectivorous birds. During the breeding season they are closely associated with human dwellings and usually nest singly or in colonies on buildings, in Europe usually in association with livestock farming (Møller 1994; Turner 2006). Being highly aerial insectivores, barn swallows need to maintain high flight efficiency and thus annual molt is slow in this species (Kiat et al. 2016), sometimes starting before autumn migration (Rubolini et al. 2002a), but most molting takes place on the wintering grounds (Turner 2006; Kiat et al. 2019; Jenni and Winkler 2020).

Recent phylogeographic analyses of the barn swallow suggest that (1) the European *H. r. rustica* populations are not genetically structured, and (2) the European *H. r. rustica* and East-Mediterranean *H. r. transitiva* populations, despite their considerable differentiation in morphological (including those sexually selected), behavioral (including migratory behavior) and life history traits, are very recently diverged and only negligibly genetically differentiated (Santure et al. 2010; Dor et al. 2010, 2012). However, the most recent analysis of complete mitogenomes of barn swallows has revealed some genetic differentiation between *H. r. rustica* and *H. r. transitiva*, as well as among populations of the former subspecies (Lombardo et al. 2022).

Study populations and procedures

We studied Eurasian barn swallows at four breeding populations in the Western Palearctic (Figure 1): in Shefayim (Israel: 32°13'N, 34°49'E), around Seville (Spain: 37°36'N, 6°14'W), around Milan (Italy: 45°05'N, 9°20'E), and near

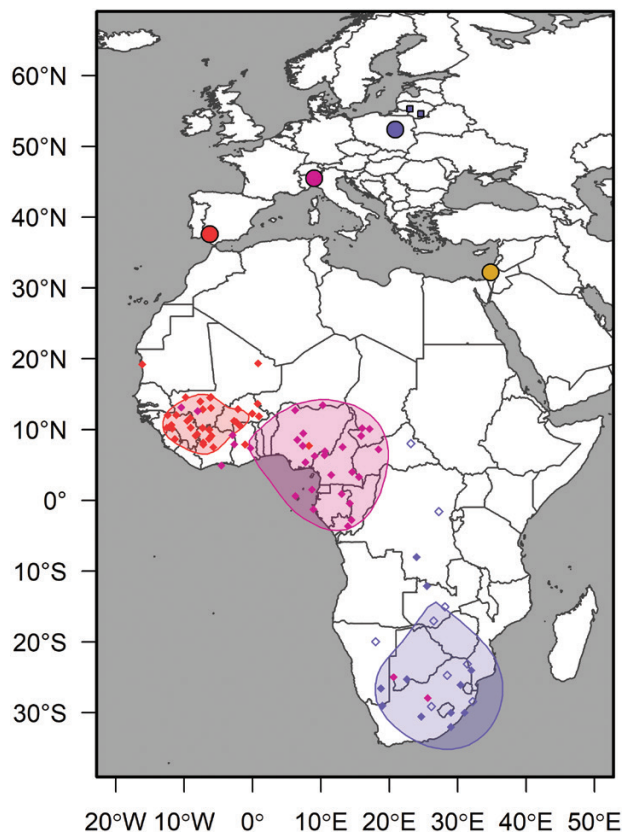


Figure 1. Eurasian barn swallow *Hirundo rustica* populations investigated in the present study. Circles represent the breeding colonies where individual morphological variables were measured. Breeding colonies in Europe belong to the subspecies *H. r. rustica* (migratory), whereas the breeding colony in Israel belongs to the subspecies *H. r. transitiva* (resident). Filled diamonds represent wintering centroids of 35, 32 and 12 individuals tagged with light-level geolocators in the Spanish, Italian and Lithuanian-Polish breeding populations (Seifert et al. 2018; Briedis et al. 2018; López-Calderón et al. 2021; Matyjasiak P, López-Calderon C, Ambrosini R, et al., unpublished). The two squares in Lithuania indicate the specific breeding colonies in which Northern European barn swallows were tagged with geolocators (we assume that migratory behavior of such individuals is the same as these from Poland). We estimated wintering areas for each breeding population as 0.5 kernel utilization distributions with R package *adehabitatHR* (Calenge 2006). In order to avoid replication, we only included one wintering centroid per individual. To increase sample size for the Lithuanian-Polish breeding population, we pooled together the 12 geolocator-tagged swallows with nine winter recoveries of barn swallows ringed in Poland. The latter nine ringing recoveries are denoted as open diamonds. The color of diamonds and kernel utilization distributions correspond to the color of breeding colonies.

Warsaw (Poland: 52°22'N, 20°52'E). Our study populations in Spain, Italy and Poland represent the nominate subspecies *H. r. rustica*, while the population from Israel belongs to the East-Mediterranean *H. r. transitiva*. Migration behavior varies considerably among these populations (Table 1). The population from Poland migrates furthest and spends the winter in southern Africa (Briedis et al. 2018; Matyjasiak P, López-Calderon C, Ambrosini R, et al., unpublished), while the transitiva population we studied in Israel is sedentary (Brown and Brown 2020). Between these extremes lie the long-distance migratory Italian population, wintering in Cameroon and surrounding countries (Liechti et al. 2015), and the shorter migrating Spanish population, flying for the winter to Ivory

Coast and surrounding countries (López-Calderón et al. 2021).

