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Comparative analysis reveals migratory swallows (Hirundinidae) have less pointed wings than residents

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The correlation between migration and wing pointedness, a pattern generally attributed to the need to reduce drag during powered straight-line flight, is well established in avian ecomorphology. However, most studies investigating this pattern have focused on relatively rounded-wing taxa, which employ different flight modes during foraging and migration. The basic assumption that migrants have comparatively pointed wings has not been questioned by analysing taxa with similar migratory and foraging flight. This study examines the correlation between migration and wing shape in swallows (Hirundinidae), a family with relatively pointed wings in which foraging flight resembles migratory flight. Using a phylogeny-based analysis, we compare the wing shape of species pairs with varying migratory habits in eight swallow genera. Surprisingly, migratory swallows have *less pointed wings* than sedentary species, and wing pointedness declines linearly with increasing migratory distance. This study represents the first published result documenting a reversal of the correlation between migration and wing pointedness found in other avian taxa. Interpreting this reversal requires a more nuanced understanding of wing ecomorphology; we hypothesize that inclement weather conditions on the breeding grounds and/or the roosting habits of migratory swallows create conflicting selective pressures that increase the cost of wing pointedness in migratory swallows. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2017, **120**, 228–235.

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INTRODUCTION

Variations in wing shape among avian taxa have been attributed to trade-offs between the demands of many ecological and behavioural variables. Variables that have been found to correlate with wing morphology include foraging mode (Marchetti, Price & Richman, 1995), habitat type (Niemi, 1985; Kaboli *et al.*, 2007), flight displays (Voelker, 2001), predation risk (Alatalo, Gustafsson & Lundbkrg, 1984; Norberg, 1990; Swaddle & Lockwood, 1998), migratory fuel load (Burns, 2003), spring phenology (Hahn *et al.*, 2015), and especially migration (Calmaestra & Moreno, 2001; Kaboli *et al.*, 2007; Milá, Wayne & Smith, 2008; see Mönkkönen, 1995; Lockwood, Swaddle & Rayner, 1998, for summaries of earlier studies). Observations of correlations between wing shape and migratory habit are particularly numerous and have a very long history in ornithological investigations (Wood & Fyfe, 1943; Palmer, 1900; Niethammer, 1937). Although generalizations are complicated by the many methodologies that have been used to describe wing shape (see Lockwood *et al.*, 1998, for a summary), the vast majority of studies have found that migrants have higher aspect ratio wings, or wings with more pointed tips, than residents. Correlations between more pointed wings and longer migratory distances have also been

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demonstrated in bats (Miller-Butterworth, Jacobs & Harley, 2003) and insects (Altizer & Davis, 2010). Based upon these correlations, it has thus been assumed that wing shape is closely tied to migratory behaviour, with migratory species possessing more pointed wings than residents.

Aerodynamic theory predicts that high aspect ratios and pointed wingtips increase the energetic efficiency of powered straight-line flight due to a reduction in induced drag (Savile, 1957; Rayner, 1988; Norberg, 1995). Experimental evidence corroborates this prediction, as pointed wingtips correlate with reduced energy expenditure during migratory flight in Swainson's thrushes (Bowlin & Wikelski, 2008). Conversely, wings with low aspect ratios and rounded tips appear more suitable for flight that requires high power at low speeds, such as foraging flight in vegetation and escape flight from the ground (Pennycuick, 1983; Swaddle & Lockwood, 1998, 2003; Burns & Ydenberg, 2002).

Despite the predictions of aerodynamic theory and the dense body of literature showing differences in wing shape between migrants and residents, the vast majority of studies have investigated the relationship between wing shape and migration within typical passerines, which have uncharacteristically rounded wings when compared with other avian taxa and employ very different modes of foraging and migratory flight (Rayner, 1988; Norberg, 1990; Lockwood *et al.*, 1998). Thus, it is unclear whether this trend is indeed universal. While a few studies have sampled widely across the spectrum of avian taxa to establish the correlation between wing shape and migration in birds in general, they have typically conducted analyses that pool data from all species analysed (see Norberg, 1995; Lockwood *et al.*, 1998, for two recent examples). As typical passerines account for more than half of all bird species and generally make up at least half of the sample species in these large-scale comparative analyses, correlations across a broad sample of taxa within this group may not be representative. For example, passerines themselves are quite heterogeneous, containing taxa that vary dramatically in wing shape, foraging style, and migratory behaviour.

