FLYING IN THE FACE OF EFFICIENCY: MIGRATORY SWALLOWS

(HIRUNDINIDAE) HAVE LESS POINTED WINGS THAN RESIDENTS

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ABSTRACT

The correlation between migration and more pointed wings is a well-established pattern in avian ecomorphology, and has been supported by a large number of studies over many decades. However, most studies have focused on taxa with relatively low aspect ratio wings, and taxa with high aspect ratio wings have scarcely been investigated except as part of large pooled datasets. While some authors have questioned whether the pattern is detectable in all taxa, the basic assumption that migrants have more pointed or similar wings compared to residents—depending on the strength of selection—has not been questioned. This study examines the correlation between migration and more pointed wings in swallows (Hirundinidae), a family with relatively high aspect ratio wings. Using phylogenetically controlled statistical methods and a well-established index of wing pointedness, I investigated the wing shape of species pairs from eight swallow genera. The present study establishes that among swallows, migratory species have less pointed wings than sedentary species, and that wing pointedness declines linearly with increasing migration distance. This study represents the first published result demonstrating a reversal of the correlation between migration and more pointed wings found in other avian taxa. Hypotheses to account for this unprecedented finding and implications for future research are discussed.

BIOGRAPHICAL SKETCH

Gernot Huber was born in Cape Town, South Africa to German parents, and grew up in Germany. He received a B.A. with Honors in Modern Thought and Literature from Stanford University in 1991. After a career in Silicon Valley and extensive travel in South America and Asia, he began to study biology at City College of San Francisco and San Francisco State University. He worked in the Eastern Sierra Nevada as a field biologist for the Point Reyes Bird Observatory (now PRBO Conservation Science) before enrolling as a graduate student in the department of Ecology and Evolutionary Biology at Cornell University. He now is a certified yoga teacher (RYT 200) and teaches yoga in Chiang Mai, Thailand.

To Marisa Guptarak, for believing in me.

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CHAPTER 1

INTRODUCTION

Variations in wing shape among avian taxa have been attributed to the trade-offs between the demands of many ecological and behavioral variables. Variables that have been found to correlate with wing shape include foraging mode (Marchetti et al. 1995), habitat type (Niemi 1985), flight displays (Voelker 2001), predation risk (Alatalo et al. 1984; Swaddle and Lockwood 1998), migratory fuel load (Burns 2003), and migration (Calmaestra and Moreno 2001; Kaboli et al. 2007; Mila et al. 2008; see Monkkonen 1995 and Lockwood et al. 1998 for summaries of earlier studies). Observations of correlations between wing shape and migratoriness are particularly numerous, and have a very long history in ornithological investigations (Frederick II ca. 1240; Niethammer 1937; Palmer 1900). Though generalizations are complicated by the large number of different 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[1]. Some researchers have also found correlations between migration and wing length (Marchetti et al. 1995; Voelker 2001; Yong and Moore 1994), but others have not (Calmaestra and Moreno 2001; Lockwood et al. 1998; Monkkonen 1995).

Aerodynamic theory predicts that high aspect ratios and pointed wingtips increase the efficiency of powered straight-line flight due to a reduction in induced drag (Norberg 1995; Rayner 1988; Savile 1957). Experimental evidence corroborates this prediction, as pointed wingtips correlate with reduced energy expenditure during

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[1] While aspect ratio and wingtip pointedness measure two different quantities, Lockwood et al. (1998) showed that their wingtip pointedness index, used in this study, has a very high correlation with the log of aspect ratio across a large and broad sample of bird species. Thus, in this paper I use the terms interchangeably to describe high aspect-ratio, pointed wings.

migratory flight in Swainson's Thrushes (Bowlin and Wikelski 2008). Conversely, wings with low aspect ratios and rounded tips are more efficient for flight that requires maneuverability and high power at low speeds, such as foraging flight in vegetation and escape flight from the ground (Burns and Ydenberg 2002; Pennycuick 1983; Swaddle and Lockwood 1998; Swaddle and Lockwood 2003).

Despite the predictions of aerodynamic theory and the large number of studies that have shown differences in wing shape between migrants and residents, the strength and universality of the correlation between wing shape and migration remain in question, largely for two reasons:

1. Aerodynamic theory predicts not only differences between migrants and residents, but differences in wing shape among species that migrate different distances (Norberg 1990). However, it has been very difficult to establish that wing shape varies with migration distance (Burns 2003; Chernetsov 2004; Mulvihill and Chandler 1990; Norberg 1995).

2. The vast majority of studies have investigated typical passerines (passerines excluding swallows), which have uncharacteristically rounded wings when compared with other avian taxa (Lockwood et al. 1998; Norberg 1990; Rayner 1988). Thus it remains unclear whether the correlation holds for taxa with less rounded wings.