All data were collected in 2019. During early breeding season (February–June) we captured adult barn swallows by intensive mist-netting at their pre-breeding roost sites (Israel) or breeding colonies (Spain, Italy and Poland) located in rural buildings. Upon capture, biometric measurements were taken, birds were ringed with a numbered metal leg-ring for later identification, and then were released. To estimate wingtip morphology, we measured the lengths of nine primary wing feathers, skipping the outermost, vestigial P10 primary. The measurements therefore encompassed the primaries from P9 (forming the leading edge of the wing) to the innermost P1 primary. The primary lengths were measured to the nearest 0.5 mm by inserting a ruler (specially designed with a fixed pin at the base) between the feather to be measured and the adjacent proximal primary feather (Jenni and Winkler 1989). The same method was used to measure the length of outermost tail feathers and thus the tail length. Right tarsus length was measured to the nearest 0.1 mm using a caliper. Body mass was measured to the nearest 0.5 g with a Pesola spring balance.

Sex was determined at capture by differences in shape of the cloacal region, and by the presence (females) or absence (males) of a brood patch (according to Svensson 1992), or later by observation of birds' behavior at the nests. For birds from the Israeli population, molecular sex determination was used because we were working in a pre-nesting roost site, too early to use external traits and due to the ineffectiveness of tail length for sex identification in this subspecies. For this purpose, 50–150 µl of blood was collected from birds from the brachial vein by venipuncture. Sex was determined using the CHD-Z and CHD-W molecular markers according to well established and previously described protocols (Saino et al. 2015).

Estimation of wingtip shape and size indicators

We quantified the wingtip morphology in barn swallows using the size-constrained Principal Component Analysis (ScPCA; Lockwood et al. 1998). ScPCA partitions the multivariate variance of handwing flight feather lengths into an isometric size component (C_1) and two shape components, wingtip pointedness/roundedness (C_2) and concavity/convexity (C_3). These components are statistically independent measures of handwing morphology that help to distinguish between isometric size and shape when analyzing wingtip shape variation (Figure 2; Lockwood et al. 1998). The isometric size component (C_1) reflects wing length. Pointedness/roundedness (C_2) reflects the length of the outermost primary feathers relative to the innermost ones. In pointed wings, the outermost primary feathers are relatively long, shifting the wing tip towards the leading edge of the wing. Concavity/convexity (C_3) reflects the length of the intermediate primaries in relation to both the outermost and innermost primaries and describes the shape of the handwing trailing edge.

We applied ScPCA to primary (P1–P9) length measurements (which were collected in the field) by means of the *sizepca* v.6.0 software (Lockwood et al. 1998). Because barn swallows show sexual dimorphism in wing length and size (and in some other morphological variables, including tail length and body mass; Bañbura 1986; Møller 1994), we conducted the analysis separately for males and females. We extracted three size-constrained principal components from

Table 1. Seasonal migration distances covered by study populations of Eurasian barn swallows *Hirundo rustica* and sample sizes obtained in these populations

Study populations	Mean (range) Great Circle distance (km)	Wintering area	Sources	Sample size (males, females)
Israel (Shefayim)	0 (0–500)*	Eastern Mediterranean (the Levant)	Brown and Brown (2020)	48 (23, 25)
Spain (Seville)	2980 (2250–3620)	West Africa	López-Calderón et al. (2021)	69 (38, 31)
Italy (Milan)	4500 (3600–5200)	Central and west-central Africa	Liechti et al. (2015)	375 (200, 175)
Poland (Warsaw)	8500 (5000–9000)	Southern Africa (south of the equator)	Briedis et al. (2018), Matyjasiak P, López-Calderon C, Ambrosini R, et al., unpublished	114 (58, 56)

*The population we studied in Israel is resident.

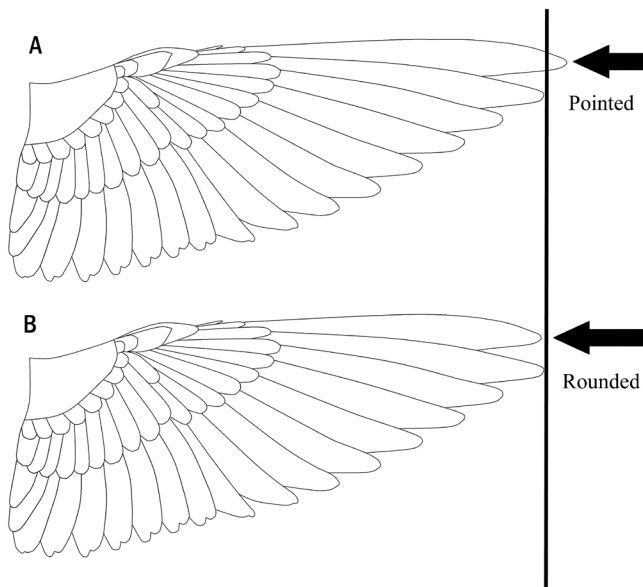


Figure 2. Representations of pointed (A) and rounded (B) wingtips in male and female Eurasian barn swallows. Arrows highlight the differences in relative length of the two outermost primary wing feathers, which mostly contribute to differences in wing pointedness among individuals.

the primary length data on either sex (Table S1). The first component (C_1) reflected wing length and size, by definition (Table S1; Lockwood et al. 1998). In the case of the two shape components, the signs of the component loadings suggest that the second components (C_2) were vectors of increasing wingtip pointedness, while the third components (C_3) were vectors of increasing wingtip trailing edge concavity (Table S1). Hence, high values of wingtip isometric size, pointedness and concavity were associated with longer wings, more pointed wingtips and more concave outline of the handwing trailing edge, respectively (Lockwood et al. 1998).