Very few studies have specifically looked for a correlation between migratory behaviour and wing shape in taxa with high wing aspect ratios, and none have examined taxa with similar flight behaviour during migration and foraging (Winkler & Leisler, 1992; Burns, 2003; Minias *et al.*, 2015). Swallows (Hirundinidae) are an ideal taxon to test the universality of the correlation between migratory behaviour and wing shape because all species have relatively high aspect ratio wings and migratory flight resembles foraging flight (Winkler, 2006), potentially indicating a less severe trade-off between flight modes that might reduce the difference in wing shape between migratory and resident species. All swallow species are coursing aerial insectivores that almost exclusively catch airborne insects while flying continuously in unobstructed air spaces (Turner, 2004). Swallows travel very large distances on foraging bouts compared with typical passerines, and fly continuously while foraging (Turner & Rose, 1989). While most passerines migrate in relatively high-altitude nocturnal flights (averaging 1050 m above the ground), swallows generally migrate during the day at relatively low altitudes (averaging about 450 m above ground level) and feed on the wing during migration (Turner, 2004; Winkler, 2006; Alerstam *et al.*, 2011; Mateos-Rodríguez & Liechti, 2012). Thus, migratory flight in swallows resembles foraging flight, and foraging flight in swallows is dependent on straight-line flight as well as manoeuvrability. Compared with other passerines (and many non-passerine taxa), both migratory and non-migratory swallow species appear to have wings highly adapted for efficient straight-line flight: In experiments using doubly labelled water to measure flight costs, swallows use 50–70% less energy during flapping flight than other passerine species of similar size (Hails, 1979). This study investigates whether the correlation between wing pointedness and migratory habit applies in an avian family in which even resident species have highly pointed wings.

MATERIAL AND METHODS

Measurements

Two species were selected from each of eight swallow genera. Each species pair included one long- or medium-distance migrant species and one resident or short-distance migrant species (Table 1). Ten adult specimens were measured from each species (where available, Table 1). In order to account for any intraspecific differences in migratory distance, the specimens were drawn from both the breeding and wintering grounds across the geographic range of each species. Only specimens not undergoing primary moult were used. Data from males and females were pooled in the analysis, as a preliminary investigation on a subset of specimens found no significant difference in wingtip pointedness between males and females.

For each specimen, the lengths of primaries two through nine of the left wing were measured using a metal ruler with a pin at the zero mark. If any primaries on the left wing were damaged, the right wing was used instead. Primary lengths were measured to within 0.5 mm accuracy as the distance from

Table 1. Sample sizes and estimated migration distances for included species (for species that have both resident and short-distance migrant subspecies, specimens were selected from resident subspecies and migration distance is indicated as zero)

Measured species	N	Migratory distance (km)
Cecropis daurica	10	3300
Cecropis striolata	9	0
Delichon urbicum	10	5940
Delichon nipalensis	10	660
Hirundo rustica	10	5940
Hirundo angolensis	10	0
Notiochelidon cyanoleuca	10	1980
Notiochelidon pileata	6	0
Progne subis subis	10	6600
Progne modesta	10	0
Riparia riparia	10	7260
Riparia paludicola	10	0
Stelgidopteryx serripennis	10	2640
Stelgidopteryx ruficollis	10	0
Tachycineta bicolor	10	1980
Tachycineta cyaneoviridis	10	0

the tip of the feather to its insertion point in the skin. Unlike the measurement of primary distances, primary length measurements are highly repeatable (Berthold & Friedrich, 1979; Lockwood *et al.*, 1998). All measurements were taken by GHH, and repeated measurements on a sub-sample of specimens in this study confirmed the repeatability of measurements. Wingtip pointedness was calculated using a variant of principal components analysis called size-constrained components analysis, as described in Lockwood *et al.* (1998). In this methodology, the first component (C_1) isolates size-related variation, while the second (C_2) describes the pointedness of the wingtip. C_2 was used in this study to determine wingtip pointedness, with higher C_2 values (less negative numbers) indicating more rounded wings.

Migration distances were estimated using the species range maps in Turner (2004). Migration distance was measured as the distance in mm between the estimated geographic means of the breeding and wintering grounds indicated on the maps, and converted to km by multiplying these distances by the factor indicated by the map scale (Marchetti *et al.*, 1995).

