Biological Journal of the Linnean Society, 2022, **XX**, 1–8. With 2 figures.

Hand-Wing Index as a surrogate for dispersal ability: the case of the Emberizoidea (Aves: Passeriformes) radiation

AXEL ARANGO[1,2,*], JESÚS PINTO-LEDEZMA[3], OCTAVIO ROJAS-SOTO[1],
ANDREA M. LINDSAY[4], CHASE D. MENDENHALL[5] and FABRICIO VILLALOBOS[1,*]

[1]*Red de Biología Evolutiva, Instituto de Ecología, A.C. - INECOL, Xalapa, Mexico*
[2]*Programa de Doctorado en Ciencias, Instituto de Ecología, A.C. - INECOL, Xalapa, Mexico*
[3]*Departament of Ecology, Evolution & Behavior, University of Minnesota, Minneapolis, MN 55455, USA*
[4]*Powdermill Nature Reserve, Carnegie Museum of Natural History, Rector, PA 15677, USA*
[5]*Section of Birds, Carnegie Museum of Natural History, Pittsburgh, PA 15213, USA*

Received 28 March 2022; revised 20 May 2022; accepted for publication 26 May 2022

Measuring the dispersal ability of birds is particularly challenging and thus researchers have relied on the extended use of morphological proxies as surrogates for such ability. However, few studies have tested the relationship between morphological proxies and other dispersal-related traits. In this study, we test the relationship of the most commonly used morphological proxy for dispersal—the Hand-Wing Index (HWI)—with traits highly associated with dispersal abilities, such as geographic range size, migratory behaviour and migratory distances. We used the Emberizoidea superfamily to evaluate these relationships and measured the HWI of 2520 individuals from 431 species (almost half of all the species in the superfamily). We first estimated the phylogenetic signal of HWI and searched for the best evolutionary model to explain its variation. We then performed PGLS analyses to assess the relationships between HWI and dispersal abilities. Our results showed that HWI has a strong phylogenetic signal and is positively related to dispersal abilities. Our findings support the use of HWI as a viable morphological proxy for dispersal in birds.

ADDITIONAL KEYWORDS: dispersal proxies – wing morphology – migration – Neotropical birds.

INTRODUCTION

Dispersal is a universal process with consequences for the ecology and evolution of species (Gadgil, 1971; Bowler & Benton, 2005; Burgess *et al.*, 2016; Claramunt, 2021). For example, dispersal determines colonization and recruitment rates of new individuals into populations across space, potentially governing gene flow within metapopulations (Kokko & Lopez-Sepulcre, 2006; Burgess *et al.*, 2016). As such, dispersal is an important process underlying the conservation and recovery of wildlife populations in habitat change and loss (Claramunt *et al.*, 2012; Smith *et al.*, 2014; Kennedy *et al.*, 2016; Sheard *et al.*, 2020). Moreover, dispersal traits can also help us understand species distributions (Ree & Smith, 2008) and responses to biological invasions (Capinha *et al.*, 2015), climate change (Travis *et al.*, 2013) and land-use changes (Bregman *et al.*, 2014).

However, measuring dispersal is often difficult since it requires expensive and complicated methods (Claramunt & Wright, 2017; Sheard *et al.*, 2020). Despite improved technologies and much effort to directly measure animal movement, dispersal data is scant. For instance, the most comprehensive dispersal data for vertebrates contain only 75 bird species [(Paradis *et al.*, 1998), recently expanded to 114 in Weeks *et al.* (2022)] and 57 mammal species (Tucker *et al.*, 2018). The inherent difficulty of directly measuring dispersal has led to the widespread use of biometric indices as proxies for dispersal abilities (Claramunt & Wright, 2017; Sheard *et al.*, 2020; Fudickar *et al.*, 2021). In birds, wing shape metrics are the most common dispersal proxies given their relationship with flight efficiency and mobility (Mönkkönen, 1995; Lockwood *et al.*, 1998; Claramunt, 2021). Moreover, in many species the wing shape of birds has evolved under the selection pressures of

---

*Corresponding authors. E-mail: axlarango@gmail.com; fabricio.villalobos@gmail.com

migration (Lockwood *et al.*, 1998; Dawideit *et al.*, 2009; Kennedy *et al.*, 2016; Sheard *et al.*, 2020), where migratory birds have more elongated wings compared to closely related non-migratory species (Lockwood *et al.*, 1998).