Statistical analyses

The dataset comprised 606 individuals with a full set of biometric measurements (Table 1). To assess errors in primary length measurements, we used biometrics taken from 20 individuals captured twice in the same breeding season to calculate repeatability estimates (intra-class correlation

coefficients, r ; Falconer and Mackay 1996). Measurements of the length of individual primary feathers were characterized by small measurement errors (no larger than the phenotypic variation between individuals), as evidenced by their high repeatability ($0.91 \leq r \leq 0.99$, $20.8 \leq F_{19,1} \leq 154.7$, all $P < 0.001$; $N = 20$). Such high repeatability is typical of primary length measurements (Jenni and Winkler 1989; Lockwood et al. 1998). Thus, our primary length measurements were sufficiently precise to allow use in statistical analyses.

We relied on linear models to analyze the relationships between isometric wingtip length and shape indices and migratory behavior in our study populations. We built separate full models with each wingtip length or shape index as a response variable, including population (four-level factor), sex as a binary variable ('female' = 0, 'male' = 1), and tail length, tarsus length and body mass as continuous covariates (to control for variation in body size). We also included in each full model all two-way population or sex by tail length, tarsus length or body mass interactions. Non-significant interactions ($P > 0.05$) were removed in a single step.

The population factor encoded the origin of the barn swallows studied, and thus an increasing gradient in seasonal migration distance (from the sedentary Israeli population to the farthest migrating Polish population). As we tested the hypothesis that wingtip length, pointedness and concavity would increase with migration distance, we took the Israeli population as the reference (default) level in all models. Input variables were centered (mean subtracted) and scaled (divided by 2 SD) prior to analyses to facilitate interpretation and comparison of effect sizes based on parameter estimates (Gelman 2008). Effect estimates are reported with their associated standard errors. Models were fitted using IMB SPSS Statistics v.27 software.

Results

Linear model controlling for the independent effects of sex and body size variables showed that isometric wingtip length component (C_1) in barn swallows increased significantly with migration distance, but this was only true for the group of migratory populations (Spanish, Italian and Polish; Table 2, Figure 3A). In the sedentary Israeli population, isometric wingtip length was similar to that of the highly migratory Polish population, while it was significantly greater than in the other migratory populations (i.e., the Spanish and

Table 2. Results of linear models of barn swallow isometric wingtip length (C_1), pointedness (C_2) and concavity (C_3) indices in relation to population-specific migratory behavior (population factor: four Western Palearctic populations from Israel, Spain, Italy and Poland representing an increasing gradient in seasonal migration distance)

Response variable	Explanatory variables	Estimate \pm SE	t^a	P
Isometric wingtip length (C_1 score) ($df = 596$)	Intercept	0.257 \pm 0.066	3.90	< 0.001
	Population: Spain	-0.471 \pm 0.080	5.89	< 0.001
	Population: Italy	-0.169 \pm 0.067	2.53	0.012
	Population: Poland	0.066 \pm 0.078	0.85	0.398
	Sex	0.354 \pm 0.061	5.77	< 0.001
	Tail length	0.516 \pm 0.060	8.54	< 0.001
	Tarsus length	-0.021 \pm 0.038	0.54	0.589
	Body mass	0.124 \pm 0.045	2.75	0.006
	Sex \times tail length	0.507 \pm 0.117	4.33	< 0.001
	Sex \times body mass	-0.199 \pm 0.086	2.32	0.021
Wingtip pointedness (C_2 score) ($df = 598$)	Intercept	-0.302 \pm 0.070	4.34	< 0.001
	Population: Spain	0.160 \pm 0.098	1.63	0.103
	Population: Italy	0.335 \pm 0.074	4.56	< 0.001
	Population: Poland	0.407 \pm 0.088	4.65	< 0.001
	Sex	0.249 \pm 0.065	3.82	< 0.001
	Tail length	0.322 \pm 0.064	5.03	< 0.001
	Tarsus length	0.093 \pm 0.045	2.07	0.039
	Body mass	-0.032 \pm 0.044	0.73	0.465
Wingtip concavity (C_3 score) ($df = 598$)	Intercept	-0.017 \pm 0.072	0.23	0.818
	Population: Spain	-0.121 \pm 0.100	1.21	0.227
	Population: Italy	0.037 \pm 0.076	0.49	0.626
	Population: Poland	0.039 \pm 0.089	0.44	0.660
	Sex	0.086 \pm 0.066	1.30	0.193
	Tail length	0.108 \pm 0.066	1.64	0.102
	Tarsus length	0.100 \pm 0.046	2.20	0.028
	Body mass	-0.032 \pm 0.042	0.76	0.445

Reference (default) level at which the intercept was calculated was 'Israel'. Sex was included as a binary variable with zero indicating 'female' and one indicating 'male'. All non-categorical model terms were centered to mean 0 and rescaled to 2 SD to facilitate interpretation and comparisons.