Statistics and analysis

Previous studies on migration and wing shape have found differences in significance between analyses that accounted for phylogenetic relatedness among taxa and those that did not (Marchetti *et al.*, 1995; Voelker, 2001). Thus, despite evidence that migration and wing shape are relatively labile traits evolutionarily (Berthold *et al.*, 1992; Egbert & Belthoff, 2003), we attempted to account for relatedness using phylogenetically independent contrasts (PICs).

PICs are commonly used to control for confounding phylogenetic effects, but require that the analysed variables be expressed as continuous variables. However, establishing that wing shape varies linearly with migration distance has been difficult, with only one study finding a significant correlation between migration distance and a wing shape index when using PICs (Marchetti *et al.*, 1995).

Because of the trade-offs between statistical methods and their differing requirements for parameter estimation, two different types of phylogenetically controlled statistical tests were conducted:

1. One-way analysis of variance (ANOVA) on the wingtip pointedness of the 16 species with nine a priori contrasts: one contrast of all migrants and all residents, and eight additional contrasts evaluating each species pair independently. Sequential Bonferroni corrections for multiple comparisons were applied to control for an inflated Type 1 error rate (Holm, 1979). This analysis used a two-state character for migration: 'migrants' being species with mean distances of over 1000 km between breeding and wintering grounds, and 'residents' with distances 0–1000 km.
2. Linear regression on 15 PICs of wingtip pointedness and migration distance coded as a continuous variable (Felsenstein, 1985).

Phylogenetically independent contrasts were created using the package 'ape' version 2.2-2 (Paradis, Claude & Strimmer, 2004) and the R statistical program version 2.8.1. To conduct the PICs analysis, the most recent and complete Hirundinidae phylogenetic analysis available (Sheldon *et al.*, 2005) was pruned to 14 of the 16 species studied herein. Assuming monophyly of genera, the two species missing from the Sheldon *et al.* consensus tree, *Cecropis striolata* and *Progne modesta*, were added to the pruned tree as sisters to congeners. In Sheldon *et al.* (2005), branch lengths for the family-level tree were taken from the Bayesian consensus tree of two mitochondrial genes, cytb and ND2, while the branch length for *C. striolata* was calculated from a separately analysed Bayesian consensus tree of Hirundo (*s. l.*) based only on cytb sequences (Sheldon *et al.*, 2005). The branch length of *C. striolata* was transformed to correspond with branch lengths from the cytb/ND2 tree under the assumption of a linear relationship between the indices (see Fig. 1; also Mönkkönen, 1995, for a similar approach). For

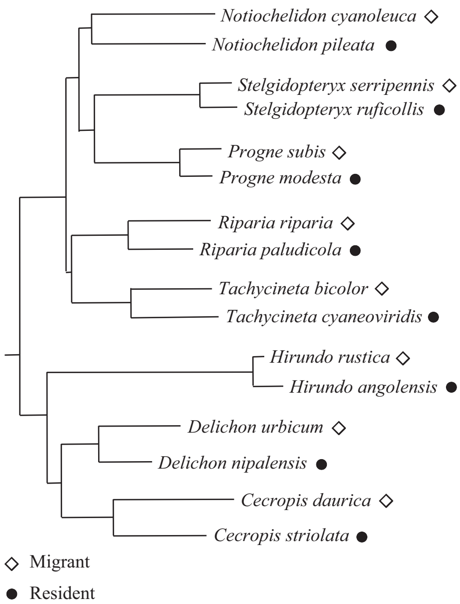

Figure 1. Phylogenetic relationships (and proportional branch lengths) among species included in this study, modified from Sheldon *et al.* (2005).

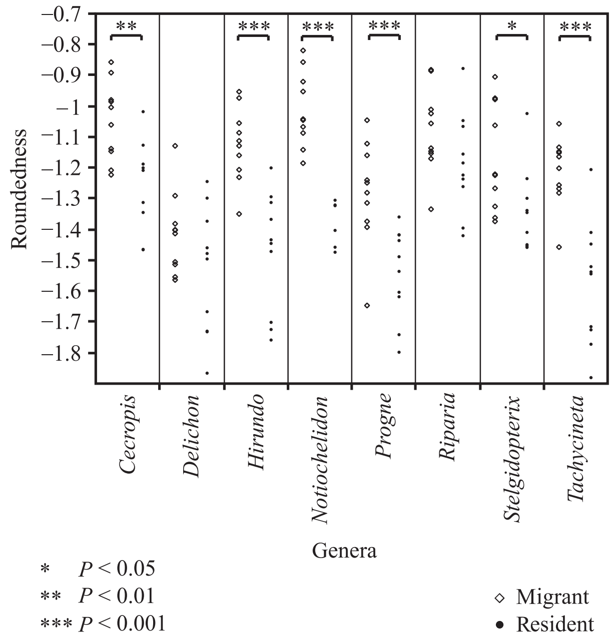

Figure 2. Plot of roundedness (C_2) values for all included individuals by species. Congeneric species are paired, with each migratory species to the left of the resident species. Lower roundedness scores (more negative values) indicate a more pointed wing. Brackets and asterisks above species pairs indicate the significance of the species-pair contrasts within the ANOVA.