Several wing shape metrics such as aspect ratio, Kipp's distance, wing pointedness and Hand-Wing Index (HWI) are known to correlate with flight efficiency and metabolic demands; traits thought to be critical in bird dispersal abilities (Claramunt *et al.*, 2012; Claramunt & Wright, 2017). For instance, avian aerodynamic models have shown that wings with a high aspect ratio are more efficient for long-distance flights (Pennycuick, 2008). The HWI, which is positively correlated with aspect ratio (Lockwood *et al.*, 1998; Claramunt *et al.*, 2012) and can be measured using museum specimen skins, has become the predominant proxy for bird dispersal abilities in macroecological and macroevolutionary studies (Claramunt *et al.*, 2012; Bitton & Graham, 2015; Kennedy *et al.*, 2016; White, 2016; Stoddard *et al.*, 2017; Sheard *et al.*, 2020; Stojanovic *et al.*, 2020). HWI, as a proxy of dispersal ability, has also been suggested to influence historical distribution and colonization dynamics in corvids (Kennedy *et al.*, 2016), thamnoflilids, and tyrannids (Capurucho *et al.*, 2020). However, few studies have directly addressed the relationship between HWI and other dispersal-related traits (Lockwood *et al.*, 1998; Dawideit *et al.*, 2009; Baldwin *et al.*, 2010), including a couple of recent studies relating it to natal dispersal distances (Claramunt, 2021; Weeks *et al.*, 2022). Natal dispersal distances are also difficult to obtain, requiring capture-mark-recapture efforts (Paradis *et al.*, 1998), and thus other traits are usually employed to describe birds' dispersal ability.

Total geographic range size, migratory behaviour and migratory distance are the most common traits used to characterize dispersal ability (Paradis *et al.*, 1998; Schwarz & Bairlein, 2004; Alzate & Onstein, 2021). Indeed, species that are good dispersers often have large geographic ranges and migrate long distances, and some are experiencing range expansion (Paradis *et al.*, 1998; Holt, 2003; Schwarz & Bairlein, 2004; Claramunt, 2021). More specifically, range size is thought to be a likely result of species' dispersal ability and its ecological and evolutionary effects on demography, colonization and gene flow (Brown *et al.*, 1996; Gaston, 2003; Lester *et al.*, 2007). For example, it is usually assumed that species with high dispersal ability can colonize different areas and thus attain large range sizes or that dispersal affects gene flow and thus local adaption and speciation, with low dispersal being associated with low gene flow and high isolation resulting in small range sizes (Lester *et al.*, 2007). Migratory behaviour has also been related to dispersal ability in several bird clades (Lockwood *et al.*, 1998; Kennedy *et al.*, 2016; Hosner *et al.*, 2017; Stoddard *et al.*, 2017). For example, it has been shown that migrant birds with high dispersal ability, such as swallows, can successfully disperse and colonize new areas through migration (Winkler *et al.*, 2017; Areta *et al.*, 2021) and that some migratory bird species appear to have expanded their distributional ranges giving origin to non-migratory species (Hosner *et al.*, 2017). Recent studies have either supported (Sheard *et al.*, 2020) or questioned (Claramunt, 2021; Weeks *et al.*, 2022) the relationship between migratory behaviour and dispersal ability, so its validity remains to be determined. These studies have mainly focused on migratory behaviour, comparing migrants vs. non-migrants without explicitly considering migratory distances (distance between breeding and wintering ranges) among migrants, which can also be an essential component of dispersal ability (Studds *et al.*, 2008).

Here, we use phylogenetic approaches to test if wing shape, as measured by HWI, is effectively related to dispersal traits (i.e. geographic range size, migratory behaviour and migratory distance). We used the Emberizoidea superfamily to conduct our investigation. The Emberizoidea superfamily was previously known as part of the New World's nine-primaried Oscines (Barker *et al.*, 2004), comprising a diverse monophyletic clade with species with contrasting geographic ranges, different migratory behaviours and distinct migratory distances (Barker *et al.*, 2015). Therefore, we consider it a particularly appropriate clade to test the relationship of HWI with differential dispersal abilities.

MATERIAL AND METHODS

Wing morphology

We used HWI, which is related to the aspect ratio of the wing and Kipp's distance (Claramunt *et al.*, 2012). We calculated HWI following Claramunt *et al.* (2012) as:

$$HWI = 100\left(\frac{WL - SL}{WL}\right)$$

We used the standard length of the closed wing (WL) and distance from the carpal joint to the tip of the first secondary feather (SL). In short, HWI values represent the elongation of the wing, where high HWI values indicate more elongated wings and low HWI values less elongated wings.

We estimated the HWI in Emberizoidea using museum specimens. The lead author measured WL and SL of 2520 individuals from 490 species (~58% of the species in the superfamily). We selected at least two males and two females when possible, excluding all specimens labelled as juveniles. We measured a mean of five individuals per species. All individuals were measured using a standard banding wing and tail ruler at the Carnegie Museum of Natural History. Despite the existence of recent wing trait databases, such as AVONET (Tobias *et al.*, 2022), we decided to use our own measurements because the same person made them. With this, we minimized the inconsistency in measurements and the error associated with the lack of data for migrant species in our clade in said database.

