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The influence of morphological variation on migration performance in a trans-hemispheric migratory songbird

Abstract: For long-distance migratory songbirds, morphological traits such as longer wings and a smaller body size are predicted to increase migration efficiency. Due to previous limitations in our ability to track the long-distance journeys of small-bodied birds, the relationship between morphology and start-to-finish migration performance has never been fully tested in free-living songbirds. Using direct-tracking data obtained from light-level geolocators, we examined the effects of morphological factors (wing and body size) on spring and fall migration performance (flight speed, duration of stopovers, total stopovers taken) of a widely distributed, trans-hemispheric migratory songbird, the purple martin (*Progne subis*) (n = 120). We found that smaller-bodied birds spent fewer days at stopovers along fall migration, but larger-bodied birds spent fewer days at stopover and took fewer stopovers during spring migration. More of the variation in fall migration performance was explained by morphology, as compared to spring migration, possibly indicating a larger influence of environmental conditions on spring performance. Overall, our results partially support long-standing and previously untested predictions regarding the influence of intrinsic factors on migration performance. Future research should examine the influence of environmental variation on migration performance as well as additional morphological traits that may contribute to migration performance.

Keywords: Purple Martin, Migration, Speed, Performance, Stopover, Body Size, Wing Length

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1 Introduction

Migration is one of the most complex and demanding patterns of animal locomotion, requiring a considerable amount of energy, directional orientation, behavioural adaptations to external factors (e.g., weather), and physiological adaptations for metabolic changes [1-2]. Although migration is performed by almost all branches of the animal kingdom [3], birds are one of the most diverse and extraordinary migrants [4]. Arctic terns (*Sterna paradisaea*), for example, are able to migrate over 80,000 km at 976 km*day[1] [5], whereas relatively small songbirds such as purple martins (*Progne subis*) can migrate up to 23,000 km at a rate of 600 km*day[1] [6]. Migration performance, i.e., the amount of time and energy spent to complete migration [2], varies between and within species, and can be influenced by external factors such as weather, as well as intrinsic factors such as individual morphology.

Theoretical models predict that more efficient migrants possess traits that enhance their migration performance, such as longer wings, which reduce drag and provide a faster flight speed [2,4,7-11]. Smaller body size (relative

to wing length) is also predicted to increase migration efficiency, since relatively larger bodies experience greater body and parasite drag due to increased surface area in contact with the resisting airflow, that is, the resisting force of airflow against the bird during flight increases proportional to its body size [12]. Thus a smaller bodied bird experiences less resistance during flight, which allows for longer potential flight times and fewer stopovers to complete migration [12]. Migration performance is directly related to reproductive success in many bird species via benefits to birds from arriving at breeding sites early to claim the most productive breeding territories and or mates [13-14]. However, intrinsic factors that promote efficient migration (i.e. long wings, small body size) may have trade-offs with other important correlates of fitness, such as foraging efficiency or the ability to evade predators [15], resulting in within-species or within-sex or age-class variability in migration performance [16]. Wing length and body size can also be affected by nutritional status during moult and development, which could result in subsequent constraints on migration performance [17]. Whether within-species variation in wing length

and body size is correlated with start-to-finish migration performance has yet to be fully tested in free-flying, long-distance migratory songbirds.