P. modesta, the branch length for *P. elegans* was substituted, as *P. elegans* was previously considered to be conspecific with *P. modesta* (Turner & Rose, 1989).

RESULTS

Mean wing pointedness varied across the 16 swallow species ($F_{15,139} = 14.19$, $P < 0.0001$; Fig. 2). More importantly, the average wing pointedness of all migrant species significantly differed from the average of all resident species after sequential Bonferroni correction, as shown by an a priori contrast between all migratory and all resident species ($P < 0.0001$; Table 2). Of eight contrasts on individual species pairs, six were significant after sequential Bonferroni correction (Table 2 and Fig. 2). In contrast to all previously published studies on wing shape and migration, however, the migratory species consistently had less pointed wings than their resident congeners.

Migratory distance and independent contrasts for wingtip roundedness were positively related (linear regression adjusted $r^2 = 0.6057$, $F = 24.04$, d.f. = 14, 1, $P = 0.00023$; Fig. 3). Cook's distance values indicate that there are no excessively influential data points in the regression. In direct contrast to results from all studies that have found a linear relationship in other avian taxa, as migratory distance increases, wingtip pointedness decreases among swallow species.

Mean wing roundedness (C_2) values for the migratory (−1.17 ± 0.18) and resident (−1.42 ± 0.21) swallow species in our study were considerably lower (indicating more pointed wings) than reported mean C_2 values for migratory species encompassing a variety of passerine and non-passerine families (−0.450 ± 0.10, Lockwood *et al.*, 1998; −0.688 ± 0.24, Fernández-Juricic *et al.*, 2006), supporting our claim that swallows have pointier wings than many passerine and non-passerine taxa.

Table 2. Results of ANOVA *a priori* contrasts on wing pointedness values of all migratory vs. all resident species and for each species pair (adjusted alpha value includes sequential Bonferroni correction)

Genus	Test *P*	Adjusted alpha value
All genera pooled	< 0.0001	0.0055
Tachycineta	< 0.0001	0.0063
Hirundo	< 0.0001	0.0071
Notiochelidon	< 0.0001	0.0083
Progne	0.0002	0.0100
Cecropis	0.0035	0.0125
Stelgidopteryx	0.0107	0.0167
Delichon	0.0708	0.0250
Riparia	0.1216	0.0500

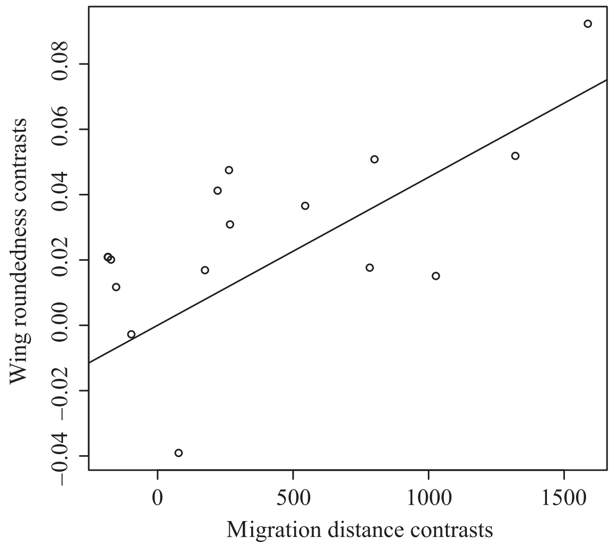

Figure 3. Scatterplot of 15 wingtip roundedness (C_2) contrasts against migration distance contrasts. The linear regression on the contrasts is significant: $r^2 = 0.6057$, $P = 0.00023$.