To establish the correlation between wing shape and migration in birds in general, some studies have sampled widely from across the spectrum of avian taxa, but they have typically conducted analyses that pool data from all species analyzed (see Lockwood et al. (1998) and Norberg (1995) for two recent examples). Since typical passerines account for more than half of all bird species and typically make up at least half of the sample species in these large-scale comparative analyses, it remains unclear whether correlations across a broad sample of taxa are significant largely due to the

significance in the highly speciose Passeriformes. If wingtip shape varies with migratory behavior because of a trade-off between migratory flight and "normal" flight, one would expect this correlation to be strongest in taxa whose wings are particularly inefficient for migratory flight, such as the short, rounded wings of typical passerines. This begs the question whether the correlation holds in avian taxa in which even resident species have relatively pointed wingtips, potentially indicating a much less severe trade-off between migratory and normal flight.

Very few studies have specifically looked for this correlation in taxa with high wing aspect ratios, and I am aware of none that have found a correlation between aspect ratio or wing pointedness and migration in birds with relatively pointed wings. One study that has analyzed non-passerines separately did find a correlation between migration and increased wing aspect ratios among non-passerine birds, but removed from the analysis three taxa with medium to high aspect ratios: pigeons (Columbidae), hummingbirds (Trochilidae), and waders (Charadriiformes) (Winkler and Leisler 1992). A separate analysis of Charadriiformes showed the opposite (non-significant) trend, with resident species trending towards higher aspect ratios, while wing shape/migration results for pigeons and hummingbirds were not reported (Winkler and Leisler 1992). A study of sandpipers of the genus *Calidris,* another taxon with high aspect ratios, also failed to find a correlation between migration distance and wing aspect ratio (Burns 2003).

Swallows (Hirundinidae) are a good example of a taxon in which all species have relatively high aspect-ratio wings and pointed wingtips. All swallow species are coursing aerial insectivores that almost exclusively catch flying insects while flying continuously in unobstructed air spaces (Turner 2004). Constrained by their common lifestyle, swallow species are similar enough in structure that morphological features have not been useful in constructing a stable swallow phylogeny (Sheldon et al. 2005).

Migratory and normal flight appear unusually similar in swallows (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. Swallows travel very large distances on foraging bouts compared with typical passerines, and they fly continuously during typical foraging (Turner 1989). Unlike most passerines, which migrate in long, high-altitude, nocturnal flights, swallows typically migrate during the day at low altitudes, and they feed on the wing while migrating (Turner 2004; Winkler 2006). Thus migratory flight in swallows resembles foraging flight, and foraging flight in swallows is dependent on efficient straight-line flight as well as maneuverability. Compared to all other passerines (and to 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 labeled water to measure flight costs, swallows used 50-70% less energy during flapping flight than other passerine species of similar size (Hails 1979). Here I investigate whether the correlation of more pointed wingtips with migratory habit applies in an avian family in which even resident species have highly pointed wings.

CHAPTER 2

METHODS

Measurements

Two species were selected from each of eight swallow genera. Each species pair included one long-distance or medium-distance migrant species and one resident or short-distance migrant (see Table 1).

Table 1. *Sample sizes and migration distances for included species. For species that have resident and short-distance migrant sub-species, specimens were selected from resident subspecies when migration distance is indicated as zero.*

species	# specimens	migr. dist. (km)	migratory category
Cecropis daurica	10	3300	long-distance
Cecropis striolata	9	0	resident
Delichon urbicum	10	5940	long-distance
Delichon nipalensis	10	660	resident/short-distance
Hirundo rustica	10	5940	long-distance
Hirundo angolensis	10	0	resident
Notiochelidon cyanoleuca	10	1980	medium-distance
Notiochelidon pileata	6	0	resident
Progne subis subis	10	6600	long-distance
Progne modesta	10	0	resident
Riparia riparia	10	7260	long-distance
Riparia paludicola	10	0	resident
Stelgidopteryx serripennis	10	2640	medium-distance
Stelgidopteryx ruficollis	10	0	resident
Tachycineta bicolor	10	1980	medium-distance
Tachycineta cyaneovividis	10	0	resident

The specimens used in this analysis came from the American Museum of Natural History, the Cornell University Museum of Vertebrates, the Museo Argentino de Ciencias Naturales "Bernadino Rivadavia", and the Peabody Museum of Natural History at Yale University. Ten adult specimens were measured from each species (where available, see Table 1). Only specimens not undergoing primary molt were used. Each specimen was inspected for the simultaneous presence of old and new primaries, and if a mixture of old and new feathers was present, the specimen was not used. Both males and females were included in the sampling, and a preliminary investigation on a subset of specimens found no significant difference in wingtip pointedness between males and females (see also Bowlin and Winkler in press for a lack of sex differences in pointedness in Tree Swallows). Thus data from males and females were pooled in the analysis.

For each specimen, I measured the lengths of primaries two through nine of the left wing using a metal ruler with a pin inserted at the zero mark. If any primaries on the left wing were damaged, the right wing was used instead. Primary lengths were measured to one millimeter accuracy as the distance from 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 and Friedrich 1979; Jenni and Winkler 1989; Lockwood et al. 1998). Repeated measurements on a sub-sample of specimens in this study confirmed the high repeatability of the measurements. Wingtip pointedness was calculated using a variant of principle components analysis called size-constrained components analysis, as described in Lockwood et al. (1998). Using this methodology, the first component (C_1) isolates size-related variation, the second (C_2) describes the pointedness of the wingtip, and the third component (C_3) describes convexity of the wing. In this study, I used C_2 to determine wingtip pointedness, with higher C_2 values indicating less pointed wings. The wingtip pointedness index C_2 used

in this study was computed using the formula from Lockwood et al. 1998, reproduced in the appendix.