Phylogenetic and geographic data

We used the Maximum Clade Credibility (MCC) tree of a calibrated species-level phylogeny of the Emberizoidea superfamily containing the relationships of 795 species (Barker *et al.*, 2015). The geographic data was obtained from BirdLife International (BirdLife International & Handbook of the Birds of the World, 2019). Unfortunately, several species (32) had their geographic data protected, so we considered only 431 species with enough data (i.e. HWI, geographic and phylogenetic data) for further analyses, where 319 species were classified as non-migrants and 112 as migrants. The excluded species did not have extreme HWI or range size values (Supporting Information, Figs S1, S2), thus we do not expect them to influence our results. Our final set of species comprises representatives of different clades within the superfamily Emberizoidea, such as Parulidae ($N = 78$), Icteridae ($N = 75$), Passerellidae ($N = 83$), Cardinalidae ($N = 33$), Emberizidae ($N = 16$) and Thraupidae ($N = 133$).

Geographic range, migrant behaviour and migratory distance

We obtained geographic range size by calculating the sum of polygon areas corresponding to ranges where birds were year-round residents, breeding and wintering for all species considered in the analyses. Before the area calculation, all polygons were projected to an equal-area projection (Eckert VI). Next, we designated 112 species as migrants based on spatially separate breeding and wintering ranges reported by the BirdLife maps. Migrant species represented mainly Parulidae ($N = 42$), Passerellidae ($N = 28$), Icteridae ($N = 13$), Cardinalidae ($N = 10$) and Emberizidae ($N = 10$) families. Finally, for each migrant species, we calculated migratory distance as the geodesic distance between the midpoints of the breeding and wintering ranges using the equidistant cylindrical projection and the 'geodist' package for R (Padgham *et al.*, 2020).

Phylogenetic analyses

We evaluated the phylogenetic signal of HWI using Pagel's lambda and Blomberg's K using the R package 'phytools' (Revell, 2012) to test for phylogenetic independence of the trait. We also evaluated and compared the fit of the most common models of trait evolution (i.e. Brownian Motion, Ornstein–Uhlenbeck, Early Burst and White Noise) to identify the evolutionary processes underlying the observed variation of HWI among species (Münkemüller *et al.*, 2012). To assess the relationship between wing morphology and other traits widely regarded as indicative of dispersal abilities (e.g. range size, migratory distance and migratory behaviour), we used phylogenetic regressions (PGLS) and PhyloANOVA using the 'phytools' and 'caper' R packages (Orme *et al.*, 2018). We assessed the relationship between HWI—as a predictor variable—and geographic range size—as a response variable—comparing the fit of two PGLS models, one including and one excluding migratory behaviour (migrant and non-migrant). Then, considering only the 112 migrant species, we fitted a third PGLS model to test the relationship between HWI and migratory distance. Finally, we performed a PhyloANOVA to determine if migratory behaviour influenced wing shape by comparing the HWI between migrants and non-migrants. Geographic range size was log-transformed to account for the large difference in the area across some species (i.e. small islands to most of the North American continent).

RESULTS

The HWI of Emberizoidea species had a mean value of 21.44 (median: 21.34), whereas the non-migrants had an average HWI of 19.14 and the migrant species of 26.98. The lowest value (HWI 6.43) was *Arremon phaeopleurus* (Caracas brushfinch)—a member of the Passerellidae family confined to the western mountains of Venezuela—and the highest values (HWI = 39.47) belonged to *Calcarius pictus* (Smith's longspur) and *Plectrophenax nivalis* (snow bunting), both migratory species of the Calcariidae family (BirdLife International & Handbook of the Birds of the World, 2019).

HWI showed significant phylogenetic signal ($\lambda = 0.831$, $P < 0.01$; $K = 0.452$, $P < 0.01$). The Ornstein–Uhlenbeck (OU) model showed the best fit for explaining HWI evolution ($\alpha = 0.120$; $\sigma^2 = 11.78$; phylogenetic half-life = 5.73; Supporting Information, Table S1). We found a positive and significant relationship between HWI and geographic range size in both the general model ($\beta = 0.169$; pseudo-$R^2 = 0.158$; $P < 0.01$, $\lambda = 0.44$; Supporting Information, Fig. S3) and the model accounting for migratory behaviour (pseudo-$R^2 = 0.237$; $P < 0.01$; $\lambda = 0.437$; Fig. 1a). This relationship remained positive and significant for both migrants ($\beta = 0.149$; $P < 0.01$) and non-migrants ($\beta = 0.0747$; $P < 0.01$). The

