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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Body mass and wing shape explain variability in broad-scale bird species distributions of migratory passerines along an ecological barrier during stopover

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Abstract Migrating birds are under selective pressure to complete long-distance flights quickly and efficiently. Wing morphology and body mass influence energy expenditure of flight, such that certain characteristics may confer a greater relative advantage when making long crossings over ecological barriers by modifying the flight range or speed. We explored the possibility, among light (mass <50 g) migrating passerines, that species with relatively poorer flight performance related to wing shape and/or body mass have a lower margin for error in dealing with the exigencies of a long water crossing across the Gulf of Mexico and consequently minimize their travel time or distance. We found that species-mean fat-free body mass and wing tip pointedness independently explained variability among species distributions within ~50 km from the northern coast. In both spring and autumn, lighter (i.e., slower flying) species and species with more rounded wings were concentrated nearest the coastline. Our results support the idea that morphology helps to shape broad-scale bird distributions along an ecological barrier and that migration exerts some selective force on passerine morphology. Furthermore, smaller species with less-efficient flight appear constrained to stopping over in close proximity to ecological barriers, illustrating the importance of coastal habitats for small passerine migrants.

Keywords Flight · Ecophysiology · Gulf of Mexico · Migration · Passerine

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Introduction

Across the globe, billions of migratory passerine birds travel great distances between breeding and non-breeding grounds, often flying long distances over large, inhospitable areas (e.g., deserts or oceans) at some point during the trip (Alerstam 1993; Berthold 1993). Most passerines must repeatedly stop their migratory flights to rest and refuel. When and where birds stop during migration have important consequences for migrants. Birds that stopover in areas of high resource availability are potentially able to deposit fuel at a faster rate (Klaassen 1996; Jenni and Schaub 2003), which may be especially important directly after or before embarking on a long, energetically expensive flight (Moore and Kerlinger 1987). Birds not able to stop in food-rich areas when energy reserves are insufficient or weather conditions are not conducive to flight (e.g., headwinds; precipitation) may be forced to land in lower quality habitats (e.g., Gauthreaux 1971; Buler and Moore 2011). The process of stopover site

selection is influenced by a hierarchy of factors operating at different scales including preferred migratory route, conditions experienced during flight (e.g., weather), available information about the landscape below while aloft (e.g., habitat; proximity to barrier), habitat quality, and intrinsic factors such as a bird's endogenous time program, energetic condition, age, sex, or morphology (Hutto 1985; Moore and Aborn 2000; Jenni and Schaub 2003; Moore et al. 2005; Chernetsov 2006; Buler et al. 2007; LaFleur et al. 2016).

Examining the habitat use patterns of migrants at various scales can deepen our understanding of the process of stopover site selection and help to reveal the influence of different factors in shaping migrant stopover distributions. For example, Buler et al. (2007) examined forest bird stopover distributions along the northern Gulf of Mexico coast and found a residual negative linear relationship between bird density aggregated across species and proximity to the coastline in both spring and autumn after accounting for other factors that influenced migrant distributions (e.g., forest cover and food availability). This relationship indicates that migrants, in general, tend to concentrate near the coastline. However, individual bird species exhibited variability in the magnitude and direction of this relationship, with some having greater concentrations inland from the coast. This variability in the broad-scale coastal concentrations among species might be related to morphological differences among species tied to their flight capabilities.

Flight performance related to wing shape and/or body mass could influence travel time or distance when crossing wide barriers. Bird species with longer and relatively more pointed wings migrate farther and fly faster than those with shorter, more rounded wings (Yong and Moore 1994; Marchetti et al. 1995; Lockwood et al. 1998; Arizaga et al. 2006; Lam et al. 2015), but see Mönkkönen (1995). Furthermore, flight speed is positively correlated with body mass (Hedenström and Alerstam 1992). Thus, smaller and/or less-efficient flyers should have less of a margin for error in dealing with the exigencies of a long water crossing across the Gulf of Mexico and are under greater physiological constraint to minimize their travel time or distance to make the crossing. This constraint could manifest as a pattern of more acute concentrations of poor flyers at the edge of a barrier.

Our objective was to test the hypothesis that differences in the stopover distributions among migrating passerine species near large crossings of water or desert may be explained, in part, by species-level variability in physiological flight capability using data from Buler et al. (2007) and more recently collected morphological data. Specifically, we examined the relationship of the residual magnitude of the change in bird stopover density with proximity to the coastline with several morphological characteristics known to influence flight performance among several migrant passerine species along the northern coast of the Gulf of Mexico.