Migration distances were determined using the species range maps in Turner (2004). Migration distance was measured as the distance in kilometers between the geographic means of the breeding and wintering grounds.

Statistics

Phylogenetically independent contrasts (PICs) have become standard procedure for the analysis of ecological adaptations across multiple taxa. However, in the literature on avian wing shape and migration, PICs have not yet become standard practice (see Marchetti (1995), Monkkonen (1995), Voelker (2001), and Burns (2003) for exceptions). PICs were designed to circumvent the problem of trait values being similar in several taxa not because of adaptation, but because of phylogenetic inertia (Felsenstein 1985). A number of studies have demonstrated that applying PICs in the analysis of conserved traits, like brain size, can produce significantly different results because the confounding influence of correlations due to common descent are removed from the analysis (Felsenstein 1985; Garland et al. 1992).

The study of bird migration has demonstrated that evolutionarily speaking migration is a highly labile trait. A number of phylogenetic studies have determined that the sister species of migratory taxa are often resident species, and vice versa, indicating that migratoriness has evolved repeatedly and independently in many taxa (Helbig 2003; Kondo and Omland 2007; Outlaw and Voelker 2006; Outlaw et al. 2003). In addition, many bird species have both migratory and resident populations, and shifts between sedentariness and migratoriness in the span of a few decades have been observed in populations of several bird species (Able and Belthoff 1998; Berthold et al. 1992; Mayr 1926). Wing shape appears to be an equally labile trait, as

wing shape changes have been shown to correlate with changes in migration distance over time periods as short as several decades (Egbert and Belthoff 2003). Nonetheless, some studies on migration and wing shape have found differences in significance between the results of statistical analyses that did and did not control for phylogenetic independence (Marchetti et al. 1995; Voelker 2001). These results suggest that the use of methods to control for phylogenetic inertia — whether PICs, or other available techniques — is advisable despite the apparent lability of migration as an evolutionary trait.

The phylogeny of swallows is well understood (Sheldon et al. 2005) and a PICs analysis is straightforward as long as one avoids analyzing a discrete dependent variable (such as a migration character with character states "migratory" and "resident"). PICs rely on a Brownian motion model of evolution to construct contrasts, and the Brownian motion model can realistically only be used with continuous traits (Garland et al. 1993). Some attempts have been made to circumvent this problem, for example by integrating Sewall Wright's threshold model, which posits that polygenic variation underlies the expression of discrete characters (Wright 1934). A Brownian motion model of evolution can be applied to the underlying polygenic variation, making the use of PICs with two state characters feasible (Felsenstein 2005). However, such methods have not yet been developed and tested to the degree that they have found wide acceptance.

Thus, until tools for binary characters become more widely available, using PICs in the analysis of wing shape and migration means that migratory behavior needs to be expressed as a continuous variable, such as actual distance traveled in kilometers or degrees latitude. However, as stated in the introduction, establishing that wing shape varies with migration distance has been difficult, and I am aware of only one study that has found a significant correlation between migration distance and a wing

shape index when using PICs (Marchetti et al. 1995). Another study using PICs applied a sign test instead of a linear regression to compare the contrasts, and was thus able to show a correlation without the need to demonstrate a linear relationship between distance and pointedness (Monkkonen 1995). A third study found a correlation using PICs, but only looked at wing length, not wing shape (Voelker 2001).

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

1. A 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; Miller 1981; Rice 1989). This analysis utilized a two-state character for migration ("long- or medium-distance migrant", and "resident or short-distance migrant").

2. A linear regression of wingtip pointedness on migration distance coded as a continuous variable, using phylogenetically independent contrasts constructed from a phylogeny of the 16 swallow species, yielding 15 independent data points (Felsenstein 1985; Harvey and Pagel 1991).

Phylogenetically independent contrasts were conducted using the package "ape" version 2.2-2 (Paradis et al. 2004) and the R statistical program version 2.8.1. To conduct the PICs analysis I used the most recent Hirundinidae phylogeny available (Sheldon et al. 2005). Branch lengths were taken from a Bayesian consensus tree of two mitochondrial genes (cytb and ND2), except for *Cecropis striolata* and *Progne*