^aThe degrees of freedom (df) are given in the first column of the table.

Italian populations; Table 2, Figure 3A). Males and females were not significantly different in terms of these relationships (Table 2). A comparison of the intercept shifts for migratory populations showed that wingtips were longer in Italian barn swallows as compared to Spanish barn swallows [estimate (SE) = 0.302 (0.057), $t_{596} = 5.36$, $P < 0.001$] and were longer in Polish barn swallows as compared to Italian birds [estimate (SE) = 0.235 (0.050), $t_{596} = 4.54$, $P < 0.001$]. Therefore, the results partly support our prediction that wingtip length would increase with migration distance.

Analysis of the effect estimates showed that wingtip pointedness component (C_2) increased consistently and significantly in the gradient of increasing migration distance, from the sedentary Israeli population to the furthest migrating Polish population (Table 2, Figure 3B). No significant sex differences were found in this relationship (Table 2). This result is entirely consistent with our prediction that wingtip pointedness would increase with increasing migration distance.

After accounting for the independent effect of sex and body size variables, no statistically significant relationship was found between wingtip concavity component (C_3) and migration distance among the four populations of barn swallows (Table 2). We therefore found no empirical support for our third prediction that wingtip concavity would increase with increasing migration distance.

Discussion

We investigated whether handwing morphology is associated with population-specific seasonal migration distance in a highly aerial insectivorous bird, the barn swallow. We found that isometric wingtip length (C_1) significantly increased with migration distance, but only among migratory populations—it was lowest in the Spanish population and highest in the Polish population. Sedentary barn swallows from the Israeli population resembled highly migratory birds from the Polish population with respect to this wing morphological trait. Second, isometric wingtip pointedness (C_2) in male and female barn swallows increased consistently and significantly with increasing migration distance, from the sedentary Israeli population to the longest migrating Polish population. Third, isometric wingtip concavity component (C_3), which reflects the wing aspect ratio, did not change significantly with increasing migration distance.

In this individual-based study, we found support for the hypothesis that Eurasian barn swallow populations undertaking longer seasonal migrations have wings with pointier handwing sections compared to less migratory populations (Table 2, Figure 3B). The novelty of this result contrasts with recent interspecific comparative studies that either found no relationship (Philips et al. 2018) or a negative relationship

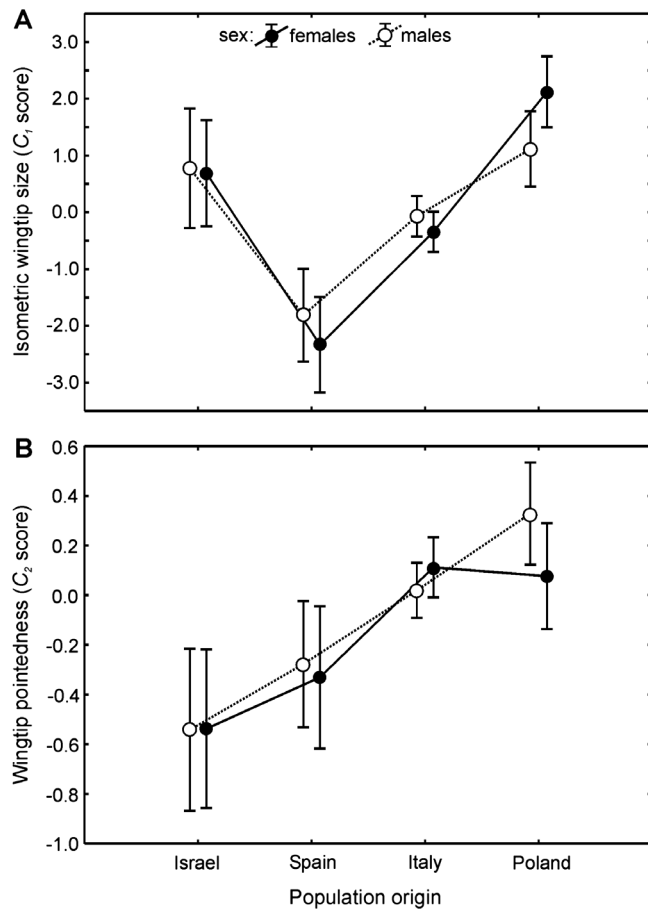


Figure 3. Variation in (A) isometric wingtip length (C_1 component) and (B) wingtip pointedness (C_2 component) in females (filled circles) and males (open circles) across four Western Palearctic populations of the Eurasian barn swallow (from Israel, Spain, Italy and Poland), representing increasing gradient of seasonal migration distance. The Israeli population is sedentary. Bars represent confidence intervals around the mean.

between pointedness and the degree of migratory behavior in hirundines (Huber et al. 2017). Previous studies on the relationship between wing morphology and migratory behavior in birds have mainly focused on passerines. Species of this clade (the order Passeriformes) are characterized (excluding hirundines) by broad wings with rounded tips and usually high wingloading, very different in shape from those favored by selection for energetically efficient sustained forward flight (Rayner 1988; Norberg 1990). The species we studied has high aspect ratio wings with pointed tips, close to the optimum from the point of view of flight energetic efficiency. Our results can thus contribute to the universality of the rule that longer migrations are associated with pointier wings (Winkler and Leisler 1992, 2005; Mönkkönen 1995; Lockwood et al. 1998; Leisler and Winkler 2003).