Materials and methods

The study area covers a 1 million hectare region within USA bordering the northern coast of the Gulf of Mexico, including nine counties within the state of Mississippi and two parishes within the state of Louisiana. Twenty-eight strip transects (500 m long × 50 m wide) were established within riparian hardwood forests along streams and within floodplain hardwood forests along major rivers (Fig. 1). Transects were placed at least 1 km apart to reduce the probability of double counting individuals, and were geographically stratified across the study area with respect to longitude and proximity to the coast. Bird surveys were conducted within the first 4 h after sunrise during two consecutive autumn (early September to the end of October 2002 and 2003) and spring seasons (mid-March to early May 2003 and 2004; for additional details, see Buler et al. 2007). Seasonal mean bird density for each selected species by transect was calculated for each sampling year and then averaged across years. We used coastline data provided by the United States Geological Survey (Watermolen 2005) to calculate the proximity of transect centers to the nearest major coastline. The distance from each transect to the nearest coastline ranged from 8.5 to 56.5 km (mean =33.0 km).

To get morphology measures at the species level (i.e., averaged across a representative sample of individuals within species), we collected wing shape data during the autumns of 2009–2011 from birds captured at a long-term bird banding station located within the Bon Secour National Wildlife Refuge along the coast of the state of Alabama, USA (30.2301°N, 88.0044°W). We also obtained data collected at a bird banding station along the southern coast of the Delaware Bay in the state of Delaware, USA (38.7837°N, 75.1647°W) during the autumn of 2011. We captured birds using mist nets and measured body mass (0.1 g), un-flattened wing chord (0.5 mm), and, from a subset of birds, the lengths of the eight distal-most primary feathers (0.5 mm) as described in Jenni and Winkler (1989). From a different subset of birds, we took two high-resolution (2592 × 1944 pixels) digital photographs of the right wing (Fig. 2). Using these photographs with Adobe Photoshop (Version CS5.1) and IMAGEJ (Abramoff et al. 2004) software, we calculated total wing area as the sum of the "body" (a.k.a. "root") box and twice the right wing area following Pennycuick (1989). We then estimated wingspan by doubling wing length and adding the width of the body box.

We used four morphological variables averaged at the species level for our analyses: aspect ratio, fat-free body mass, wing pointedness (C_2), and wing convexity (C_3). We originally considered also using species-average fat-free wing loading (average fat-free mass divided by average wing area) as a morphological variable. However, it was strongly correlated with fat-free body mass among the

Fig. 1 Map of study area along the northern Gulf of Mexico within the states of Mississippi and Louisiana USA (land *light gray*, water *white*). The locations of 28 transects (*dots*) are within riparian hardwood forests along streams and within floodplain hardwood forests along major rivers depicted as *gray lines*
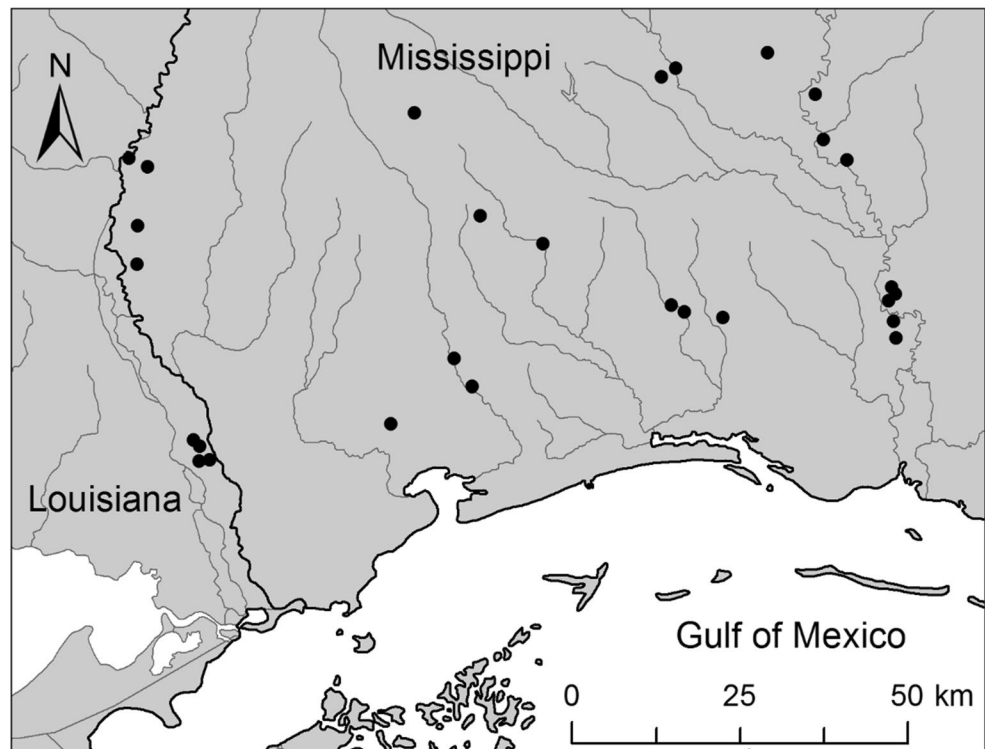