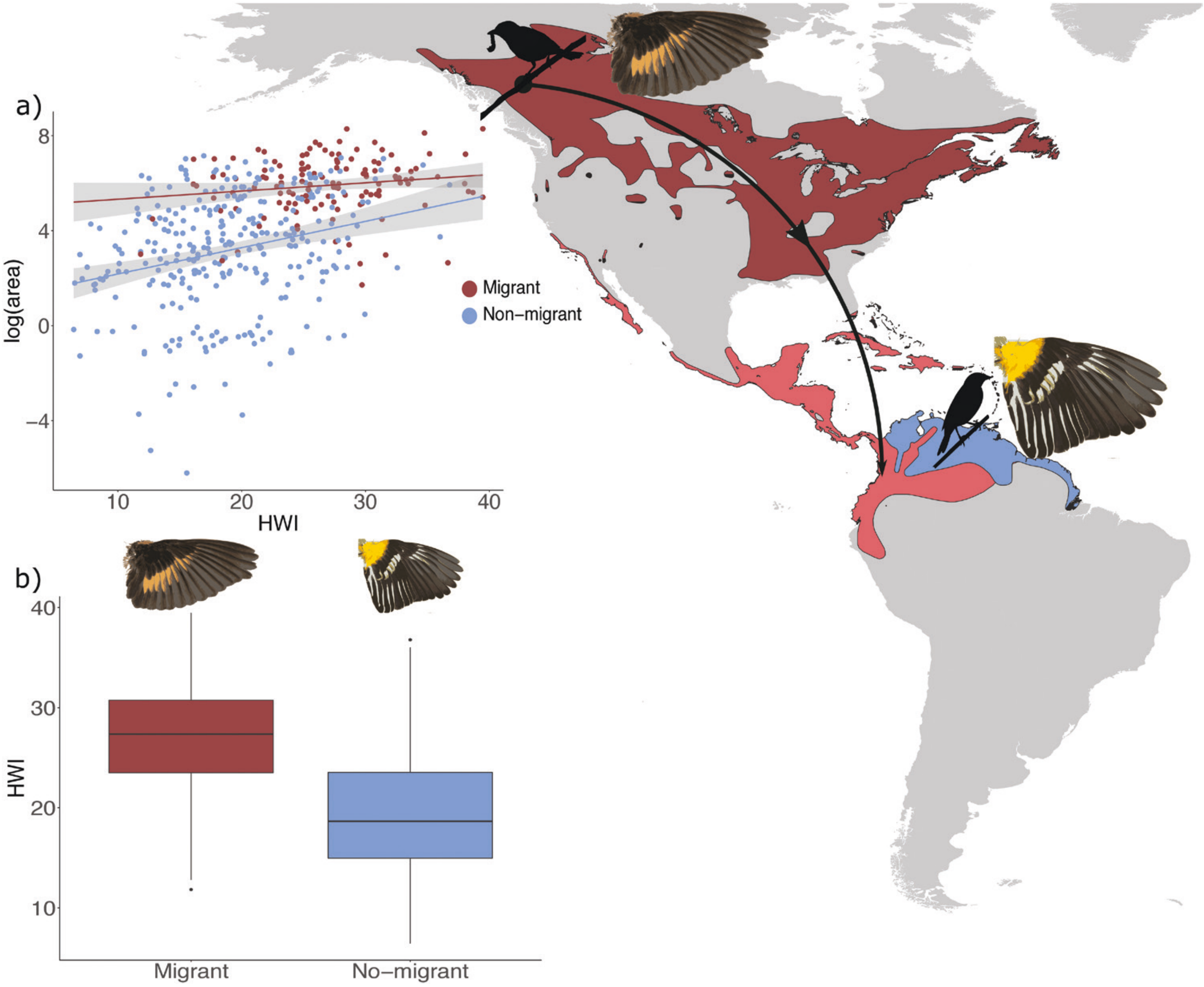

Figure 1. Birds with more elongated wings tend to have longer dispersal abilities than birds with rounder wings, as shown by their (a) geographic range size and (b) migrant behaviour. The model fitted in (a) represents the values of the PGLS where log-area was predicted by HWI considering their migratory behaviour. In the map, the areas comprising USA and Canada represent the breeding distribution and elongated wing shape of the migrant American redstart (*Setophaga ruticilla*), whereas the areas comprising Mexico, the Caribbean, Central America and northern South America represent its winter range. The range encompassing only northern South America and round wing shape represents the geographic distribution of the non-migrant yellow oriole (*Icterus nigrogularis*; HWI= 14.66).

model accounting for the migratory behaviour provided a better fit than the one excluding it (Supporting Information, Table S2). The PhyloANOVA of HWI predicted by migratory behaviour showed a significant difference in the wing shape between migrant and non-migrant species (F = 172.27; $P < 0.01$; $\lambda = 0.75$; Fig. 1b), where non-migrant species displayed rounder wings. Accordingly, the PGLS where HWI predicted migration distance showed a positive and significant relationship ($\beta = 111.492$; pseudo-$R^2 = 0.145$; $P < 0.01$; $\lambda = 0.076$; Fig. 2), implying that species with more elongated wings perform longer migratory distances.