In order to quantitatively describe wingtip morphology, we used composite measures of wingtip shape and size that control for allometry and are recommended in this type of research (see discussion in Lockwood et al. 1998). But to illustrate in real terms the magnitude of differences in wingtip pointedness between barn swallow populations differing in migratory behavior, differences in millimeters of length of primary P9 (forming the leading edge; see Figure 2) and primary P8 can be used. The mean differences in length of these

feathers (P9 minus P8) in males and females from the highly migratory Polish population vs. the less migratory Spanish population were (mean \pm SE) as follows: males 0.9 ± 0.1 mm, females 0.3 ± 0.2 mm vs. males 0.2 ± 0.2 mm, females -0.1 ± 0.2 mm (sample sizes are given in Table 1). The differences between the two populations appear small, but in magnitude they correspond to similarly quantified differences in handwing pointedness between sex and age groups of barn swallows (see calculations above and Figure 1 in Saino et al. 2017).

We found that isometric handwing length (C_1 component) did not increase with migration distance starting from the sedentary Israeli population, but this increase could only be observed within the group of migrating populations, from the Spanish to the Polish population (Figure 3A). Contrary to what we expected, barn swallows from the sedentary Israeli population closely resembled birds from the highly migratory Polish population in this flight morphological trait (Table 2). This discrepancy between expected and observed geographical trends in barn swallow handwing length could be explained by a steady genetic influx due to barn swallow migrants from populations located in the north passing through the Eastern Mediterranean (Pérez-Tris et al. 2004; Baldwin et al. 2010) and perhaps also by selection forces other than migration. This issue is certainly worth further research.

The lack of association we found between the migratory behavior of barn swallows and the concavity of their handwings (C_3 component; Table 2), a measure that closely matches the wing aspect ratio and is one of the good predictors of migratory behavior (Lockwood et al. 1998), can be explained by referring to the results of interspecific comparative studies of flight morphology and wing aerodynamics. Barn swallows and other hirundines have long, pointed wings with an above-median aspect ratio compared to bird species representing a wide range of systematic and ecological groups (Rayner 1988; Norberg 1990). Barn swallows hunt for insects in the air and therefore spend much of their lives in flight (Turner 2006). Consequently, their flight morphology should be subject to strong selection for energetically efficient flight in both highly migratory and more sedentary populations. The effect of this may be that there is little variation in wingtip shape between barn swallow populations differing in migratory distance and that it is therefore difficult to detect relationships between migratory behavior and wingtip shape of hirundines in comparative studies (as in Philips et al. 2018).

In the present study, it is worth noting that tail length was relatively strongly and positively associated with handwing length and pointedness, and to some degree with handwing concavity (Table 2). It is beyond the scope of this study to analyze the exact background of this relationship, but we will try to propose two possible explanations for it. First, the above relationship and also the increase in wingtip pointedness and length with migration distance, from southern to Northern European populations, may reflect a compensatory role of wing size and shape in relation to the aerodynamic cost of tail ornamentation (Balmford et al. 1994; Møller et al. 1995b). We would expect the covariation between tail length and wing morphology not to occur in the sedentary Israeli population, whose tail is short, sexually monomorphic, and probably does not act as a signal in sexual selection (although this issue needs to be investigated in the future). However, this covariation did not differ between the study populations (Table 2). Second, the covariation between tail length

and wing morphology may be related to the requirements of flight maneuverability during everyday foraging and migration. The forked tail, which is typical of hirundines, can produce additional lift, augmenting the lifting surface of long and pointed wings when flying slowly or making a turn (Thomas 1993, 1996; Rowe et al. 2001). Barn swallows are coursing aerial insectivores that rely on maneuverability to catch large, strong flying insects, many of which are maneuverable in their own right. They use the “fly-and-forage” migration strategy (Rubolini et al. 2002b; Turner 2006), which means they usually migrate by day, frequently flying at low altitude (up to 100 m and often just a dozen meters above the ground level). Foraging at low altitude or migrating during the day, barn swallows must be able to respond quickly to perturbations such as dynamic near-ground wind conditions (wind gradients and changing wind directions), turbulence and terrain obstacles. Large maneuverability can make them better able to control their position to be stable in the air and maintain their path during flying in turbulent conditions, or taking advantage of wind gradients near the ground, both during daily foraging and migratory flight (Thomas and Taylor 2001; Warrick et al. 2016). We would expect the relationship between tail length and wing morphology to be stronger in highly migratory populations and weaker in sedentary populations, where the two traits may evolve independently of each other. However, the results of our analyses did not support this prediction (Table 2). These are important issues to be investigated in future studies.

The difference between the results of our individual-based study and those of the comparative research by Huber et al. (2017), reporting that highly migratory hirundines have more rounded wingtips compared to more sedentary ones, is remarkable. However, it should be noticed, as Saino et al. (2017) pointed out earlier, that in Huber et al. (2017) differences between sexes in wingtip morphology were not taken into account and, consequently, the effect of sexual selection on wingtip morphology was not assessed. Male barn swallows have longer and more pointed wings than females (Saino et al. 2017). In addition, the isometric length and pointedness of the wingtip significantly covaries with the length of the tail (this study). The exceptionality of results by Huber et al. (2017) may also be due to the fact that they did not take into account the geographic origin of the measured specimens, but wingtip morphology may be related to the distance traveled between wintering and breeding sites (this study). Future comparative studies are needed that take into account all possible factors affecting wing morphology and resolve the discrepancies.