In this study, we used purple martins as a model system for examining long-distance migration performance, as they are a common, wide-ranging, long-distance migratory songbird that breeds throughout North America (Fig. 1) and migrates to South America during the winter [18]. Purple martins show extensive within-species variation in migration timing and distance, with individuals travelling between 10,000 and 22,000 km annually, depending on their breeding site [6, (Fraser et al. unpub. data)]. Within-species variation in morphological traits, such as wing length and body size, may exist within purple martins as a consequence of their broad latitudinal breeding distribution (26°N - 53°N), where differences in climate and food quality and availability could result in different selection pressures on wing or body size [19]. Purple martins also have an aerial foraging strategy, potentially making them more sensitive to trade-offs between migration performance and foraging efficiency [8]. Their foraging behaviour and/ or migration range
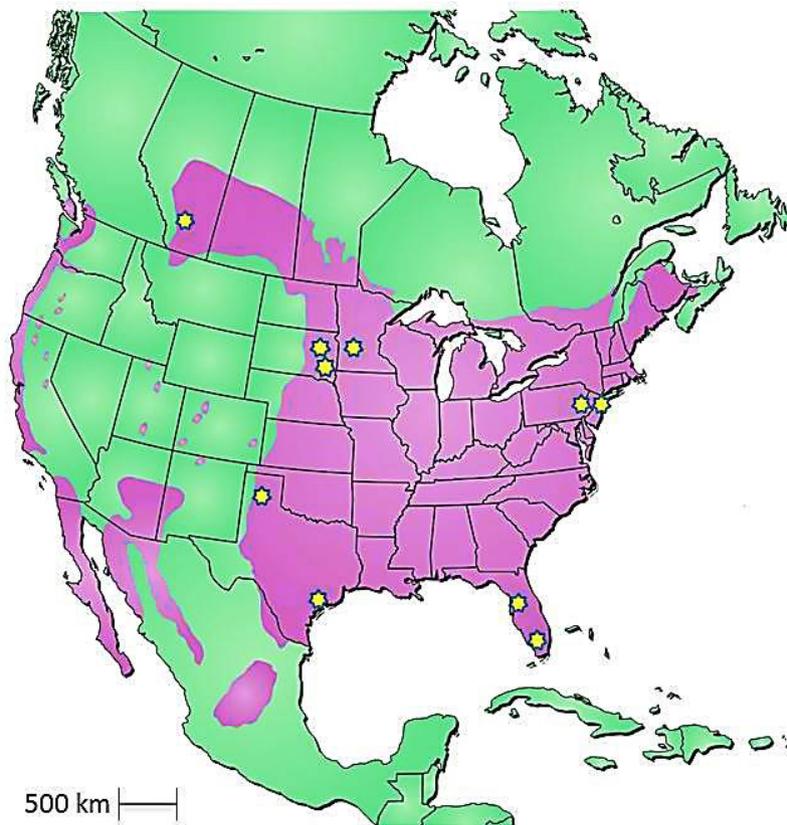
Figure 1. Research sites (indicated by yellow stars), from 2007-2013 where migration tracking devices, light-level geolocators, were deployed. The purple area shows the breeding range for purple martin (*Progne subis*). Breeding sites are (with latitude and longitudes): Lacombe (53.02°N, 112.83°W) AB; Columbia (45.62°N, 98.32°W) and Sioux Falls (43.55°N, 96.70°W), SD; Mille Lacs (45.92°N, 93.62°W), MN; Locust (40.39°N, 74.03°W), NJ; Disneyworld (28.37°N, 81.59°W) and Naples (26.15°N, 81.75°W), FL; Corpus Christi (27.70°N, 97.41°W) and Amarillo (35.04°N, 101.93°W), TX; Malvern (41.53°N, 80.07°W), PA.

are similar to other aerial insectivores (e.g., cliff swallow (*Petrochelidon pyrrhonota*)) and other passerines (e.g., Connecticut warblers (*Oporornis agilis*)), thus factors affecting migration performance in purple martins may also be applicable to similar species.

Our objective was to test the hypothesis that intraspecific variation in wing and body morphology contributes to variation in migration performance in purple martins. Using data collect across the breeding range of purple martins we examined the influence of wing length and body size on migration performance. We inferred the size of the birds through tarsus length, as this measure has been shown to be a legitimate predictor of body size for both males and females of the same species [20-21]. We predicted, based on theoretical models [2,4,7-12], that a bird with longer wings and a smaller body size would travel at a faster flight speed, stop for fewer days during migration, and take fewer stopovers to complete migration than a bird with shorter wings and a larger body size. Previous studies have examined how wing morphology affected arrival timing and energy expenditure during migration [15,22], and how wing morphology affected migration duration [23], but we present the first study to examine how intraspecific variation in wing and body morphology, across multiple sites and varying breeding latitudes, affect flight speed, total number and duration of stopovers using start-to-finish migration data. The results of our research fill a gap in our knowledge of migration behaviour and may have important implications for our understanding of the selective forces that shape the performance of long-distance migration in songbirds.

2 Material and Methods

This study was carried out in accordance with the recommendations of the Ornithological Council 'Guidelines to the Use of Wild Birds in Research' and was approved by University of Manitoba's Animal Care Committee (Animal Care Protocol Number: F14-009-1) and the York University Animal Care Committee (Animal Care Protocol Number: 2009-2W(R1)).

Geolocator Deployment– Between 2007 and 2013, we deployed 332 light-level geolocators (British Antarctic Survey, models MK10, MK12, MK14, MK20) at 10 different breeding colonies across the breeding range of purple martins (Fig. 1). Geolocators were attached to the back of the bird using a leg-loop backpack harness made of Teflon ribbon [24]. Purple martins were caught at their nest boxes using drop door or pole traps at their breeding colonies. For each individual, we measured wing length and tarsus

length and identified their sex and age. Wing length was taken by measuring the length of the flattened wing chord. Tarsus length was measured using a standard protocol [25] and was used as an indicator of overall structural body size. Purple martins were identified as either second year (SY; i.e., sub-adults), or after second year (ASY; i.e., adults) birds, based on plumage colouration [25]. Birds were recaptured at the same breeding site in the year following deployment, resulting in individual migration tracks for 120 purple martins (36% of all geolocators deployed between 2007 and 2013). Return rates of birds were not lower for birds carrying geolocators as compared to birds that were banded only [26].