Fig. 2 *Left* high-resolution (2592 × 1944 pixels) image taken of a bird wing at the banding station in Bon Secour National Wildlife Refuge, Alabama, USA. *Right* wing silhouette image produced from field photographs through Adobe Photoshop. IMAGE J software was then used to calculate total wing area as the sum of the "body" (a.k.a. "root") box and twice the *right* wing area following Pennycuick (1989). We also estimated wingspan by doubling wing length and adding the width of the body box
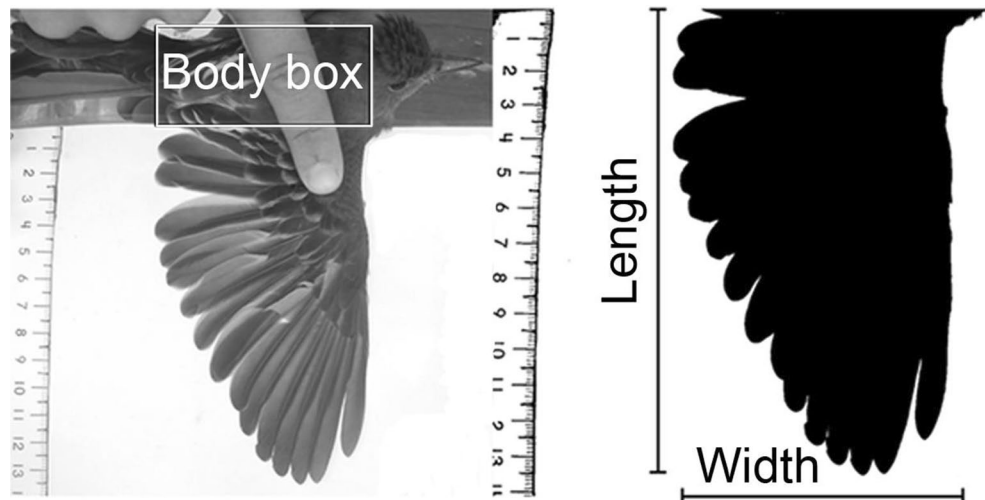
sampled species (Pearson $r = 0.95$, $df = 14$, $p < 0.001$). We decided to use fat-free mass instead of fat-free wing loading in our analysis, because sample sizes were greater for determining fat-free mass within species and it is a simpler measure. However, our interpretations could be cast in terms of wing loading based on our data set. The absolute values of all other correlations among predictor variables were <0.49. We calculated aspect ratio for each individual bird as the square of the wingspan divided by total wing area. To estimate the species-mean fat-free body mass, we used body mass, fat score (Helms and Drury 1960), and wing chord from >20 years of banding data collected primarily along the northern Gulf of Mexico coast by FRM for each focal species (total $n = 11,568$). Using this large data set and methods described by Ellegren (1989, 1992), we first performed a linear regression of body mass on fat score for the wing chord length class (1 mm increments) for each species. We then performed a second regression between the resulting intercepts of the first regression and each wing chord class. The resulting equation from the second regression allowed us to estimate the mean fat-free body mass of each species based on the species-mean wing chord length. To quantify the wingtip shape, we calculated size-constrained wing shape components C_2 and C_3

using primary feather measures according to Lockwood et al. (1998). C_2 is a measure of how pointed the wingtip is where lower values indicate a more pointed wing and higher values indicate a more rounded wing. C_3 describes convexity or concavity where increasing C_3 values corresponds to increasing convexity.

As a measure of the change in bird density with proximity to the coast (i.e., index of coastal concentration) for each bird species, we used the mean standardized regression coefficient of the linear regression between bird density and proximity to the coast after controlling for the effects of arthropod abundance, forest cover in the local landscape, habitat structure, and plant composition reported by Buler et al. (2007). A negative coefficient value indicated that the density of a species was relatively greater nearer the coastline (i.e., strong coastal concentration), while a positive value indicated that the density was relatively greater away from the coast (i.e., weak coastal concentration). We analyzed data for migrant species with ≥50 detections across all surveys and with >5 individuals measured for morphological characters.

We modeled variability in the index of coastal concentration among species (outcome variable) with each of the four morphometric predictor variables separately (species means of aspect ratio, fat-free body mass, and wing shape components C_2 and C_3) using hierarchical linear models within a Bayesian framework. We did not consider models with multiple predictors given the low sample sizes (i.e., number of species). We incorporated uncertainty in point estimates of species means (i.e., measurement error) for all variables in the models by defining the probability of the observed mean for each species as having the specified Gaussian distribution centered on the posterior estimated mean given the observed SE of the mean (from Table 1). Doing so allowed us not only to estimate parameter coefficients for predictors that take into account the uncertainty of both outcome and predictors, but it also produced updated estimates of the means of each species for each predictor variable via partial pooling. Incorporating measurement error in the models also precluded the calculation of a valid information criterion (e.g., WAIC) (McElreath 2016). Therefore, we did not compare our models within an information theoretic framework.