DISCUSSION

In contrast with the previously established and widespread pattern, migratory swallow species have independently evolved less pointed wings than their resident congeners. Six of eight congeneric swallow species pairs show significantly rounder wings in the migratory species after sequential Bonferroni correction (Table 2 and Fig. 2), and the differences in wingtip pointedness in the other two species pairs trend in the same direction. Furthermore, in swallows, wingtip pointedness decreases linearly with increasing migratory distance. The strong linear relationship between wing *roundedness* and migratory distance in swallows contrasts with the linear relationships between wing *pointedness* and migratory distance that have been found in other avian taxa (Marchetti *et al.*, 1995; Mönkkönen, 1995; Kaboli *et al.*, 2007). The general correlation between migratory habit and wing roundedness is unprecedented in the study of animal flight and runs counter to all prior research finding correlations between migratory behaviour and wing shape in avian and mammalian taxa (Mulvihill & Chandler, 1991; Marchetti *et al.*, 1995; Mönkkönen, 1995; Norberg, 1995; Norman, 1997; Lockwood *et al.*, 1998; Calmaestra & Moreno, 2001; Miller-Butterworth *et al.*, 2003; Kaboli *et al.*, 2007; Milá *et al.*, 2008).

Avian flight theory predicts that long-distance migrants, in contrast with sedentary birds, have more pointed wings with higher aspect ratios to reduce induced drag and minimize cost of transport during sustained forward flight (Savile, 1957; Rayner, 1988; Norberg, 1995). Selection should thus favour a positive relationship between wing pointedness and migratory distance if migratory performance constitutes the principal selective force governing flight morphology in migratory taxa. However, migration is just one of the many selective pressures, including habitat type (Niemi, 1985; Kaboli *et al.*, 2007), predation risk (Alatalo *et al.*, 1984; Norberg, 1990; Swaddle & Lockwood, 1998), foraging mode (Marchetti *et al.*, 1995), and sexual selection (Fernández & Lank, 2007), that influence avian wing shape. If closely related migratory and non-migratory taxa differ throughout their annual cycle in ecological and behavioural factors other than migratory habit, these groups may deviate from the established correlation between migratory behaviour and wing pointedness.

The wing shape of a given species is constrained by the conflicting morphological demands of a wide range of flight modes – each with a variety of associated ecological and behavioural correlates (Table 3). While high-speed prolonged flight, such as that necessary for migration, is generally associated with pointed wings, aerodynamic theory predicts that hovering, slow flight, acceleration, and landing benefit from more rounded wings (Norberg & Rayner, 1987). Birds taking off from the ground and flying at low speeds are constrained by power, wing inertia, and lift generation, and rounded wings are thought to facilitate slow flight by maximizing the thrust generated by flapping (Swaddle & Lockwood, 2003). Manoeuvrability imposes further constraints on flight morphology, as different types of manoeuvrability generate opposing predictions about optimal wing pointedness (Warrick, 1998). High-speed fixed-wing manoeuvring, or the ability to manoeuvre at high-speeds without flapping, is heavily relied upon by pure coursers (e.g. swifts) foraging in open areas and generally benefits from pointed wings. Conversely, low-speed flapping manoeuvring, employed by pure hawkers (e.g. flycatchers) and low-flying birds in dense habitat, is typically associated with more rounded wings. Aerial hawkers, such as swallows, rely on a combination of these two strategies, utilizing high-speed flight to capture prey closer to the ground, yet lingering in areas of elevated insect density at high altitudes (Warrick, 1998). Given the numerous selective pressures influencing optimal wing shape in avian taxa, a shift in the relative importance of the various flight modes employed by migrant vs. resident taxa could explain the previously undocumented correlation between wing roundedness and migratory distance. Here, we propose two non-mutually exclusive mechanisms that may account

Table 3. Predicted morphological and ecological correlates of different flight modes, modified from Norberg & Rayner (1987). Wing roundedness corresponds to the pointedness coefficient of Lockwood *et al.* (1998), where higher values signify more rounded wings. The plus (+) symbols indicate that higher coefficients (more rounded wings) are advantageous, while the minuses (–) denote lower optimal values.