Data Analysis – We used the software package BASTrak (British Antarctic Survey) to analyze the data retrieved from the geolocators. Purple martins are diurnal migrants [27], so we used the latitude and longitude coordinates at midnight to determine the stationary location of nightly stopover locations along the migration route. Birds were considered stationary when latitude and longitude remained constant within 2 degrees between consecutive midnight locations. Using this criterion, we were able to determine when each bird arrived and departed from a stopover site, overwintering site, or breeding site.

Using the position data derived from geolocators, we calculated migration flight speed, the total number of stopover days, the total number of stopovers, and the total distance travelled for both fall migration and spring migration. We calculated the total distance travelled during migration by measuring the distance between stopover sites from start-to-finish during fall and spring migration. Migration speed (km*day^{-1}) measured only the speed of the migrant when flying, and excluded stopover days. Speed was calculated by taking the total fall or spring migration distance over the number of days spent flying during the migration period of interest. We identified stopover days as all days spent at a particular stopover site. The total number of stopovers and the total number of stopover days for fall or spring migration were calculated by taking the sum of all stopovers and stopover days, respectively, from start-to-finish of fall or spring migration.

Statistical analyses – We first compared wing and tarsus length across age-sex classes and breeding latitudes, to document demographic patterns in morphology, using Student's t-tests and ANOVA. We then examined the influence of wing length and tarsus length on each component of migration performance: migration speed, total number of stopover days, and the total number of stopovers taken (the dependent variables) for both fall and spring migration using general linear models (GLMs). As

purple martins breeding further north must travel further on migration compared to those breeding at more southern latitudes, we included breeding latitude as a covariate in addition to wing length and tarsus length. For stopovers, we also included migration distance as a covariate, as longer distances (independent of breeding latitude) could result in more stopovers. We report the model estimates (± standard error, SE) for the effects of wing and tarsus length on measures of migration performance, as well as the results for overall model fit. All tests were performed using R [28]. Sample size differed in some cases between models because migration data were not available for all locations or individuals, as in the small number of cases of battery failure prior to spring migration, or when birds were travelling during the equinoxes, during which time latitudes could not be determined.

3 Results

We tracked 120 purple martins (Table 1) from 10 breeding colonies (Fig. 1) over 7 years. On average, wing length was 146.3 ± 0.3 mm, and tarsus length was 17.06 ± 0.17 mm. Wing length differed between sexes (t_{118} = -4.16, $P < 0.05$); males, on average, had significantly longer wings (mean ± SE = 147.57 ± 0.38 mm) than females (mean ± SE = 145.27 ±0.4 mm). Tarsus length was not significantly different between sexes (t_{116} = 0.43, $P = 0.67$; males: 16.98 ± 0.26 mm; female: 17.13 ± 0.22 mm). Wing and tarsus length were not significantly different between second year (SY) and after second year (ASY) birds (wing: t_{118} = -0.35, $P = 0.73$, SY = 146.58 ± 0.69 mm, ASY = 146.3 ± 0.33 mm; tarsus: t_{116} = -1.84, $P = 0.07$, SY = 17.78 ± 0.38 mm, ASY =16.93 ± 0.18 mm). Across the 10 breeding colonies, tarsus length varied significantly ($F_{1, 116}$ = 270.9, $r^2 = 0.7$, $P < 0.05$), where tarsus length was positively associated with breeding latitude (i.e., birds from Florida had the shortest tarsi and birds