Table 1 Species averages (±SE) of morphology characteristics

Species	Estimated fat-free body mass (g)	Wing chord length (mm)	Wing pointedness	Wing convexity	Aspect ratio	Coastal concentration index	
						Spring	Autumn
Acadian Flycatcher	11.06 ± 2.18	72 ± 0.11 (70)	−0.02 ± 0.16 (8)	−1.63 ± 0.29 (8)	5.04 ± 0.08 (8)	0.61 ± 0.37	−0.16 ± 0.18
American Redstart	6.86 ± 1.56	61 ± 0.03 (840)	0.32 ± 0.07 (27)	−1.58 ± 0.07 (27)	4.65 ± 0.03 (17)	−0.37 ± 0.40	−0.37 ± 0.17
Blue–gray Gnatcatcher	5.67 ± 2.16	51 ± 0.03 (721)	1.40 ± 0.27 (9)	−0.98 ± 0.21 (9)	4.40 ± 0.06 (14)	−0.38 ± 0.29	n/a
Eastern Wood Pewee	12.23 ± 3.84	82 ± 0.10 (133)	0.09 ± 0.24 (6)	−0.90 ± 0.45 (6)	5.51 ± 0.09 (7)	n/a	−0.53 ± 0.23
Great Crested Flycatcher	32.13 ± 7.25	98 ± 0.19 (75)	0.42 ± 0.08 (16)	−1.59 ± 0.14 (16)	4.51 ± 0.08 (14)	0.57 ± 0.38	n/a
Gray Catbird	32.23 ± 4.74	88 ± 0.02 (5202)	1.04 ± 0.14 (18)	−1.01 ± 0.12 (18)	4.48 ± 0.05 (19)	n/a	−0.29 ± 0.24
Hooded Warbler	9.01 ± 1.01	64 ± 0.04 (219)	0.56 ± 0.10 (11)	−1.48 ± 0.16 (11)	4.50 ± 0.09 (14)	−0.37 ± 0.43	−0.31 ± 0.17
Indigo Bunting	11.99 ± 2.85	65 ± 0.03 (482)	0.27 ± 0.10 (14)	−1.25 ± 0.11 (14)	4.63 ± 0.08 (13)	0.23 ± 0.41	n/a
Magnolia Warbler	6.93 ± 0.96	58 ± 0.04 (630)	0.66 ± 0.11 (11)	−1.48 ± 0.08 (11)	4.55 ± 0.07 (11)	n/a	−0.61 ± 0.25
Northern Parula	6.48 ± 7.39	55 ± 0.10 (82)	0.30 ± 0.11 (13)	−1.34 ± 0.14 (13)	4.78 ± 0.07 (10)	−0.10 ± 0.28	n/a
Prothonotary Warbler	11.36 ± 4.91	69 ± 0.08 (80)	0.45 ± 0.06 (9)	−1.57 ± 0.07 (9)	5.08 ± 0.08 (15)	−0.56 ± 0.30	n/a
Red-eyed Vireo	13.76 ± 1.77	78 ± 0.03 (1276)	0.38 ± 0.10 (11)	−0.91 ± 0.06 (11)	5.51 ± 0.04 (18)	0.30 ± 0.45	−0.63 ± 0.26
Summer Tanager	25.61 ± 5.97	92 ± 0.07 (69)	−0.08 ± 0.07 (14)	−1.30 ± 0.11 (14)	5.11 ± 0.06 (9)	0.68 ± 0.39	−0.26 ± 0.24
Tennessee Warbler	7.72 ± 2.61	63 ± 0.04 (287)	0.20 ± 0.06 (9)	−1.59 ± 0.10 (9)	5.02 ± 0.06 (15)	n/a	−0.06 ± 0.24
White-eyed Vireo	9.74 ± 1.71	60 ± 0.02 (994)	0.46 ± 0.10 (13)	−1.09 ± 0.12 (13)	4.58 ± 0.05 (14)	−0.44 ± 0.31	−0.29 ± 0.18
Wood Thrush	38.61 ± 7.75	105 ± 0.05 (408)	−0.06 ± 0.08 (13)	1.52 ± 0.13 (13)	4.76 ± 0.08 (7)	0.59 ± 0.52	0.11 ± 0.18