Summing up, the present study shows that wingtip isometric length and pointedness are associated with population-specific seasonal migration distance in the Eurasian barn swallow. Although this study covers the entire spectrum of barn swallow migratory behavior, it only considers two subspecies, including the one with the largest breeding range. Future studies are needed on more barn swallow subspecies and on other species of the Hirundinidae family to get a more comprehensive understanding of the relationship between wing morphology and migratory behavior in highly aerially foraging birds.

Acknowledgments

The late Prof. Nicola Saino contributed to planning this study. We would like to thank M. Caprioli, M. Romano, and Y. Wasserlauf for help with fieldwork, the landowners and the

staff that allowed us to collect data in farms where barn swallows breed, and A.P. Møller for commenting on the earlier draft of this work. We are thankful to the handling editor and three anonymous reviewers for their helpful suggestions and constructive criticism.

Funding

P.M. was financially supported by “the National Science Centre” grant no. DEC-2013/09/B/NZ8/03321. A.C. was partially financially supported by grant FSE-REACT EU, DM 10/08/2021 n. 1062. Field data collected in Spain was funded by research projects of the *Junta de Andalucía* (P12-RNM-2144).

Conflict of Interest

The authors declare that they have no conflict of interest.

Ethical Standards

The research conducted in this study complied with animal welfare laws of Poland (Polish Bird Ringing Centre permit No. 236/2019), Italy (Regione Lombardia, Decreto N. 599/2018; Provincia di Novara, Determinazione n. 973/2019), Spain (approval by Junta de Andalusia Local Government, 25/04/2012. Ref. DGB/JS) and Israel (NPA permit No. 2019/42152), which are the countries where the research was conducted. All applicable guidelines for the care and use of animals were followed.

Supplementary Material

Supplementary material can be found at [https://academic.oup.com/cz](https://academic.oup.com/cz/article/69/3/255/6596885).

References

- Alatalo RV, Gustafsson L, Lundberg A, 1984. Why do young passerine birds have shorter wings than older birds? *Ibis* 126:410–415.
- Alerstam T, 2009. Flight by night or day? Optimal daily timing of bird migration. *J Theor Biol* 258:530–536.
- Ambrosini R, Møller AP, Saino N, 2009. A quantitative measure of migratory connectivity. *J Theor Biol* 257:203–211.
- Baldwin MW, Winkler H, Organ CL, Helm B, 2010. Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats *Saxicola torquata*. *J Evol Biol* 23:1050–1063.
- Balmford A, Jones IL, Thomas ALR, 1994. How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution* 48:1062–1070.
- Bañbura J, 1986. Sexual dimorphism in wing and tail length as shown by the swallow *Hirundo rustica*. *J Zool* 210: 131–136.
- Bowlin MS, Wikelski M, 2008. Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. *PLoS One* 3:e2154.
- Briedis M, Kurlavičius P, Mackevičienė R, Vaišvilienė R, Hahn S, 2018. Loop migration, induced by seasonally different flyway use, in Northern European barn swallows. *J Ornithol* 159:885–891.
- Brown MB, Brown CR, 2020. Barn swallow *Hirundo rustica*., version 1.0. In: Rodewald PG editor. *Birds of the World*. Ithaca: Cornell Lab of Ornithology. doi:10.2173/bow.barswa.01.
- Calenge C, 2006. The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519.