with the longest tarsi were found in New Jersey); for every 1° increase in breeding latitude, tarsus length is predicted to increase by 0.22 mm. No significant differences in wing length were found between separate breeding colonies ($F_{1, 118}$ = 0.57, $r^2 < 0.001$, $P = 0.45$). Breeding latitude was also significantly correlated with the total distance travelled during fall migration ($F_{1, 118}$ = 149.4, $r^2 = 0.56$, $P < 0.05$) and spring migration ($F_{1, 109}$ = 218.9, $r^2 = 0.67$, $P < 0.05$). This collinear relationship prevents breeding latitude from being used in any models that have migration distance as a covariate. Two separate models were applied to the total duration of stopovers and total number of stopovers; one model using breeding latitude and one model using migration distance as a covariate. Furthermore, tarsus length was also positively correlated with both fall and spring migration distance (fall: $F_{1, 116}$ = 45.36, $r^2 = 0.28$, $P < 0.05$; spring: $F_{1, 108}$ = 75.39, $r^2 = 0.41$, $P < 0.05$), but wing length did not share any significant correlation with fall or spring migration distance (fall: $F_{1, 118}$ = 1.76, $r^2 < 0.01$, $P = 0.19$; spring: $F_{1, 109}$ = 0.23, $r^2 < 0.01$, $P = 0.63$). Using a linear model, we determined that tarsus length and wing length were not collinear ($F_{1, 116}$ = 1.09, $r^2 < 0.01$, $P = 0.3$).
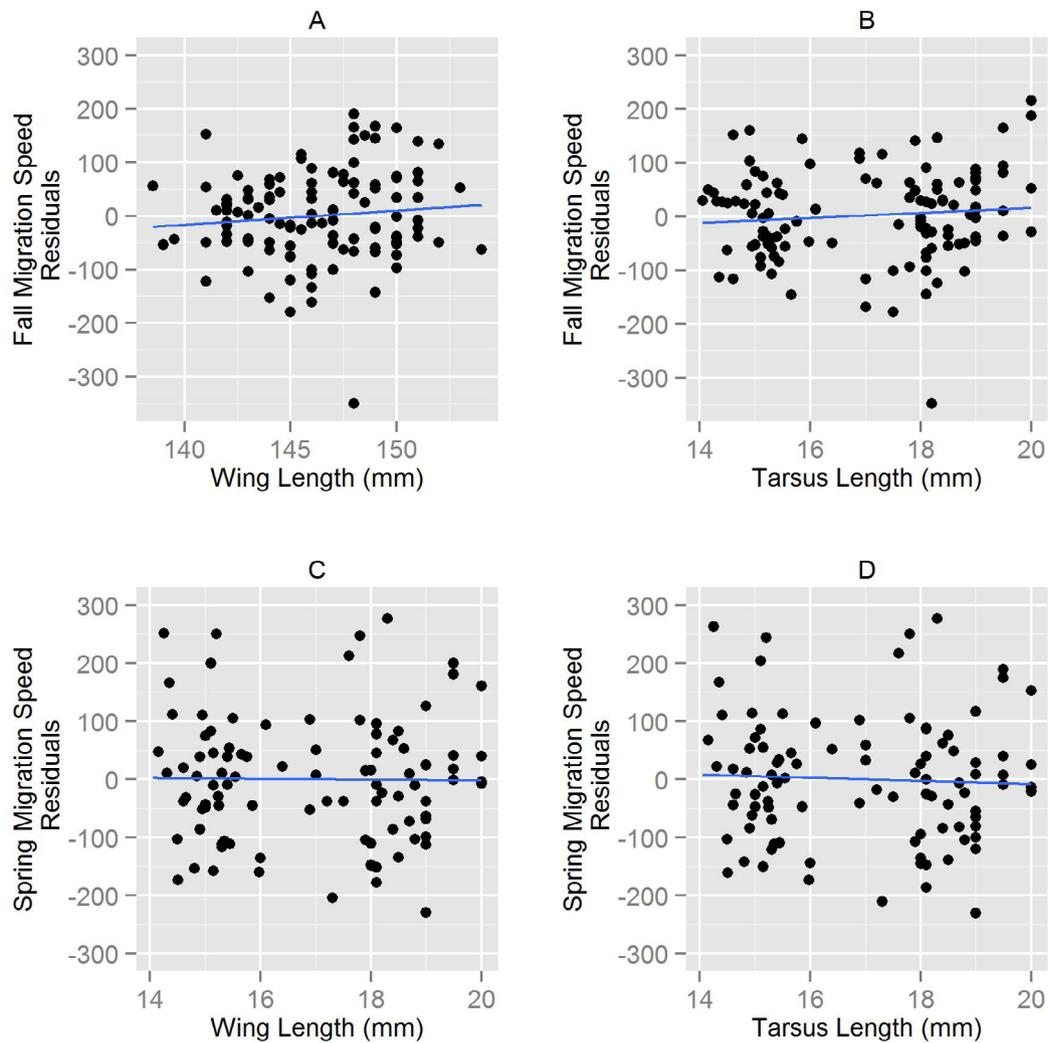
3.1 Variation in fall migration

We nested tarsus length by breeding latitude or migration distance (for stopover models) to control for variation in tarsus length between different breeding latitudes. Wing length and tarsus length were poor predictors of fall migration speed (Fig. 2A, B; $P_{wing} = 0.22$, $P_{tarsus} = 0.2$) with less than 1% of the variation explained by the model (Table 2; $F_{3, 113}$ = 1.4, $r^2 = 0.01$, $P = 0.29$).

In the model with breeding latitude as a covariate, 31% of the variation observed in the duration of fall stopovers was explained by wing length, tarsus length (nested within

Table 1. Total number of geolocators recovered from purple martins per site and per year, from 10 different sites across North America.