Mean fat-free body mass is based on median species wing chord. Fat-free body mass standard deviations are based on parameter estimates of the regression (see "Materials and methods"). Wing chord presented as median ± SE. Wing pointedness and wing convexity are wing shape component indices C_2 and C_3, respectively, described by Lockwood et al. (1998). Aspect ratio is wing span^2 wing area^{-1}. Coastal concentration indices are the standardized regression coefficient of the residual change in bird species density with proximity to the coast by season. Sample sizes are reported in parentheses where appropriate

Instead, we present the results of all four models tested for each season. We specified vague priors for the intercept and slope parameters and used a Hamiltonian Monte Carlo sampler to run the analysis with STAN (Stan Development Team 2016) using packages rstan (Guo et al. 2016) and rethinking (McElreath 2016) in program R (R Development Core Team 2016). We determined the mean pooling factor (λ) and mean R^2 across 1000 samples of the posterior distribution of each model following Gelman and Pardoe (2006). The pooling factor represents the degree to which the point estimates are pooled together based on means across species rather than estimated separately based on the raw data. The pooling factor ranges from 0 (i.e., no pooling) to 1 (i.e., complete pooling). The R^2 values represented the amount of explained variance of the posterior estimates of species-mean coastal concentration indices.

Results

We had sufficient sample sizes of wing measurements for a total of 12 species among seasons (Table 1). During both seasons, fat-free body mass and wing pointedness explained a moderate amount of variability in the coastal concentration index among species (Table 2). At least 90% of the posterior probability density of their regression coefficients were either negative or positive, respectively. Fat-free mass was more strongly related to coastal concentration index than wing pointedness in both seasons. Species with lower fat-free body mass and more rounded wings were more strongly concentrated along the coastline than heavier species and species with more pointed wings (Fig. 3). Associations were stronger during spring than autumn. Aspect ratio and wing convexity were not related to coastal concentration index for either season. There was a large amount of pooling among estimates in general. Thus, our approach to include uncertainty around the average point estimates likely helped to reduce the risk of overconfidence and spurious inference.

Discussion

We provide evidence that morphological characteristics related to the flight capability of migrating birds at a species level are associated with species stopover distributions across a broad spatial extent near the edge of a wide ecological barrier. Specifically, variability among 12 long-distance migrant passerine species in how strongly they concentrate at the coastline during migratory stopover within 50 km of Gulf of Mexico is influenced, in part, by their species-average body mass and wing tip pointedness. Lighter species and those with rounder wings departed (during autumn) and landed (in spring) in closer proximity to the barrier than heavier species and those with more pointed wings, presumably before or after flying a distance of up to 1500 km across the Gulf of Mexico. Most migrants in our study area, centered along the northern coast, engage in trans-Gulf crossings (Lowery 1946; Moore et al. 1990; Gauthreaux and Belser 1999), and their distributions within 50 km of the coastline likely represent the initial landfall or departure points when negotiating the crossing (Gauthreaux 1971; Gauthreaux and Belser 1999; Gauthreaux et al. 2006; LaFleur et al. 2016).

Species with a greater body mass may experience advantages through increased flight speed (i.e., shortened crossing time) and less susceptibility to wind drift and turbulence than lighter (i.e., slower flying) species (Lindhe-Norberg et al. 2000; Calmaestra and Moreno 2001; Alerstam et al. 2007). Thus, heavier species may make faster and more directed flights across the Gulf. This may leave them with relatively greater energy reserves upon finishing the crossing and energy to continue flying inland. Alternatively, it can take 18–24 h for migrants to cross the Gulf of Mexico

Table 2 Mean posterior standardized regression coefficient of linear models for each species-mean morphology measure predicting coastal concentration index among passerine species along the northern Gulf of Mexico coast by season

Model predictor	Season							
	Spring ($n = 12$ species)				Autumn ($n = 11$ species)			
	Coefficient	Cum. P	R^2	λ	Coefficient	Cum. P	R^2	λ
Fat-free mass	0.03 (0.00 to 0.06)	0.99	0.68	0.86	0.01 (−0.00 to 0.03)	0.93	0.41	0.83
Wing pointedness	−0.68 (−1.47 to 0.01)	0.97	0.58	0.64	−0.30 (−0.77 to 0.19)	0.90	0.22	0.80
Wing convexity	−0.16 (−1.02 to 0.70)	0.66	−0.19	0.28	−0.25 (−0.76 to 0.25)	0.85	−0.17	0.87
Wing aspect ratio	0.08 (−0.30 to 0.45)	0.68	0.01	0.09	−0.09 (−0.39 to 0.20)	0.73	−0.30	0.46