DISCUSSION

We showed that bird wing morphology, specifically HWI, has a strong phylogenetic signal and shows positive and significant relationships with biogeographical and ecological traits related to dispersal abilities. Our results support recent findings relating HWI and direct measures of natal dispersal distances (Claramunt, 2021; Weeks *et al.*, 2022). Specifically, we found that Emberizoidea species with more elongated wings have larger geographic range sizes, regardless of their migratory behaviour (Fig. 1a; Supporting

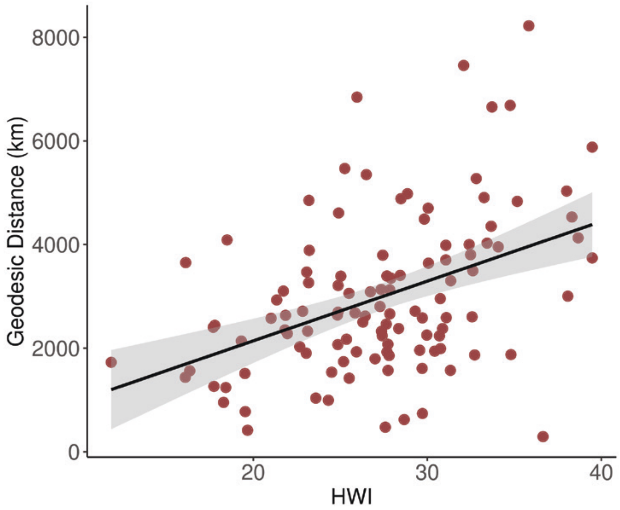

Figure 2. Positive relationship of HWI with geodesic distance between breeding and wintering areas of migrant species.

Information, Table S2). We also found that migratory species tend to have more elongated wings than non-migratory species (Fig. 1b). Even among migratory species, wing shape is significantly related to their migratory distance (Fig. 2).

HWI of emberizoid species showed a significant phylogenetic signal, suggesting that the wing shape of species across the Emberizoidea radiation is more similar among closely related than distantly related species. This finding was supported by the two most common measures of phylogenetic signal; Pagel's lambda and Blomberg's K. Moreover, our model-fitting approach indicated that the evolution of HWI can be explained by a constrained evolutionary process that supports phylogenetic niche conservatism (i.e. the tendency of species to retain ancestral characteristics; Münkemüller *et al.*, 2012), as suggested by the best-fitting OU model. A similar finding of strong, but higher, phylogenetic signal was found for the relatively short-winged birds of the Furnariidae family (median HWI = 15.7, Pagel's lambda = 0.99) by Claramunt *et al.* (2012). However, contrary to our findings for Emberizoidea, these authors found that a Brownian motion model best-explained wing shape evolution in the Furnariids. These differences between Emberizoidea and Furnariidae clades, although being different taxonomic levels, indicate distinct evolutionary pathways of their wing shape that may depend on their particular ecological and evolutionary settings. For example, emberizoids are more geographically widespread and ecologically varied than furnariids (Barker *et al.*, 2015; Winkler *et al.*, 2020) which may ultimately determine the strength and direction of evolution (Harmon, 2019). In addition, compared to Furnariidae, Emberizoidea comprises a higher number of migratory species that, in turn, have more elongated wing shapes than their non-migrant sister species (Lockwood *et al.*, 1998; Alerstam *et al.*, 2003). This difference in wing shape among closely related species within the Emberizoidea would increase trait variation within the whole clade, thus decreasing the values of its phylogenetic signal compared to the Furnariidae.

Although the relationship between geographic range size and dispersal abilities has been challenged in recent years (Lester *et al.*, 2007), the ecological and evolutionary explanations for this relationship, such as the ability of highly dispersive species to colonize different areas and/or to reduce gene flow and extinction risk, remain widely accepted (Alzate & Onstein, 2021). In fact, a recent meta-analysis by Alzate & Onstein (2021) found that, in birds, the positive relationship between geographic range size and dispersal proxies (e.g. wing morphology, flight efficiency, natal dispersal distance) is persistent at diverse taxonomic and spatial scales. Likewise, the relationship between HWI and dispersal has been questioned, arguing that other morphological measurements that affect flight efficiency (e.g. aspect ratio, lift-to-drag ratio) may better explain dispersal abilities in birds (Claramunt, 2021). Nonetheless, our findings confirm the recent ones made by Sheard *et al.* (2020), showing that geographic range size is a significant predictor of wing shape and vice versa. The significant relationship between HWI and geographic range size in different avian lineages indicates the high viability of HWI as a dispersal proxy for birds when direct dispersal measures are unavailable.

Migratory behaviour has also been shown to influence the wing shape of bird species (Mönkkönen, 1995; Lockwood *et al.*, 1998; Sheard *et al.*, 2020). For example, the recent global analysis of Sheard *et al.* (2020) found that migratory behaviour was a strong predictor of HWI across avian radiation and suggested that this metric is mechanistically linked to flight ability and the capacity to overcome geographic barriers. Agreeing with this global finding, we found that wing shape of Emberizoidea is significantly different between migratory and non-migratory species, and species that participate in lengthy seasonal migrations tend to have more elongated wings better suited for faster and more efficient flights (Lockwood *et al.*, 1998). In contrast, two more recent studies (Claramunt, 2021; Weeks *et al.*, 2022) on smaller species sets (75 and 114, respectively) did not find differences in natal dispersal distances between migratory and non-migratory species, mainly due to philopatry in the former, but that such dispersal distances are still positively related with HWI. Still, other studies found a relationship between flight efficiency, as described by migratory behaviour (Winkler *et al.*, 2017; Areta *et al.*, 2021) and HWI (Hosner *et al.*, 2017), and dispersal via range expansion, suggesting altogether that dispersal may indeed be related to migration but constrained by factors such as philopatry (Claramunt, 2021) and the dependence of successful colonization on other species requirements [e.g. niche breath, trophic level or population abundance (Gaston, 2003)].