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modesta, which do not appear in this tree. Branch lengths for *C. striolata* were taken from a Bayesian consensus tree of Hirundo (*sensu lato*) based on cytb sequences (Sheldon et al. 2005). I transformed the *C. striolata* branch lengths to correspond with branch lengths from the cytb/ND2 tree under the assumption of a linear relationship between the indices ((see Figure 1; also Monkkonen 1995 for a similar approach).
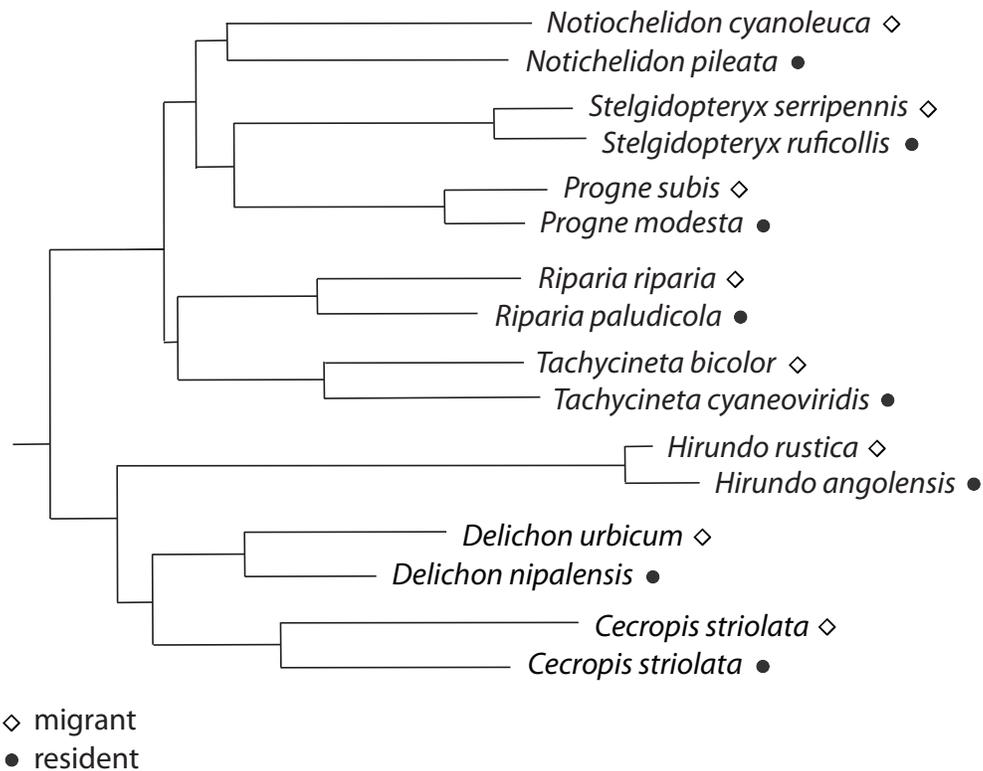

◇ migrant
● resident

Figure 1. *Phylogeny of species included in this study, based on Sheldon et al. (2005).*

For *P. modesta*, branch lengths for *P. elegans* were substituted. *P. elegans* is likely the species most closely related to *P. modesta* among the *Progne* species included in the phylogeny, and was previously considered to be conspecific with *P. modesta* (Turner 1989).

CHAPTER 3

RESULTS

An ANOVA shows that there are significant differences among the mean wing pointedness values of the 16 swallow species $(F_{15, 139} = 14.19, P < 0.0001$; see Figure 2). More importantly, an a priori contrast between all migratory and all resident species shows that the average of the mean of all migrant species is significantly different from the average of all resident species after sequential Bonferroni correction $(P < 0.0001$; see Table 2). Of eight contrasts on individual species pairs, six are significant after sequential Bonferroni correction (see Table 2 and Figure 2). Unlike in all previously published studies on wing shape and migration, however, the migratory species consistently have *less* pointed wings than their resident congeners.

Table 2. *Results of ANOVA a priori contrasts on wing pointedness values of all migratory versus all resident species and for migrants versus residents in individual species pairs. Adjusted alpha value is the alpha value after applying sequential Bonferroni corrections.*