Wing pointedness and wing convexity are wing shape component indices C_2 and C_3, respectively, described by Lockwood et al. (1998). Aspect ratio is wing span^2 wing area^{-1}. The 95% credible interval range is presented in parentheses. The cumulative posterior probability density (Cum. P) of coefficients greater or less than zero is presented. Mean R^2 and mean pooling factor (λ) of 1000 samples from the posterior distribution of each linear model are also presented
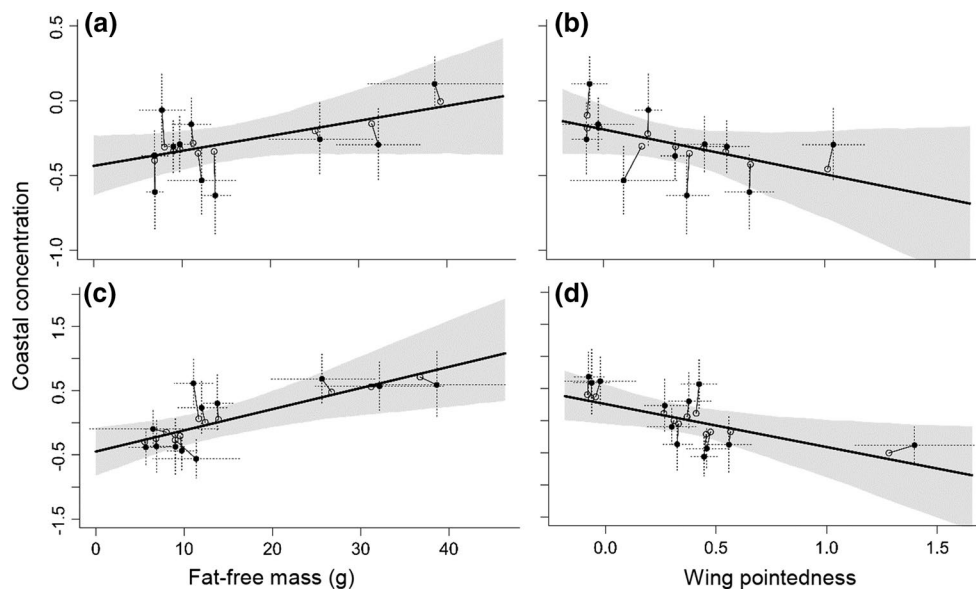
Fig. 3 Regression plots of the relationship between coastal concentration index and mean fat-free mass or mean wing pointedness among 11 bird species during autumn (**a**, **b**) and 12 bird species during spring (**c**, **d**) along the northern coast of the Gulf of Mexico. *Solid points* are the observed mean values for each species with *dashed lines* depicting observed standard errors of means (i.e., measurement error). *Open points* are the posterior means. *Thin solid lines* connect pairs of points for the same species to depict shrinkage of posterior means from partial pooling. The *thick solid line* is the *maximum a posteriori* regression line with the shaded region depicting the 95% credible interval of the regression line

(Gauthreaux and Belser 1999; Deppe et al. 2015). Thus, in the case of spring migration, the fastest birds begin arriving around mid-day and may fly farther inland because they have more time to search for suitable stopover habitat during daylight hours. Late arrivals may not make landfall until late in the day and simply put down at the immediate coastline.

Although less strong than the relationship with body mass, species characterized by more rounded wings were more concentrated nearer the coastline than species with more pointed wings. This is likely because a pointed wing shape reduces drag by smoothly shedding wingtip vortices that create drag (Lockwood et al. 1998). Pointed wings allow for more efficient flight by lowering the energy demand per unit distance traveled while increasing power (Norberg 1990; Yong and Moore 1994; Norberg 1995b; Bowlin and Wikelski 2008). Thus, species with more pointed wings could have relatively more energy to fly to more suitable or higher quality habitat inland to refuel before continuing their migration.

Flight characteristics are subject to selection pressures outside the needs for migration (e.g., foraging; predator escape; mating displays) (Rayner 1988; Norberg 1990, 1995a). That said, wing characteristics that aid in flight efficiency and speed during migration could be selected for if they confer birds an advantage, allowing them to travel farther and faster than birds with less-efficient wing shape (Pennycuick 1975; Yong and Moore 1994; Bowlin 2007). While much research has focused on wing shape in relation

to migration distance or between migrant and resident birds (Rayner 1988; Winkler and Leisler 1992; Senar et al. 1994; Mönkkönen 1995; Lockwood et al. 1998; Voelker 2001; Corman et al. 2014), we have an incomplete understanding of how flight performance, measured by wing morphology and body mass, relates to stopover distributions of migrating birds.