- Carvalho Provinciato IC, Araújo MS, Jahn AE, 2018. Drivers of wing shape in a widespread Neotropical bird: A dual role of sex-specific and migration-related functions. *Evol Ecol* 32:379–393.
- Claramunt S, 2021. Flight efficiency explains differences in natal dispersal distances in birds. *Ecology* 102:e03442.
- Corman AM, Bairlein F, Schmaljohann H, 2014. The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. *Behav Ecol Sociobiol* 68:391–402.
- Dor R, Safran RJ, Sheldon FH, Winkler DW, Lovette IJ, 2010. Phylogeny of the genus *Hirundo* and the Barn Swallow subspecies complex. *Mol Phylogenet Evol* 56:409–418.
- Dor R, Safran RJ, Vortman Y, Lotem A, McGowan A et al., 2012. Population genetics and morphological comparisons of migratory European *Hirundo rustica rustica* and sedentary East-Mediterranean *Hirundo rustica transitiva* barn swallows. *J Hered* 103:55–63.
- Evans MR, 1998. Selection on swallow tail streamers. *Nature* 394:233–234.
- Evans MR, Thomas ALR, 1997. Testing the functional significance of tail streamers. *Proc R Soc B* 264:211–217.
- Falconer DS, Mackay TFC, 1996. *Introduction to Quantitative Genetics*. 4th edn. Harlow: Pearson-Prentice Hall.
- Fernández-Juricic E, Blumstein DT, Abrica G, Manriquez L, Adams LB et al., 2006. Relationships of anti-predator escape and post-escape responses with body mass and morphology: A comparative avian study. *Evol Ecol Res* 8:731–752.
- Fiedler W, 2005. Ecomorphology of the external flight apparatus of blackcaps *Sylvia atricapilla* with different migration behavior. *Ann N Y Acad Sci* 1046:253–263.
- Förschler MI, Bairlein F, 2011. Morphological shifts of the external flight apparatus across the range of a passerine (Northern Wheatear) with diverging migratory behaviour. *PLoS One* 6:e18732.
- Forstmeier W, Keßler A, 2001. Morphology and foraging behaviour of Siberian *Phylloscopus* warblers. *J Avian Biol* 32:127–138.
- Fudickar AM, Partecke J, 2012. The flight apparatus of migratory and sedentary individuals of a partially migratory songbird species. *PLoS One* 7:e51920.
- Gelman A, 2008. Scaling regression inputs by dividing by two standard deviations. *Stat Med* 27:2865–2873.
- Hedenström A, Møller AP, 1992. Morphological adaptations to song flight in passerine birds: A comparative study. *Proc R Soc B* 247:183–187.
- Huber GH, Turbek SP, Bostwick KS, Safran RJ, 2017. Comparative analysis reveals migratory swallows (Hirundinidae) have less pointed wings than residents. *Biol J Linn Soc* 120:228–235.
- Jenni L, Winkler R, 1989. The feather-length of small passerines: A measurement for wing-length in live birds and museum skins. *Bird Study* 36:1–15.
- Jenni L, Winkler R, 2020. *Moult and Ageing of European Passerines*. London: Bloomsbury Publishing PLC.
- Keast A, 1996. Wing shape in insectivorous passerines inhabiting New Guinea and Australian rain forests and eucalypt forest/eucalypt woodlands. *Auk* 113:94–104.
- Kiat Y, Izhaki I, Sapir N, 2016. Determinants of wing-feather moult speed in songbirds. *Evol Ecol* 30:783–795.
- Kiat Y, Izhaki I, Sapir N, 2019. The effects of long-distance migration on the evolution of moult strategies in Western-Palaearctic passerines. *Biol Rev* 94:700–720.
- Leisler B, Winkler H, 2003. Morphological consequences of migration in passerines. In: Berthold P, Gwinner E, Sonnenschein E editors. *Avian Migration*. Berlin Heidelberg: Springer-Verlag, 175–186.
- Liechti F, Scandola C, Rubolini D, Ambrosini R, Korner-Nievergelt F et al., 2015. Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population. *J Avian Biol* 46:254–265.
- Lockwood R, Swaddle JP, Rayner JMV, 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *J Avian Biol* 29: 273–292.
- Lombardo G, Rambaldi Migliore N, Colombo G, Capodiferro MR, Formenti G et al., 2022. The mitogenome relationships and phylogeography of barn swallows *Hirundo rustica*. *Mol Biol Evol* 39:msac113. doi:10.1093/molbev/msac113.
- López-Calderón C, Magallanes S, Marzal A, Balbontín J, 2021. The migration system of barn swallows *Hirundo rustica* breeding in southwestern Spain and wintering across west Africa. *Ardeola* 68:335–354.
- MacPherson MP, Jahn AE, Mason NA, 2022. Morphology of migration: associations between wing shape, bill morphology and migration in kingbirds (*Tyrannus*). *Biol J Linn Soc* 135:71–83.
- Marchetti K, Price T, Richman A, 1995. Correlates of wing morphology with foraging behaviour and migration distance in the genus *Phylloscopus*. *J Avian Biol* 26:177–181.
- Matyjasiak P, Marzal A, Navarro C, de Lope F, Møller AP, 2009. Fine morphology of experimental tail streamers and flight manoeuvrability in the house martin *Delichon urbica*. *Funct Ecol* 23:389–396.
- Matyjasiak P, Matyjasiak J, de Lope F, Møller AP, 2004. Vane emargination of outer tail feathers improves flight manoeuvrability in streamerless hirundines, *Hirundinidae*. *Proc R Soc B* 271:1831–1838.
- Matyjasiak P, Olejniczak I, Boniecki P, Møller AP, 2013. Wing characteristics and spring arrival date in barn swallows *Hirundo rustica*. *Acta Ornithol* 48:81–92.
- Milá B, Wayne RK, Smith TB, 2008. Ecomorphology of migratory and sedentary populations of the yellow-rumped warbler *Dendroica coronata*. *Condor* 110:335–344.
- Møller AP, 1994. *Sexual Selection and the Barn Swallow*. Oxford: Oxford University Press.
- Møller AP, 1995. Sexual selection in the barn swallow *Hirundo rustica*. V. Geographic variation in ornament size. *J Evol Biol* 8:3–19.
- Møller AP, Barbosa A, Cuervo JJ, de Lope F, Merino S et al., 1998. Sexual selection and tail streamers in the barn swallow. *Proc R Soc B* 265:409–414.
- Møller AP, Chabi Y, Cuervo JJ, de Lope F, Kilpimaa J et al., 2006. An analysis of continent-wide patterns of sexual selection in a passerine bird. *Evolution* 40:856–868.
- Møller AP, de Lope F, Lopez Caballero JM, 1995a. Foraging cost of a tail ornament: Experimental evidence from two populations of barn swallows *Hirundo rustica* with different degrees of sexual size dimorphism. *Behav Ecol Sociobiol* 37:289–295.
- Møller AP, de Lope F, Saino N, 1995b. Sexual selection in the barn swallow *Hirundo rustica*. VI. Aerodynamic adaptations. *J Evol Biol* 8:671–687.
- Mönkkönen M, 1995. Do migrant birds have more pointed Wings? A comparative study. *Evol Ecol* 9:520–528.
- Neto JM, Gordinho L, Belda EJ, Marín M, Monrós JS et al., 2013. Phenotypic divergence among West European populations of reed bunting *Emberiza schoeniclus*: The effects of migratory and foraging behaviours. *PLoS One* 8:e63248.
- Norberg UM, 1990. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Berlin, Heidelberg: Springer-Verlag.
- Norberg UM, Rayner JM, 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. *Philos Trans R Soc B* 316:335–427.
- Outlaw DC, 2011. Morphological evolution of some migratory *Ficedula* flycatchers. *Contrib Zool* 80:279–284.
- Pennycuik CJ, 1975. Mechanics of flight. In: Farner DS, King JR, Parkes KC editors. *Avian Biology*. Vol. 5. New York: Academic Press, 1–73.
- Pérez-Tris J, Bensch S, Carbonell R, Helbig A, Tellería JL, 2004. Historical diversification of migration patterns in a passerine bird. *Evolution* 58:1819–1832.
- Phillips AG, Töpfer T, Böhning-Gaese K, Fritz SA, 2018. Evidence for distinct evolutionary optima in the morphology of migratory and resident birds. *J Avian Biol* 49:e01807.
- Rayner JMV, 1988. Form and function of avian flight. In: Johnston RF, editor. *Current Ornithology*. Vol. 5. Boston (MA): Springer, 1–66.