While the relationship between dispersal and migration needs further testing for its generality, our findings and those of others (e.g. Sheard *et al.*, 2020) prove that migratory birds have more elongated wings that non-migrants. The mechanisms of this morphological-migratory relationship remain elusive, mainly because of the dual possibility that migratory behaviour selects for wing shape or vice versa (Mönkkönen, 1995). Migration or nomadism would generate selection for more elongated wings (Stojanovic *et al.*, 2020). At the same time, sedentarism would favour the selection for rounder wings benefiting from increased manoeuvrability for foraging and predator avoidance or diet and substrate specialization (Bitton & Graham, 2015). Accordingly, recent studies (Bitton & Graham, 2015; Stojanovic *et al.*, 2020), including our findings, suggest that wing shape may result from the pressure of particular movement needs, such as displacement and foraging (Claramunt, 2021).

We also described a positive and significant relationship between HWI and migratory distances in migratory species. This finding may have resulted from the complex interaction between dispersal ability, migratory behaviour, morphological adaptations (Claramunt, 2021) and the non-linearity of migratory distances caused by stopovers (Parker, 1994). On the one hand, the sustenance of long-distance migratory flights cannot be accounted for by morphology alone (Claramunt, 2021), requiring physiological adaptations (Baldwin *et al.*, 2010). On the other hand, the stopovers that birds conduct throughout their migrations (Mehlman *et al.*, 2005) might undermine the flight efficiency provided by their wing shape for dispersal. Stopovers, in this case, would give resting stops that could prevent migrants from using their optimal dispersal distance given their wing shape or allow non-efficient fliers to migrate long distances. Nonetheless, migrants with less efficient wings (i.e. rounder-shaped wings) would still be more affected by adverse weather conditions (Saino *et al.*, 2010) and would have closer stopovers (Buler *et al.*, 2017). Therefore, migrants with rounder wings would have shorter migratory distances due to a lack of energy or time for straying further away from their natal distribution (Claramunt, 2021), reinforcing our results that migratory distance is positively related to the wing shape.

Our findings confirm that HWI is significantly and positively related to traits indicative of birds' dispersal and flight abilities. Although additional evidence suggests that other measurements, such as the drag-to-lift ratio, might perform slightly better in predicting natal dispersal for birds (Claramunt, 2021), the relative ease of measurement of HWI—primarily via museum specimens—compared to other morphological traits, makes it an accessible proxy for dispersal when available.

ACKNOWLEDGEMENTS

We thank the Posgrado en Ciencias of Instituto de Ecología, A.C. (INECOL). We acknowledge the support provided by the Consejo Nacional de Ciencia y Tecnología of México (CONACyT) for the scholarship to A.A. (No. 838518) and the Ciencia Basica project to F.V. (No. A1-S-34563). We also thank the Carnegie Museum of Natural History, the Powdermill Avian Research Center, and all its personnel. Special thanks to Dr. John Wenzel for the support provided to A.A. while conducting this research. We thank the editor and two anonymous reviewers for the insightful comments and suggestions that certainly improved our manuscript. A.A. and F.V. conceived the study and wrote the first draft, A.A. collected the data and conducted the analyses. A.A., F.V., J.P-L. and O.R-S. discussed and interpreted the results. All authors contributed to the final version of the manuscript. We have no conflicts of interest to declare.

DATA AVAILABILITY

Data files and analyses are described at: https://github.com/fabro/Emberizoid_dispersal. Distribution data can be requested at: http://datazone.birdlife.org/species/requestdis.

REFERENCES

Alerstam T, **Hedenström A**, **Åkesson S. 2003.** Long-distance migration: evolution and determinants. *Oikos* **103:** 247–260.

Alzate A, **Onstein RE. 2021.** Understanding the relationship between dispersal and range size. *bioRxiv*, doi: 10.1101/2021.09.29.462346, 1 October 2021, preprint: not peer reviewed.

Areta JI, **Salvador SA**, **Gandoy FA**, **Bridge ES**, **Gorleri FC**, **Pegan TM**, **Winkler DW. 2021.** Rapid adjustments of migration and life history in hemisphere-switching cliff swallows. *Current Biology* **31:** 2914–2919.

Baldwin MW, **Winkler H**, **Organ CL**, **Helm B. 2010.** Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats (*Saxicola torquata*). *Journal of Evolutionary Biology* **23:** 1050–1063.

Barker FK, **Burns KJ**, **Klicka J**, **Lanyon SM**, **Lovette IJ. 2015.** New insights into New World biogeography:

an integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *The Auk: Ornithological Advances* **132:** 333–348.