Flight performance may act on distributions of individuals within species in ways that we were unable to test. For example, bird distributions relating to wing shape may differ by age and sex among individuals within species. In general, younger birds have shorter, more rounded wings than older birds, which are hypothesized to assist naïve, inexperienced birds more susceptible to predation in predator escape (Alatalo et al. 1984; Pérez-Tris and Tellería 2001). Males of some passerine species have longer wings or more pointed wings than females, potentially giving them an adaptive advantage in flight performance (Hedenstrom and Moller 1992; Corman et al. 2014). Males of many passerine species are known to arrive earlier on breeding grounds than females. Thus, although we did not have adequate sample sizes to test for morphometric differences as it relates to time of season, there may be variability in wing morphology between early and late migrating birds. Females and younger birds generally carry more fat during migrations, as well (Yong and Moore 1994; Bowlin 2007), and flight performance is influenced by fat load, with flight performance of individuals decreasing as their mass increases

(Hedenström 1992). Heavier individuals within species with higher fuel loads tend to have decreased maneuverability and speeds, but increased flight distances (Hedenström 1992; Pennycuick 2008). We encourage further study into how flight performance of individuals within species may influence broad-scale distributions of migrants. For example, are broad-scale patterns at the species level matched by patterns of individuals within species? If so, we might expect body mass and wing tip shape of individuals within species to vary with proximity to the coastline.

Given that smaller species with less-efficient flight may be more constrained to use habitats within close proximity to ecological barriers, it is important that these species have access to high-quality stopover habitat adjacent to barriers. Within North America, the coastal forests that provide suitable stopover habitat in close proximity to the Gulf of Mexico coast are rapidly disappearing and what remains is under risk of human development (Crossett et al. 2004; Buler and Moore 2011). As valuable coastal stopover habitat is damaged, migrants will be forced to fly greater distances, which may decrease the likelihood of a successful migration for some individuals or species.

Author contribution statement JJB, RJL, and FRM conceived and designed the study. JJB, JAS, and TJZ collected field data. RJL processed the image data. JJB processed the survey data. JAS and TJZ processed the banding data. JJB analyzed the data. JJB, RJL, JAS, and TJZ wrote the manuscript. FRM provided editorial advice.

Compliance with ethical standards

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

References

Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics Int 11:36–42

Alatalo RV, Gustafsson L, Lundberg A (1984) Why do young passerine birds have shorter wings than older birds? The Ibis 126:410–415

Alerstam T (1993) Bird Migration. Cambridge University Press, New York

Alerstam T, Rosén M, Bäckman J et al (2007) Flight speeds among bird species: allometric and phylogenetic effects. PLoS Biol 5:e197

Arizaga J, Campos F, Alonso D (2006) Variations in wing morphology among subspecies might reflect different migration distances in Bluethroat. Ornis Fennica 83:162

Berthold P (1993) Bird migration. Oxford University Press, New York

Bowlin MS (2007) Sex, wingtip shape, and wing-loading predict arrival date at a stopover site in the Swainson's Thrush (*Catharus ustulatus*). Auk 124:1388–1396

Bowlin MS, Wikelski M (2008) Pointed wings, low wing loading and calm air reduce migratory flight costs in songbirds. PLoS ONE 3:e2154

Buler JJ, Moore FR (2011) Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. J Ornithol 152:S101–S112

Buler JJ, Moore FR, Woltmann S (2007) A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802

Calmaestra R, Moreno E (2001) A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in passeriformes. Ardea 89:407–416

Chernetsov N (2006) Habitat selection by nocturnal passerine migrants en route: mechanisms and results. J Ornithol 147:185–191

Corman A-M, Bairlein F, Schmaljohann H (2014) The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. Behav Ecol Sociobiol 68:391–402

Crossett KM, Culliton TJ, Wiley PC, Goodspeed TR (2004) Population trends along the coastal United States: 1980–2008. National Oceanic and Atmospheric Administration, Silver Spring

Deppe JL, Ward MP, Bolus RT et al (2015) Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proc Natl Acad Sci 112:E6331–E6338. doi:10.1073/pnas.1503381112

Ellegren H (1989) Hur kan vikt och vinglängd användas för att uppskatta mängden lagrat fett hos flyttande fåglar?–en metodstudie hos höstflyttande blåhakar Luscinia s. svecica. Vår Fågelärld 48:75–85

Ellegren H (1992) Estimated effects of age and sex on the fat-free body mass of autumn migrating bluethroats Luscinia s. svecica. Ardea 80:255–259

Gauthreaux SA (1971) A radar and direct visual study of passerine spring migration in southern Louisiana. Auk 88:343–365

Gauthreaux SA, Belser CG (1999) Bird migration in the region of the Gulf of Mexico. In: Adams NJ, Slotow RH (eds) Proceedings of the 22nd International Ornithological Congress. Birdlife South Africa, Durban, pp 1931–1947

Gauthreaux SA, Belser CG, Welch CM (2006) Atmospheric trajectories and spring bird migration across the Gulf of Mexico. J Ornithol 147:317–325

Gelman A, Pardoe I (2006) Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. Technometrics 48:241–251