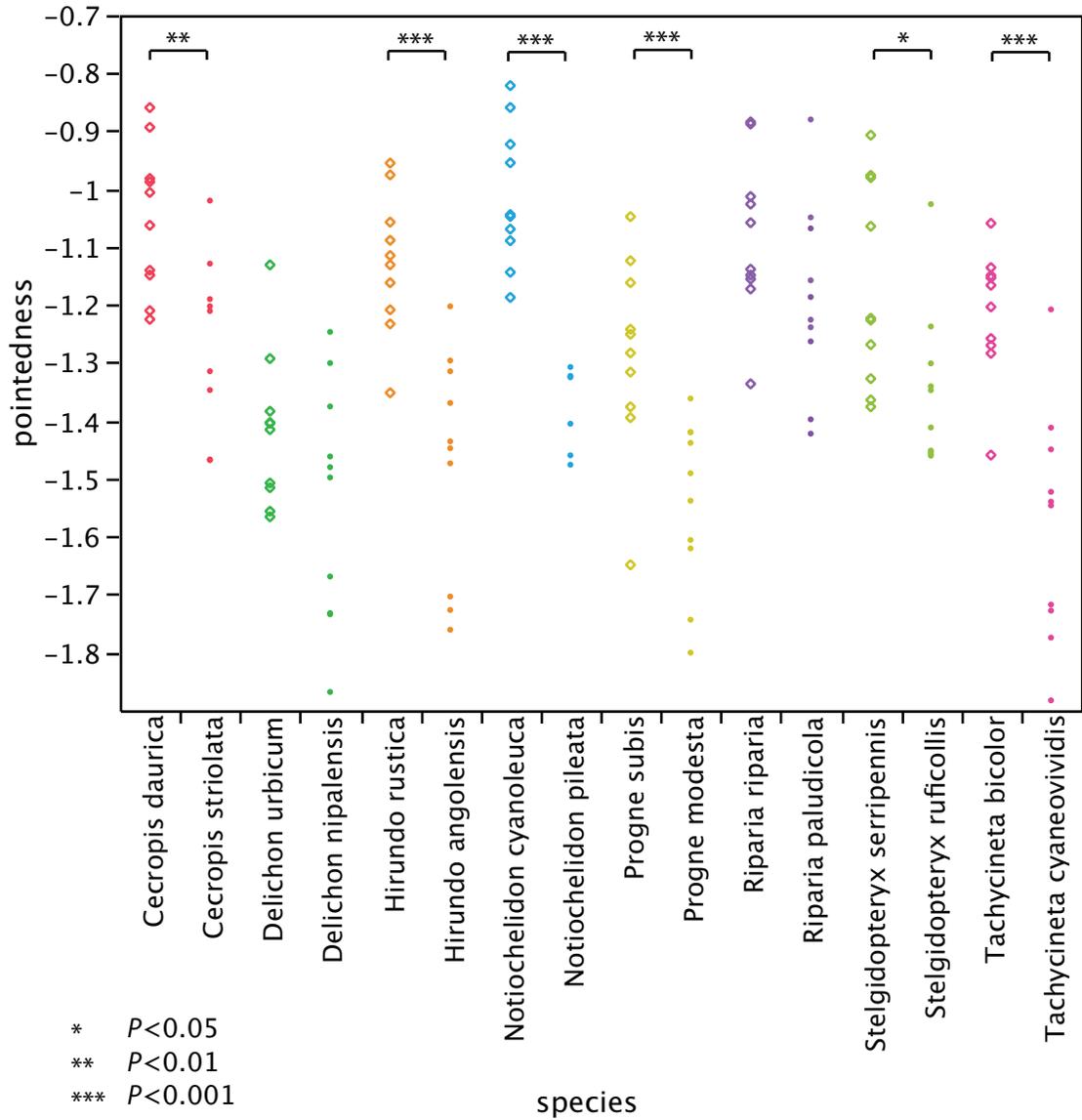| genus	test *P*	adjusted alpha value	significant
all genera pooled	< 0.0001	0.0055	yes
Tachycineta	< 0.0001	0.0063	yes
Hirundo	< 0.0001	0.0071	yes
Notiochelidon	< 0.0001	0.0083	yes
Progne	0.0002	0.01	yes
Cecropis	0.0035	0.0125	yes
Stelgidopteryx	0.0107	0.0167	yes
Delichon	0.0708	0.025	no
Riparia	0.1216	0.05	no

Figure 2. *Plot of pointedness values for all included species. Open diamonds indicate migratory species, while filled circles indicate residents. Congeneric species are paired, with each migratory species preceding the resident one. Lower pointedness scores (more negative values) indicate a more pointed wing. Brackets above species pairs indicate the significance of species-pair contrasts within the ANOVA.*

A linear regression on the independent contrasts for wingtip pointedness and

migration distance yielded a significant relationship between migration distance and

wingtip pointedness (linear regression adjusted $R^2 = 0.6057$, $F = 24.04$, df = 14, 1,

$P = 0.00023$; Figure 3).