Year	Naples, Florida	Corpus Christi, Texas	Disney, Florida	Amarillo, Texas	Locust, New Jersey	Malvern, Pennsylvania	Sioux Falls, South Dakota	Columbia, South Dakota	Mille Lacs, Minnesota	Lacombe, Alberta
2007	0	0	0	0	0	2	0	0	0	0
2008	0	0	0	0	0	3	0	0	0	0
2009	0	0	0	0	0	11	0	0	0	0
2010	0	0	0	0	0	0	0	0	0	0
2011	0	0	0	0	11	15	4	6	4	0
2012	0	0	0	0	0	15	0	0	0	2
2013	3	13	22	8	0	0	0	0	0	1

Figure 2. Influence of wing length (A, C) and tarsus length (B, D) on fall and spring migration speed. Dependent variable (y-axis) for (A) and (C) are the residuals of tarsus length nested in breeding latitude against migration speed. Dependent variable for (B) and (D) are the residuals of wing length and breeding latitude against migration speed.

Table 2. Summary of statistical analysis from the general linear models, comparing the sample size, r², and P-values of models with breeding latitude or migration distance of purple martins as an extrinsic covariate. Tarsus length was used as an indicator of overall body size.

Dependent variables	Independent variables	Extrinsic covariate	n	r²	P
Fall migration speed (km*day⁻¹)	Wing length, Tarsus length	Breeding latitude	116	0.01	0.29
Total duration (days) spent at fall stopovers	Wing length, Tarsus length	Breeding latitude	115	0.31	<0.05
		Fall migration distance	115	0.36	<0.05
Total number of fall stopovers	Wing length, Tarsus length	Breeding latitude	58	<0.01	0.53
		Fall migration distance	58	<0.01	0.31
Spring migration speed (km*day⁻¹)	Wing length, Tarsus length	Breeding latitude	97	0.02	0.22
Total duration (days) spent at spring stopovers	Wing length, Tarsus length	Breeding latitude	99	0.02	0.22
		Spring migration distance	97	0.09	<0.05
Total number of spring stopovers	Wing length, Tarsus length	Breeding latitude	56	<0.01	0.5
		Spring migration distance	54	0.12	<0.05

breeding latitude), and breeding latitude (Table 2; $F_{3, 112}$ = 18.34, r^2 = 0.31, $P < 0.05$) but the morphological factors were poor predictors of the duration of fall stopovers (P_{wing} = 0.2, P_{tarsus} = 0.8). The model with fall migration distance as the covariate explained a greater amount of variation in the duration of fall stopovers (Table 2; $F_{3, 112}$ = 22.15, r^2 = 0.36, $P < 0.05$). In this model, wing length was, again, not a significant predictor (Fig. 3A; $P = 0.07$) but tarsus length, when nested in fall migration distance, was positively correlated with the duration of fall stopovers (Fig. 3B; $P < 0.05$).

Using breeding latitude as a covariate, the model was a poor predictor of the total number of fall stopovers (Table 2; $F_{3, 55}$ = 0.75, $r^2 < 0.01$, $P = 0.53$); the morphological variables were not significant predictors of the total number of fall stopovers (P_{wing} = 0.57, P_{tarsus} = 0.27). Applying fall migration distance in the model explained more variation in the total number of fall stopovers than applying breeding latitude as a covariate but the model was still a poor predictor (Table 2; $F_{3, 55}$ = 1.24, $r^2 < 0.01$, $P = 0.31$) and the variables were also insignificant (Fig. 4A, B; P_{wing} = 0.69, P_{tarsus} = 0.08).

3.2 Variation in spring migration

Variation in spring migration speed could not be explained by wing length or tarsus length, after correcting for variation in tarsus length between different breeding latitudes (Table 2; $F_{3, 94}$ = 0.87, $r^2 < 0.01$, $P = 0.46$). The morphological factors were also not significant predictors of spring migration speed in the model (Fig. 2C, D; P_{wing} = 0.27, P_{tarsus} = 0.21).

The duration of spring stopovers could not be predicted by wing length or tarsus length, in the model with breeding latitude (Table 2; $F_{3, 96}$ = 1.49, r^2 = 0.02, $P = 0.22$), but tarsus length was a significant predictor of the duration of spring stopovers when we used spring migration distance as a covariate (P_{tarsus} < 0.05). Tarsus length was negatively correlated with the duration of spring stopovers (Fig. 3D), a contrast to the positive correlation tarsus length showed with the duration of fall stopovers (Fig. 3B). Although the model with spring migration distance is significant, only 9% of the variation observed in the duration of spring stopovers could be explained by the morphological factors (Table 2; $F_{3, 94}$ = 4.07, r^2 = 0.09, $P < 0.05$).