Barker FK, **Cibois A**, **Schikler P**, **Feinstein J**, **Cracraft J. 2004.** Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences* **101:** 11040–11045.

BirdLife International, Handbook of the Birds of the World. **2019.** *Bird species distribution maps of the world. Version 2019.1*. Available at: http://datazone.birdlife.org/species/requestdis

Bitton P, **Graham BA. 2015.** Change in wing morphology of the European starling during and after colonization of North America. *Journal of Zoology* **295:** 254–260.

Bowler DE, **Benton TG. 2005.** Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* **80:** 205–225.

Bregman TP, **Sekercioglu CH**, **Tobias JA. 2014.** Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biological Conservation* **169:** 372–383.

Brown JH, **Stevens GC**, **Kaufman DM. 1996.** The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* **27:** 597–623.

Buler JJ, **Lyon RJ**, **Smolinsky JA**, **Zenzal TJ**, **Moore FR. 2017.** Body mass and wing shape explain variability in broad-scale bird species distributions of migratory passerines along an ecological barrier during stopover. *Oecologia* **185:** 205–212.

Burgess SC, **Baskett ML**, **Grosberg RK**, **Morgan SG**, **Strathmann RR. 2016.** When is dispersal for dispersal? Unifying marine and terrestrial perspectives. *Biological Reviews* **91:** 867–882.

Capinha C, **Essl F**, **Seebens H**, **Moser D**, **Pereira HM. 2015.** The dispersal of alien species redefines biogeography in the Anthropocene. *Science* **348:** 1248–1251.

Capurucho JM, **Ashley MV**, **Tsuru BR**, **Cooper JC**, **Bates JM. 2020.** Dispersal ability correlates with range size in Amazonian habitat-restricted birds. *Proceedings of the Royal Society B* **287:** 20201450.

Claramunt S. 2021. Flight efficiency explains differences in natal dispersal distances in birds. *Ecology* **102:** e03442.

Claramunt S, **Derryberry EP**, **Remsen JV**, **Brumfield RT. 2012.** High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences* **279:** 1567–1574.

Claramunt S, **Wright NA. 2017.** Using museum specimens to study flight and dispersal. In: Webster MS, ed. *Emerging frontiers in collections-based ornithological research: the extended specimen. Studies in Avian Biology 50*. Chicago: American Ornithological Society 127–143.

Dawideit BA, **Phillimore AB**, **Laube I**, **Leisler B**, **Böhning-Gaese K. 2009.** Ecomorphological predictors of natal dispersal distances in birds. *Journal of Animal Ecology* **78:** 388–395.

Fudickar AM, **Jahn AE**, **Ketterson ED. 2021.** Animal migration: an overview of one of nature's great spectacles. *Annual Review of Ecology, Evolution, and Systematics* **52:** 479–497.

Gadgil M. 1971. Dispersal: population consequences and evolution. *Ecology* **52:** 253–261.

Gaston KJ. 2003. *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Harmon LJ. 2019. Phylogenetic comparative methods: learning from trees. *EcoEvoRxiv*, doi: 10.32942/osf.io/e3xnr, 20 May 2019, preprint: not peer reviewed.

Holt RD. 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* **5:** 159–178.

Hosner PA, **Tobias JA**, **Braun EL**, **Kimball RT. 2017.** How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes). *Proceedings of the Royal Society B: Biological Sciences* **284:** 20170210.

Kennedy JD, **Borregaard MK**, **Jønsson KA**, **Marki PZ**, **Fjeldså J**, **Rahbek C. 2016.** The influence of wing morphology upon the dispersal, geographical distributions and diversification of the Corvides (Aves; Passeriformes). *Proceedings of the Royal Society B: Biological Sciences* **283:** 20161922.

Kokko H, **Lopez-Sepulcre A. 2006.** From individual dispersal to species ranges: perspectives for a changing world. *Science* **313:** 791.

Lester SE, **Ruttenberg BI**, **Gaines SD**, **Kinlan BP. 2007.** The relationship between dispersal ability and geographic range size. *Ecology Letters* **10:** 745–758.

Lockwood R, **Swaddle JP**, **Rayner JM. 1998.** Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* **29:** 273–292.

Mehlman DW, **Mabey SE**, **Ewert DN**, **Duncan C**, **Abel B**, **Cimprich D**, **Sutter RD**, **Woodrey M. 2005.** Conserving stopover sites for forest-dwelling migratory landbirds. *The Auk* **122:** 1281–1290.

Mönkkönen M. 1995. Do migrant birds have more pointed wings?: a comparative study. *Evolutionary Ecology* **9:** 520–528.

Münkemüller T, **Lavergne S**, **Bzeznik B**, **Dray S**, **Jombart T**, **Schiffers K**, **Thuiller W. 2012.** How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* **3:** 743–756.