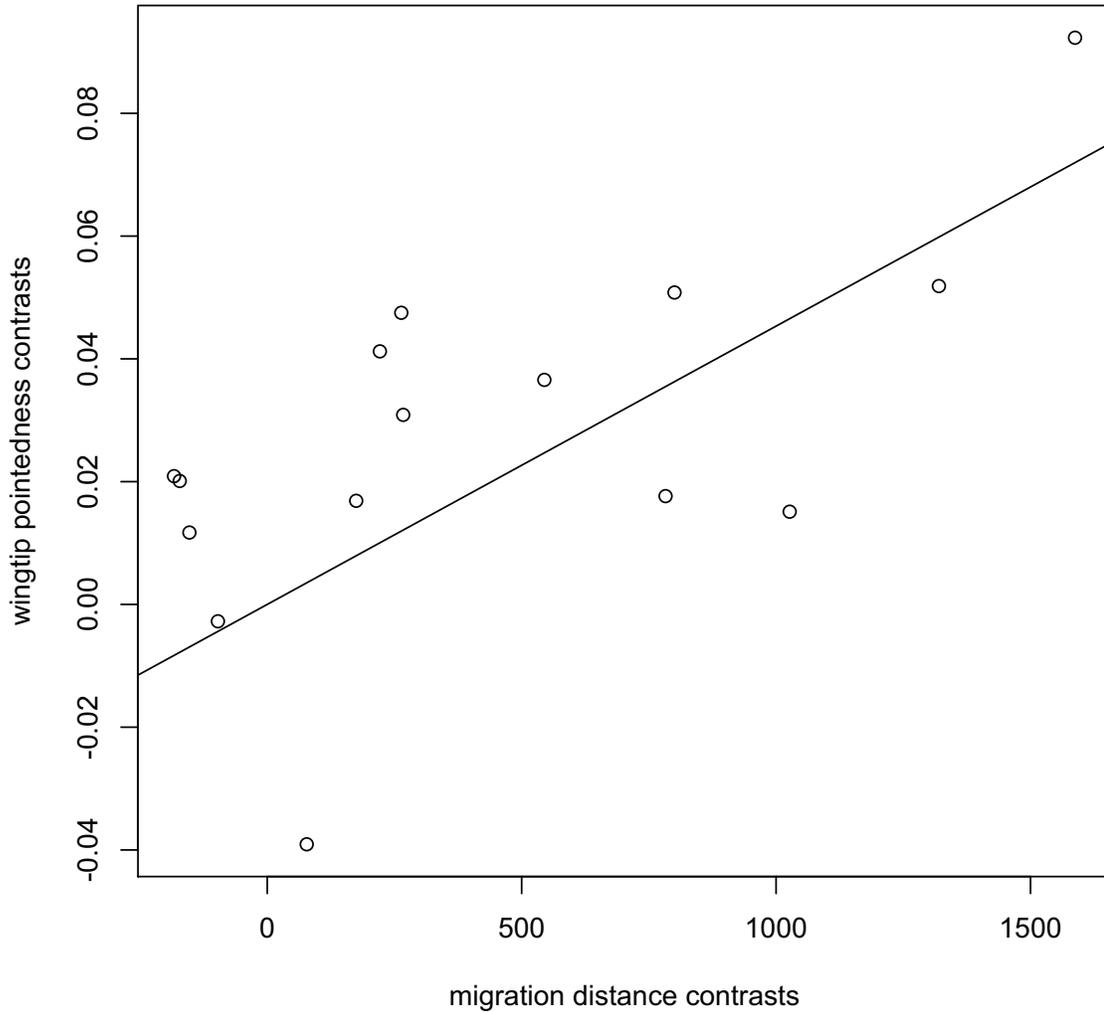***Figure 3.*** *Scatter plot of 15 wingtip pointedness contrasts against migration distance contrasts. The linear regression on the contrasts is significant:* $R^2 = 0.6057$, $P = 0.00023$.

An analysis of Cook's distance values indicated that there are no excessively influential data points. In contrast to results from all other studies that found a linear relationship, as migration distance increases, wingtip pointedness decreases.

CHAPTER 4

DISCUSSION

The general pattern that migratory birds have more pointed and higher aspect ratio wings than resident forms is well established among typical passerines, and has been confirmed in broad studies incorporating both non-passerines and passerine taxa (Lockwood et al. 1998; Norberg 1995). It has also been established among non-passerines in at least one large-scale study that investigated non-passerines separately from passerines (Winkler and Leisler 1992). However, this pattern has scarcely been investigated independently in taxa with more pointed wings. While some researchers have questioned the universality of the correlation between pointed wings and migratory behavior, hypotheses as to why this pattern may not be universal have focused on insufficiently strong selection pressures (Keast 1980; Niemi 1985), or evidence that pointedness may sometimes correlate with aspects of migratory behavior other than total migration distance (Burns 2003). To my knowledge, the basic assumption that more pointed wings are generally advantageous for migration — and that migrants thus either have more pointed or similar wings compared to residents, depending on the strength of selection — has never been questioned.

Among swallows, the passerine family with the highest aspect ratio wings, the pattern that migratory birds have more pointed wings is reversed. Migrant swallow species have significantly less pointed wings than resident species, a finding that is unprecedented in ornithological research. Six out of eight congeneric swallow species pairs show significantly less pointed wings in the migratory species after sequential Bonferroni correction (see Table 2 and Figure 2). The differences in wingtip pointedness in the other two species pairs trend in the same direction.

Not only do migrant swallows have less pointed wings than non-migrants, the wingtip pointedness decreases linearly with increasing migration distance: using

phylogenetically independent contrasts, a linear regression of migration distance contrasts on wingtip pointedness contrasts yields a highly significant linear relationship (see Figure 3). The strong inverse linear relationship between wing pointedness and migration distance in the passerine family Hirundinidae is reversed compared to the linear relationships between wing pointedness and migration distance that have been found in other avian taxa (Kaboli et al. 2007; Marchetti et al. 1995; Monkkonen 1995).

The findings presented here indicate that exceptions to the prevailing, established pattern of migrants having more pointed wings are not limited to cases in which no significant differences in wing shape exist between migrants and residents. In the family Hirundinidae, the correlation between wingtip shape and migration is reversed compared to the pattern found in all other avian taxa in which a correlation has been established (Calmaestra and Moreno 2001; Kaboli et al. 2007; Lockwood et al. 1998; Marchetti et al. 1995; Mila et al. 2008; Monkkonen 1995; Mulvihill and Chandler 1991; Norberg 1995; Norman 1997). The prediction stated in the introduction that a potentially reduced trade-off between migratory and foraging flight in swallows might reduce the selection for differential wing shape in migrants is repudiated. Migratory habit correlates strongly with more rounded wings in swallows, in contrast to all previously published results in birds.