Wing length and tarsus length were poor predictors of the total number of stopovers taken during spring migration when breeding latitude was applied as a covariate (Table 2; $F_{3, 53}$ = 0.8, $r^2 < 0.01$, $P = 0.5$; P_{wing} = 0.42, P_{tarsus} = 0.22) but tarsus length was a significant predictor

when nested in spring migration distance (P_{tarsus} < 0.05). Tarsus length was negatively correlated with the total number of spring stopovers (Fig. 4B). The model using spring migration distance as a covariate explained more variance in the total number of spring stopovers (Table 2; $F_{3, 51}$ = 3.47, r^2 = 0.12, $P < 0.05$) than the model with breeding latitude.

4 Discussion

We found that variation in body size correlated with en-route migration performance in a long-distance migratory songbird, whereby in fall, smaller-bodied birds (inferred through tarsus length) took fewer stopovers while in spring, larger-bodied birds complete migration with fewer individual stops and fewer total days spent at stopovers. Our fall migration results support predictions that energy expenditure during migration is modulated by variation in body morphology, subsequently influencing the number of stopover days needed for refueling during migration. We also found that wing length was not significantly different between different breeding colonies but larger-bodied birds were found at higher latitude colonies. The novelty of this result contrasts with previous studies that showed variation in wing length across different latitudes [29-30]. We speculate that wing length may be influenced by external factors, such as variation in climate [30], as well as ecological demands, such as selection for shorter wings to allow for greater aerial manoeuvrability at breeding sites with high predation rates [31].

The stopover models (total duration of stopovers and the total number of stopovers) required two models to control for variation in body size (one with breeding latitude and another with migration distance as a covariate). Comparing the two models revealed that greater variation in the total duration of stopovers and the total number of stopovers was explained in the model that included migration distance. The significance of migration distance in these models suggests the migration strategy adopted by larger-bodied birds differs from smaller-bodied birds, as a result of adaptation to longer migration distance.