Orme D, **Freckleton R**, **Thomas G**, **Petzoldt T**, **Fritz S**, **Isaac N**, **Pearse W. 2018.** *caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 1.0.1.* Available at: https://cran.r-project.org/web/packages/caper/caper.pdf [accessed 15 June 2022].

Padgham M, **Summer MD**, **Karney CF. 2020.** *Package 'geodist': fast, dependency-free geodesic distance calculations*. Available at: https://cran.r-project.org/web/packages/geodist/geodist.pdf [accessed 9 October 2020].

Paradis E, **Baillie SR**, **Sutherland WJ**, **Gregory RD. 1998.** Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67:** 518–536.

Parker III TA. 1994. Habitat, behavior, and spring migration of cerulean warbler in Belize. *American Birds* **48:** 70–75.

Pennycuick CJ. 2008. *Modelling the flying bird*. London: Academic Press.

Ree RH, **Smith SA. 2008.** Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* **57:** 4–14.

Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3:** 217–223.

Saino N, **Rubolini D**, **von Hardenberg J**, **Ambrosini R**, **Provenzale A**, **Romano M**, **Spina F. 2010.** Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds. *Functional Ecology* **24:** 658–669.

Schwarz CJ, **Bairlein F. 2004.** Dispersal and migration. *Animal Biodiversity and Conservation* **27:** 297–298.

Sheard C, **Neate-Clegg MHC**, **Alioravainen N**, **Jones SEI**, **Vincent C**, **MacGregor HEA**, **Bregman TP**, **Claramunt S**, **Tobias JA. 2020.** Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications* **11:** 1–9.

Smith BT, **McCormack JE**, **Cuervo AM**, **Hickerson MJ**, **Aleixo A**, **Cadena CD**, **Perez-Eman J**, **Burney CW**, **Xie X**, **Harvey MG. 2014.** The drivers of tropical speciation. *Nature* **515:** 406–409.

Stoddard MC, **Yong EH**, **Akkaynak D**, **Sheard C**, **Tobias JA**, **Mahadevan L. 2017.** Avian egg shape: form, function, and evolution. *Science* **356:** 1249–1254.

Stojanovic D, **Neeman T**, **Heinsohn R. 2020.** Overlap in the wing shape of migratory, nomadic and sedentary grass parrots. *Journal of Avian Biology* **51:** e02586.

Studds CE, **Kyser TK**, **Marra PP. 2008.** Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of the National Academy of Sciences* **105:** 2929–2933.

Tobias JA, **Sheard C**, **Pigot AL**, **Devenish AJ**, **Yang J**, **Sayol F**, **Schleuning M. 2022.** AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters* **25:** 581–597.

Travis JMJ, **Delgado M**, **Bocedi G**, **Baguette M**, **Bartoń K**, **Bonte D**, **Boulangeat I**, **Hodgson JA**, **Kubisch A**, **Penteriani V. 2013.** Dispersal and species' responses to climate change. *Oikos* **122:** 1532–1540.

Tucker MA, **Böhning-Gaese K**, **Fagan WF**, **Fryxell JM**, **van Moorter B**, **Alberts SC**, **Ali AH**, **Allen AM**, **Attias N**, **Avgar T. 2018.** Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* **359:** 466–469.

Weeks BC, **O'Brien BK**, **Chu JJ**, **Claramunt S**, **Sheard C**, **Tobias JA. 2022.** Morphological adaptations linked to flight efficiency and aerial lifestyle determine natal dispersal distance in birds. *Functional Ecology*. https://doi.org/10.1111/1365-2435.14056

White AE. 2016. Geographical barriers and dispersal propensity interact to limit range expansions of Himalayan birds. *The American Naturalist* **188:** 99–112.

Winkler DW, **Billerman SM**, **Lovette IJ. 2020.** Ovenbirds and woodcreepers (Furnariidae), version 1.0. In: Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS, eds. *Birds of the world*. Ithaca: Cornell Laboratory of Ornithology. Available at: https://doi.org/10.2173/bow.furnar2.01

Winkler DW, **Gandoy FA**, **Areta JI**, **Iliff MJ**, **Rakhimberdiev E**, **Kardynal KJ**, **Hobson KA. 2017.** Long-distance range expansion and rapid adjustment of migration in a newly established population of barn swallows breeding in Argentina. *Current Biology* **27:** 1080–1084.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Comparison among different evolutionary models (Ornstein–Uhlenbeck, Brownian motion, Early Burst and White Noise) fitted to HWI for the Emberizoidea superfamily.
Table S2. Akaike scores for the PGLS models relating HWI and geographic range area
Figure S1. Distribution of HWI in Emberizoidea, the blue-coloured bars indicate species for which geographic range area could not be calculated using the methods stated in the manuscript.
Figure S2. Geographic range size predicted by HWI with the inclusion species whose area could not be calculated using the methods stated in the manuscript. The approximate geographic range size of these species (No-geodata) was acquired from the Bird Life DataZone and the IUCN Red List.
Figure S3. Positive, general relationship of HWI and geographic range size for Emberizoidea.