One potential limitation of this study is that it does not include information on wing loading, a measurement that cannot easily be obtained from museum specimens with closed wings. Aspect ratio and wing loading are the primary determinants of flight ability, and thus it would be useful to know if wing loading differs between migrant and resident swallows. However, existing data from a broad collection of other taxa indicates that wing loading does not significantly correlate with migratory behavior (Calmaestra and Moreno 2001; Lockwood et al. 1998; Marchetti et al. 1995;

Winkler and Leisler 1992).

The results of this paper may seem counterintuitive, but I believe this impression results largely from a common misrepresentation of the tradeoff in wing shape between residents and migrants. The tradeoff has frequently been described as the tradeoff between efficient straight-line flight and maneuverability (Calmaestra and Moreno 2001; Mila et al. 2008; Rayner 1988; Savile 1957; Winkler and Leisler 1992). Both migratory and resident swallows require significant maneuverability to capture aerial insects that can and do take evasive action, while it seems reasonable to hypothesize that migrant swallows have an increased need for efficient straight-line flight as has been demonstrated in other migrants. When the tradeoff is described as one between efficiency and maneuverability, the wingtip pointedness data for swallows appears to run counter to logic. However, describing the trade-off as one between maneuverability and efficient straight-line flight does not apply to the type of maneuverability primarily employed in aerial insectivory. Instead, the tradeoff is more accurately described as one between efficient flight (both straight *and* curved) on the one hand, and acceleration performance on the other. Efficient flight (both straight and curved) benefits from more pointed wings, while acceleration performance increases with a more rounded wing shape.

The reason why the trade-off has often been characterized as one between straight flight efficiency and maneuverability is that among birds with relatively rounded wings, maneuverability does improve with more rounded wings. However, two very different types of maneuvering flight exist in birds (Warrick 1998). Only one of them benefits from rounded wings, but the type associated with rounded wings also happens to be the only one that is well studied and well understood. Rounded wings are the morphological adaptation that enables typical passerines and other birds to generate maximum power to make tight turns at very low speeds, to accelerate

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quickly, and to take off from the ground quickly and steeply. Warrick calls this low-speed, flapping maneuvering facultative maneuverability. However, there is another type of maneuverability that is not dependent on maximum power generation and rounded wings, and this form of maneuvering flight appears to be what is primarily employed by coursing aerial foragers such as swallows and swifts (Warrick 1998). Warrick calls this second type of maneuverability fixed-wing or intrinsic maneuverability. Intrinsic maneuverability is determined by wing loading, with larger wings relative to body mass decreasing the minimum turning radius (Norberg 1995) and thus increasing maneuverability. Secondarily, intrinsic maneuverability is improved by high wing aspect ratios because high aspect-ratio wings generate less induced drag, particularly during maneuvering (Warrick 1998).

To summarize, high aspect-ratio wings not only have the well-known effect of improving the efficiency of straight-line flight, they also improve the efficiency of higher speed intrinsic maneuvering, while diminishing acceleration performance and facultative maneuvering. Low aspect ratio wings diminish the efficiency of straight-line flight and intrinsic maneuvering while improving acceleration and low speed facultative maneuvering. The wing shape tradeoff for birds with low aspect ratio wings like typical passerines is a fairly straight-forward one between the requirement for acceleration and slow maneuvering imparted by foraging on the ground or in vegetation and by the associated increased predation risk on the one hand, and increased efficiency during migration on the other. However, among swallows, it appears that the efficiency of both normal foraging flight and migration benefit from more pointed wings, and that neither flight mode imposes a requirement for low speed maneuverability or strong acceleration. These complementary requirements beg the question why there is a significant difference in wing shape between migratory and resident swallows, and why it is the migrant swallows that have more rounded wings.

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One hypothesis is that migratory swallows have an increased need for steep takeoff from low roosting perches, because migratory swallows roost in large aggregations close to the ground where they are subject to relatively heavy predation. On migration and on their wintering grounds, migratory swallows roost primarily in low vegetation such as tall grass and reed beds (Turner 2004). In contrast, resident swallows are more likely to roost singly or in small groups in or near their nests even in the non-breeding season, or in small aggregations that do not regularly attract aerial predators (Skutch 1960; Winkler 2006). In one study of a large roost of Barn Swallows wintering in Africa, typically more than 95% of swallows departing from the roost in the morning flew almost straight up, climbing at maximum rates to avoid predation by African Hobbies (*Falco cuvieri*) and other aerial predators (Bijlsma and van den Brink 2005). (The remainder also accelerated rapidly, but departed in a flight path as horizontal as possible to hide in the tall grass.) Higher aspect ratio wings compromise maximum acceleration and climbing rate, and high acceleration performance is necessary for fast take-off from the ground or from a low perch. Indeed, birds with very high wing aspect ratios have a very difficult time with take-off from low perches, and some, such as swifts and frigatebirds, are completely unable to take off from flat ground. Pennycuick (1983) has demonstrated how variation in wing shape of birds that should all benefit from high aspect-ratio wings differs with roosting habits and especially with take-off patterns. A similar pattern may exist among swallow species, with migratory species having more stringent requirements for rapid and steep takeoff from low perches because of their habit of roosting in large flocks in low vegetation, where they may be subject to strong predation pressures. The combination of roosting low to the ground combined with the need for fast acceleration to avoid predators attracted by large roosts favors more rounded wings.