4.1 Fall migration performance

Larger birds (as measured by tarsus length) had more stopover days during fall migration, which may be due to a higher requirement of energy to power flight or having to
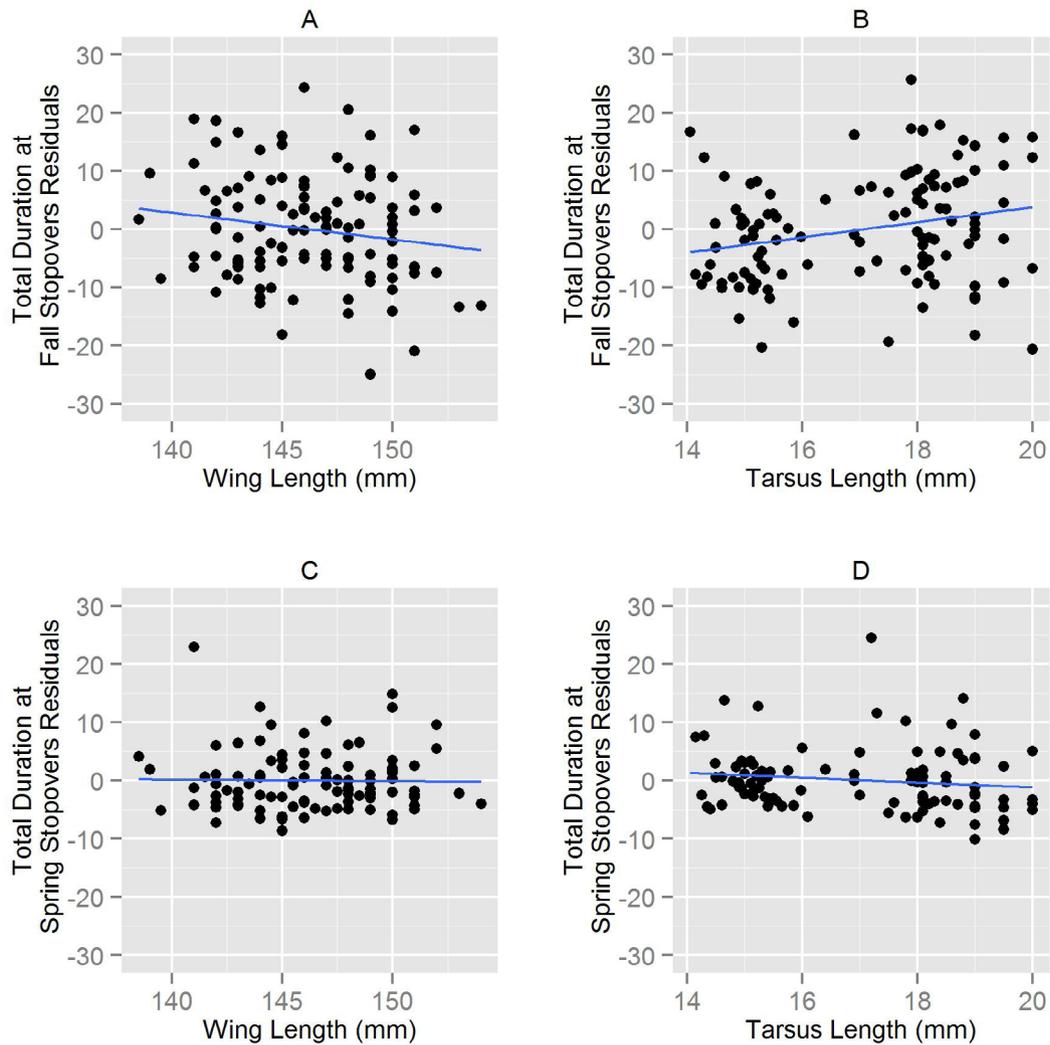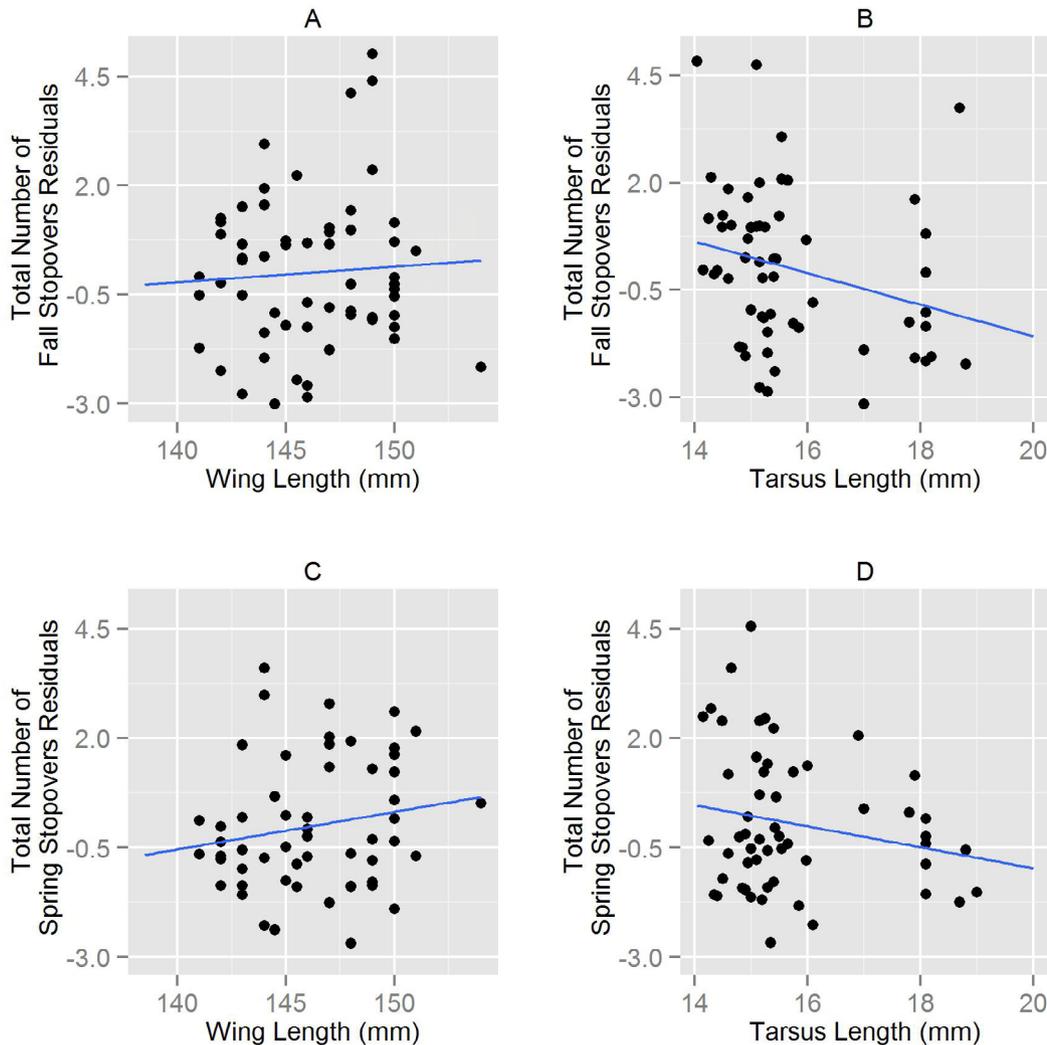
Figure 3. Influence of wing length (A, C) and tarsus length (B, D) on the total number of days spent at stopovers on fall and spring migration. Dependent variable (y-axis) for (A) and (C) are the residuals of tarsus length nested in migration distance against the total duration spent at stopovers on migration. Dependent variable for (B) and (D) are the residuals of wing length and migration distance against the total duration spent at stopovers on migration.

travel further on fall migration, resulting in an increased rate of fuel expenditure [4,32]. Body size (tarsus length) and wing length were poor predictors of migration flight speed and the total number of stopovers taken on fall migration. Our results do not support the theoretical models proposed by Pennycuick [32] that larger birds must fly faster than smaller birds to achieve the same distance travelled during migration. A previous study [15] of another neotropical, long-distance migratory songbird, the Swainson's thrush (*Catharus ustulatus*), found that individuals with more pointed wingtips and a lower wing loading arrived earlier during spring migration, which could be a result of faster flight speed, or fewer stopovers.