Guo J, Lee D, Sakrejda K, et al (2016) rstan: R Interface to Stan

Hedenström A (1992) Flight performance in relation to fuel load in birds. J Theor Biol 158:535–537

Hedenström A, Alerstam T (1992) Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. J Exp Biol 164:19–38

Hedenstrom A, Moller A (1992) Morphological adaptations to song flight in passerine birds: a comparative study. In: Proceedings of the Royal Society B: Biological Sciences, pp 183–187

Helms CW, Drury WHJ (1960) Winter and migratory weight and fat field studies on some North American buntings. Bird-banding 31:1–40

Hutto RL (1985) Habitat selection by nonbreeding, migratory land birds. In: Cody ML (ed) Habitat selection in birds. Academic Press Inc., Orlando, pp 455–476

Jenni L, Schaub M (2003) Behavioural and physiological reactions to environmental variation in bird migration: a review. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer-Verlag, Berlin, pp 155–171

Jenni L, Winkler R (1989) The feather-length of small passerines: a measurement for wing-length in live birds and museum skins. Bird Study 36:1–15

Klaassen M (1996) Metabolic constraints on long-distance migration in birds. J Exp Biol 199:57–64

LaFleur JM, Buler JJ, Moore FR (2016) Geographic position and landscape composition explain regional patterns of migrating landbird distributions during spring stopover along the northern coast of the Gulf of Mexico. Landsc Ecol 31:1697–1709

Lam L, McKinnon EA, Ray JD et al (2015) The influence of morphological variation on migration performance in a trans-hemispheric migratory songbird. Anim Migr. doi:10.1515/ami-2015-0005

Lindhe-Norberg U, Brooke AP, Trewhella WJ (2000) Soaring and non-soaring bats of the family Pteropodidae (flying foxes, *Pteropus* spp.): wing morphology and flight performance. J Exp Biol 203:651

Lockwood R, Swaddle J, Rayner J (1998) Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. J Avian Biol 29:273–292

Lowery GH (1946) Evidence of trans-Gulf migration. Auk 63:175–210

Marchetti K, Price T, Richman A (1995) Correlates of wing morphology with foraging behaviour and migration distance in the genus Phylloscopus. J Avian Biol 26:177–181

McElreath R (2016) Rethinking: Statistical rethinking book package (R package version 1.59)

Mönkkönen M (1995) Do migrant birds have more pointed wings?: a comparative study. Evol Ecol 9:520–528

Moore FR, Aborn DA (2000) Mechanisms of en route habitat selection: how do migrants make habitat decisions during stopover? Stud Avian Biol 20:34–42

Moore FR, Kerlinger P (1987) Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54

Moore FR, Kerlinger P, Simons TR (1990) Stopover on a Gulf Coast barrier island by spring trans-gulf migrants. Wilson Bulletin 102:487–500

Moore FR, Woodrey MS, Buler JJ, et al (2005) Understanding the stopover of migratory birds: a scale dependent approach. In: Ralph CJ, Rich TD (eds) Bird conservation implementation and integration in the Americas: proceedings of the third international partners in flight conference. USDA Forest Service, Gen. Tech. Rep. PSW-GTR-191, pp 684–689

Norberg UM (1990) Vertebrate flight: mechanics, physiology, morphology, ecology and evolution. Spring-Verlag, Berlin

Norberg UM (1995a) How a long tail and changes in mass and wing shape affect the cost for flight in animals. Funct Ecol 9:48–54

Norberg UM (1995b) Wing design and migratory flight. Isr J Zool 41:297–305

Pennycuick CJ (1975) Mechanics of flight. Avian Biol 5:1–75

Pennycuick CJ (1989) Bird flight performance : a practical calculation manual. Oxford University Press, Oxford

Pennycuick CJ (2008) Modelling the flying bird. Elsevier, New York

Pérez-Tris J, Tellería JL (2001) Age-related variation in wing shape of migratory and sedentary Blackcaps Sylvia atricapilla. J Avian Biol 32:207–213

Rayner JMV (1988) Form and function in avian flight. Current ornithology. Plenum Press, New York, pp 1–66

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Senar JC, Lleonart J, Metcalfe NB (1994) Wing-shape variation between resident and transient wintering Siskins Carduelis spinus. J Avian Biol 25:50–54

Stan Development Team (2016) Stan modeling language users guide and reference manual, Version 2.10.0

Voelker G (2001) Morphological correlates of migratory distance and flight display in the avian genus Anthus. Biol J Lin Soc 73:425–435

Watermolen J (2005) Hydrologic Unit Boundaries: National Atlas of the United States

Winkler H, Leisler B (1992) On the ecomorphology of migrants. Ibis 134:21–28

Yong W, Moore FR (1994) Flight morphology, energetic condition, and the stopover biology of migrating thrushes. Auk 111:683–692