Interestingly, the two swallow species pairs that show no significant difference in wing shape may lend additional support to the migratory roost predation hypothesis. Among the two species pairs that do not show a significant difference in wing shape, both species of one pair have relatively pointed wings (genus *Delichon*), while both species of the other pair have relatively rounded wings (genus *Riparia*) (see Figure 2).

If the migratory roost predation hypothesis is accurate, we would expect the migratory *Delichon* species (House Martin, *Delichon urbicum*), which has a wing shape typical of resident swallows, to not be subject to the predation pressures of other migratory swallows. The House Martin winters in Africa and Southeast Asia, but it is seen in much smaller numbers on its wintering grounds in Africa than would be expected based on its breeding numbers (Moreau 1972). Their general absence from large swallow roosts on the wintering grounds means that they are less subject to predation at these roosts than other migratory swallows, which could explain why their wings are not adapted for strong acceleration. On the other hand, *Riparia paludicola* (Brown-throated Sand Martin) has the most rounded wing of the non-migratory swallow species in this study. Unlike most other resident swallows, *R. paludicola* roosts in the winter in large flocks in reed beds (Turner 1989), and thus according to the roost predation hypothesis should have an increased need for acceleration compared to other resident swallow species, and thus be subject to stronger selection for more rounded wings.

The results of this study raise the question whether the correlation between rounded wings and migration is unique to swallows, or whether it is a more general trend among coursing aerial insectivores, or even holds for other avian taxa with relatively pointed wings. It is conceivable that migration may impose an increased need for acceleration on other taxa with high aspect-ratio wings, if conditions during migration and on the wintering grounds necessitate roosting closer to the ground,

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and/or subject them to higher predation risks that can be ameliorated by increased acceleration ability.

Previously published data on wing shape/migration correlations in other taxa with pointed wings suggests that the correlation between rounded wings and migration may exist in taxa other than swallows. As mentioned in the introduction, Winkler and Leisler (1992) conducted a broad investigation specifically of non-passerine taxa to test whether the wing shape/migration correlation that was established largely in typical passerines holds in other taxa. They did find significantly higher aspect ratios among migrants, but they excluded 3 taxa from the analysis, namely Charadriiformes (waders), Columbidae (pigeons and doves), and Trochilidae (hummingbirds). Charadriiformes, a taxon with relatively high wing aspect ratios, was analyzed separately and yielded a non-significant but opposing trend, with resident species having higher aspect ratio wings than migrants (Winkler and Leisler 1992). In their parallel analysis of passerines, Winkler and Leisler excluded Hirundinidae (swallows) and Parulidae (New World warblers). Results for Parulidae were reported separately and mirror those of passerines in general, while results for Hirundinidae were not reported.

The only recent study that specifically looked into the wing shape/migration correlation in a relatively high aspect-ratio taxon (*Calidris* sandpipers), did not find a correlation between pointed wings and migration distance (Burns 2003). Burns used phylogenetically independent contrasts to test for a linear regression between wing pointedness and migration distance, and found a very weak non-significant effect.

What little data has been published on high aspect-ratio taxa seems to suggest at least the possibility of an inverse relationship existing in more than one such taxon. No correlation between migration and more pointed wings has been found in the few taxa with high aspect-ratio wings that have been investigated separately, and some of

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the data at least trends towards an inverse relationship. However, to test this hypothesis, additional studies similar to this one need to be conducted in other taxa with relatively pointed wings. If similar trends are found in other high aspect-ratio taxa, a more broadly defined hypothesis based on stronger selection for acceleration performance among migrants shows promise, as other taxa also show increased flocking behavior among migrants, and such flocks may also attract increased attention from predators.

The present study provides evidence that correlations between changes in morphology and ecological variables such as migratory behavior may not apply across all avian taxa, even when multiple broad studies have confirmed such correlations. In addition to testing whether the pattern described here exists in other taxa with relatively pointed wings, further study of the aerodynamics of a more diverse range of wing shapes is needed to refine our understanding of the changing tradeoffs in aerodynamic performance across the entire range of bird wing shapes. In particular, increased study of the aerodynamics of high aspect-ratio bird wings is needed to better understand the mechanics of maneuvering in birds with relatively pointed wings. The results of this study caution against generalizations about the aerodynamics of bird wings derived from the in-depth study of birds with a narrow and non-representative range of wing shapes.

APPENDIX

WINGTIP POINTEDNESS INDEX

The wingtip pointedness index C_2 used in this study was created using size-corrected component analysis, a modification of principle component analysis that isolates size variation by incorporating a rigorous geometric model of size. The index was designed and tested using a large and diverse avian dataset, and is described in more detail in Lockwood et al. (1998). Q_1 is the length of distal-most primary feather (excluding vestigial primaries), Q_2 is the length of the second most distal primary, and so forth. The C_2 index is computed as follows, with larger values of C_2 indicating a less pointed wing:

$$C_2 = \ln(3.332 Q_1^{-3.490} Q_2^{-1.816} Q_3^{-0.893} Q_4^{-0.003} Q_5^{0.829} Q_6^{1.351} Q_7^{1.661} Q_8^{2.363})$$

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