More pointed wingtips are often associated with longer wings [8], but our results revealed longer wings do not contribute to greater migration performance, contrary to our predictions.

Male purple martins had significantly longer wings than females but body size was similar between sex classes. However, our results do not suggest this confers any advantages to their migration performance, as we did not find longer wings to have any significant effect on fall or spring migration performance. We found no significant differences in morphology by age class, indicating that sub-adult (second year) and adult (ASY) birds could perform similarly during fall migration. This

Figure 4. Influence of wing length (A, C) and tarsus length (B, D) on the total number stopovers taken on fall and spring migration. Dependent variable (y-axis) for (A) and (C) are the residuals of tarsus length nested in migration distance against the total number of stopovers taken on migration. Dependent variable for (B) and (D) are the residuals of wing length and migration distance against the total number of stopovers taken on migration.

contrasts with previous studies, which show that younger birds have shorter wings and related poorer migration performance [16,31]. However, our younger age-class (SY) birds were completing their second fall and spring migration (as opposed to their inaugural migrations) and thus it is perhaps not surprising that their morphology during their second year was not significantly different than that of older adults. Examining other measures of wing morphology (in addition to wing length), such as aspect ratio and wing loading, which are predicted to have direct effects on migration performance [4,8], may provide insight on potential sex- or age-dependent differences in factors driving these traits.

4.2 Spring migration performance

In contrast to fall migration, larger bodied birds tended to spend fewer days at stopovers and took fewer stopovers to complete spring migration. It is possible that larger-bodied birds are better able to tolerate adverse weather during early spring at breeding sites. Martins, like other aerial insectivores, are susceptible to early-spring cold snaps, and thus natural selection could result in larger-bodied birds being favoured to arrive earlier at breeding sites [33]. During a cold spring, smaller-bodied birds might be at a thermoregulatory disadvantage [34], in contrast to fall migration when food is abundant, weather is generally

more favourable, and small bodies are advantageous for flight efficiency [32]. Sex-differences in migration performance are usually most apparent in spring, when males initiate migration and arrive at breeding sites earlier than females [35]. However, our results suggest that within-species variation in morphology is not an important component of migration performance in spring, and sex-differences in wing size are unlikely to account for any observed protandry in purple martins. However, overall models for spring migration performance were weaker than for fall migration performance.

Selection pressures on morphology may differ between spring and fall migration in that extrinsic factors, such as environmental conditions, play a larger role in shaping spring migration performance. Prey availability and abundance may differ between spring and fall migration for many migratory songbirds [36], which has been found to affect migration performance [37] resulting in behavioural differences between the two migration periods. It has yet to be tested whether spring phenology and available resources (i.e., variation in insect emergence and abundance as a result of temperature differences) at stopover sites affects spring migration performance in martins. An investigation into habitat quality of stopover sites during spring migration may reveal differences in physiological condition within-species that contributes to spring migration performance [38]. Endogenous timing factors likely also play a role, given strong selection for early arrival at breeding sites in spring. A previous study [6] found that purple martins did not depart for spring migration earlier or migrate at a faster rate in response to warmer temperatures and an earlier spring, suggesting endogenous schedules may not be very flexible to changing environmental conditions.

In conclusion, we tested long-standing predictions about the influence of morphological traits on migration performance in purple martins. However, we emphasize that because purple martins adopt a fly-and-forage strategy [39], which is uncommon among typical long-distance migratory songbirds, our results are more applicable to other species with a similar migration range and behaviour, such as other swallows. We found strong evidence that variation in body size contributes to overall migration performance, whereby smaller-bodied birds spent fewer days at stopovers during fall migration, but larger-bodied birds spent fewer days at stopovers and took fewer stopovers to complete spring migration. We found considerable variation in migration performance within purple martins, so it is important to examine what factors contribute to intraspecific variation, such as how optimization of migration performance may result in a

trade-off with foraging ability and provisioning rates. We recommend examining other factors that may influence or limit migration performance, as wing-morphology characteristics in purple martins may contribute to or be under selection to support other life-history functions, such as terrestrial and aerial predator avoidance, or to enhance foraging or provisioning ability, in addition to migration performance.

Conflict of Interest: We, the authors of this study, declare that we do not have any conflicts of interest.

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