- Rowe LV, Evans MR, Buchanan KL, 2001. The function and evolution of the tail streamer in hirundines. *Behav Ecol* 12:157–163.
- Rubolini D, Gardiazabal Pastor A, Pilastro A, Spina F, 2002b. Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. *J Avian Biol* 33:15–22.
- Rubolini D, Massi A, Spina F, 2002a. Replacement of body feathers is associated with low premigratory energy stores in a long-distance migratory bird, the barn swallow *Hirundo rustica*. *J Zool* 258:441–447.
- Saino N, Bazzi G, Gatti E, Caprioli M, Cecere JG et al., 2015. Polymorphism at the clock gene predicts phenology of long-distance migration in birds. *Mol Ecol* 24:1758–1773.
- Saino N, Rubolini D, Ambrosini R, Romano A, Parolini M et al., 2017. Sex- and age-dependent morphology and selection on wing shape in the barn swallow *Hirundo rustica*. *J Avian Biol* 48:1441–1450.
- Santure AW, Ewen JG, Sicard D, Roff DA, Møller AP, 2010. Population structure in the barn swallow *Hirundo rustica*: A comparison between neutral DNA markers and quantitative traits. *Biol J Linn Soc* 99:306–314.
- Seifert N, Ambrosini R, Bontempo L, Camin F, Liechti F et al., 2018. Matching geographical assignment by stable isotopes with African non-breeding sites of barn swallows *Hirundo rustica* tracked by geolocation. *PLoS One* 13:e0202025.
- Sheard C, Neate-Clegg MHC, Alioravainen N, Jones SEI, Vincent C et al., 2020. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nat Commun* 11:1–9.
- Svensson L, 1992. *Identification Guide to European Passerines*. 4th edn. Stockholm: British Trust for Ornithology.
- Swaddle JP, Lockwood R, 1998. Morphological adaptations to predation risk in passerines. *J Avian Biol* 29:172–176.
- Thomas ALR, 1993. On the aerodynamics of birds' tails. *Philos Trans R Soc B* 340:361–380.
- Thomas ALR, 1996. The flight of birds that have wings and a tail: Variable geometry expands the envelope of flight performance. *J Theor Biol* 183:237–245.
- Thomas ALR, Taylor GK, 2001. Animal flight dynamics. I. Stability in gliding flight. *J Theor Biol* 212:399–424.
- Turner A, 2006. *The Barn Swallow*. London: T&AD Poyser.
- Vágási CI, Pap PL, Vincze O, Osváth G, Erritzøe J et al., 2016. Morphological adaptations to migration in birds. *Evol Biol* 43:48–59.
- Voelker G, 2001. Morphological correlates of migratory distance and flight display in the avian genus *Anthus*. *Biol J Linn Soc* 73:425–435.
- Wang X, Clarke JA, 2015. The evolution of avian wing shape and previously unrecognized trends in covert feathering. *Proc R Soc B* 282:20151935.
- Warrick DR, 1998. The turning- and linear-maneuvering performance of birds: The cost of efficiency for courting insectivores. *Can J Zool* 76:1063–1079.
- Warrick DR, Hedrick TL, Biewener AA, Crandell KE, Tobalske BW, 2016. Foraging at the edge of the world: low-altitude, high-speed manoeuvring in barn swallows. *Philos Trans R Soc B* 371:20150391.
- Winkler H, Leisler B, 1992. On the ecomorphology of migrants. *Ibis* 134:21–28.
- Winkler H, Leisler B, 2005. To be a migrant: ecological burdens and chances. In: Greenberg R, Marra PP eds. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Baltimore: The Johns Hopkins University Press, 79–86.