Flight mode	Wing roundedness	Ecological correlates
High-speed sustained flight (Norberg & Rayner, 1987)	–	Migration (Mönkkönen, 1995; Lockwood *et al.*, 1998; Fiedler, 2005; Milá *et al.*, 2008; Altizer & Davis, 2010; Baldwin *et al.*, 2010; Minias *et al.*, 2015)
Hovering & slow flight (Norberg & Rayner, 1987)	+	Prey capture – gleaners/hawkers (Warrick, 1998)
High-speed fixed-wing manoeuvring (Warrick, 1998)	–	Prey capture – pure coursers (Warrick, 1998)
Low-speed flapping manoeuvring (Warrick, 1998)	+	Habitat density (Lockwood *et al.*, 1998), foraging height (Marchetti *et al.*, 1995), aerial display (Fernández & Lank, 2007)
Acceleration, take-off & landing (Pennycuick, 1983; Lockwood *et al.*, 1998; Warrick, 1998; Brewer & Hertel, 2007; Fernández & Lank, 2007)	+	Predator avoidance (Norberg & Rayner, 1987), prey capture – gleaners/hawkers (Warrick, 1998)

for this shift in flight modes and contribute to our unexpected finding in swallows.

The first potential explanation of this shift between resident and migratory taxa may be the need to forage during periods of low food availability or inclement weather at higher latitudes. While resident swallows breed in climates assumed to be relatively stable and predictable, migratory birds breeding at high latitudes occasionally experience cold snaps or episodes of unseasonably cold weather, especially immediately following or prior to migration. During periods of poor weather, swallows are known to adjust their foraging behaviour in order to take advantage of denser and more stable insect populations at lower heights (Turner, 2010). For example, both purple martins (*Progne subis*) and barn swallows (*Hirundo rustica*) forage closer to the ground or nearer to vegetation in windy or cold weather (Doughty & Fergus, 2002; Evans, Bradbury & Wilson, 2003). Capturing aerial insects in cluttered habitat (i.e. closer to vegetation) requires increased reliance on low-speed flapping manoeuvring so as to avoid obstacles (Lockwood *et al.*, 1998). Migratory swallows may thus possess more rounded wings in order to forage more effectively during the periods of low food availability associated with unpredictable weather conditions at higher latitudes.

Alternatively, rounded wings in long-distance migrants may have evolved as a consequence of the distinct roosting habitats of migratory and resident swallows and their respective take-off requirements during the non-breeding season. Outside of the breeding period, migratory swallows primarily roost in large numbers in low vegetation such as tall grasses and reed beds (van den Brink, Bijlsma & van der Have, 2004; Bijlsma & van den Brink, 2005). In contrast, resident swallows tend to roost singly near their nests or in small aggregations in trees, burrows, or the rafters of buildings (Skutch, 1960; Turner, 2004). Although resident individuals occasionally join larger roosts of migrants (Skutch, 1960), resident species generally roost higher off the ground than migratory swallows. The roosts of migratory swallows can contain millions of individuals (van den Brink *et al.*, 2004; Bijlsma & van den Brink, 2005), and the inhabitants rely on highly synchronized manoeuvres when leaving and entering the roost so as to escape aerial predators. For example, Bijlsma & van den Brink (2005) documented over 90% of flock members departing from a roost of 1.5 million migratory barn swallows in under 10 min. Given the established trade-off between wing pointedness and take-off performance, migratory species may require more rounded wings to ascend in a coordinated fashion from roosts in low vegetation. Indeed, the wing pointedness of birds that generally benefit from high aspect ratio wings for improved gliding performance varies with roosting habits and take-off patterns, such that species have the highest aspect ratio wings possible given their most difficult take-off requirement (Pennycuick, 1983). Although pointed wings may decrease the cost of transport during migratory flight, the roosting habits of migratory swallows during the non-breeding season may have necessitated the evolution of rounded wings to minimize the threat of predation during coordinated acceleration from roosts in low vegetation.

While we provide two possible explanations that may account for the previously undocumented relationship between wing roundedness and migratory distance, further research is needed to fully understand the drivers underlying this pattern. Systematic time budget analyses of migratory and resident swallows promise to shed light on the mechanisms responsible for relatively rounded wings in migratory swallows by clarifying the amount of time allocated to various flight-related activities. Likewise, the utilization of wind tunnels and high-speed video imagery to examine trade-offs between flight modes across varying degrees of wing pointedness could provide additional insight into constraints on wing morphology in migratory and resident taxa.

Regardless of the specific mechanisms underlying this pattern, this study is the first to question the universal nature of the correlation between migratory behaviour and wing pointedness, especially in taxa with relatively high aspect ratio wings that employ similar modes of migratory and foraging flight. Our study stresses the importance of considering all selective pressures that influence wing shape throughout the annual cycle when interpreting patterns of ecomorphology and highlights opportunities to refine our knowledge of the interplay between the selective forces shaping foraging, migratory, and escape flight across latitudes in order to enhance our understanding of wing shape evolution.

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