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RESEARCH ARTICLE

Functional Ecology

Morphological adaptations linked to flight efficiency and aerial lifestyle determine natal dispersal distance in birds

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Abstract

- Natal dispersal—the movement from birthplace to breeding location—is often considered the most significant dispersal event in an animal's lifetime. Natal dispersal distances may be shaped by a variety of intrinsic and extrinsic factors, and remain poorly quantified in most groups, highlighting the need for indices that capture variation in dispersal among species.
- 2. In birds, it is hypothesized that dispersal distance can be predicted by flight efficiency, which can be estimated using wing morphology. However, the use of morphological indices to predict dispersal remains contentious and the mechanistic links between flight efficiency and natal dispersal are unclear.
- 3. Here, we use phylogenetic comparative models to test whether hand-wing index (HWI, a morphological proxy for wing aspect ratio) predicts natal dispersal distance across a global sample of 114 bird species. In addition, we assess whether HWI is correlated with flight usage in foraging and daily routines.
- 4. We find that HWI is a strong predictor of both natal dispersal distance and a more aerial lifestyle.
- 5. Our results support the use of HWI as a valid proxy for relative natal dispersal distance, and also suggest that evolutionary adaptation to aerial lifestyles is a major factor connecting flight efficiency with patterns of natal dispersal.

KEYWORDS

bird traits, dispersal, functional traits, morphology, natal dispersal

1 | INTRODUCTION

Dispersal is a fundamental ecological and evolutionary process, influencing survival, population dynamics and biogeography (Pigot & Tobias, 2015). Within populations, dispersal is a critical factor regulating resource competition (Waser, 1985) and exposure to parasites and predation (Connell, 1971; Janzen, 1970), as well as

inbreeding (Greenwood et al., 1978), demography and population genetics (Clobert et al., 2012; Greenwood & Harvey, 1982). At larger spatiotemporal scales, dispersal can shape patterns of geographical range expansion and overlap (Pigot & Tobias, 2015), thereby influencing diversification rates by determining the likelihood of secondary contact and rates of gene flow (Claramunt et al., 2012; Diamond et al., 1976; Weeks & Claramunt, 2014). Despite its general

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importance, however, dispersal is difficult to quantify in a standardized way across numerous species and direct comparative analyses of the correlates and drivers of dispersal distances remain surprisingly limited.

While dispersal can potentially refer to several different forms of movement, the most relevant to ecological and evolutionary theories is natal dispersal, or the travel between birth and breeding sites. In mobile organisms, such as birds, long-distance migration may involve the movement of individuals over much greater distances, yet avian migrants tend to have strong philopatry, with relatively low natal dispersal. Thus, long-distance migration can be considered a strategy for persisting in seasonal environments rather than dispersal in its traditional sense (Winger et al., 2019). The approximate distance travelled during migration is well known for almost all birds, in line with detailed datasets on avian distributions, phylogenetic history (Jetz et al., 2012), morphology (Sheard et al., 2020; Tobias et al., 2022) and dietary niche (Wilman et al., 2014). However, largescale studies of bird natal dispersal distances are lacking.

One source of information on natal dispersal is long-term bird banding, but the relevant data are time-intensive to collect and currently limited to very few well-studied regions, such as the British Isles (Paradis et al., 1998). Separating natal dispersal from seasonal migration is also not straightforward. Individual movement dynamics can be revealed by other technologies, including GPS trackers (e.g. Oliver et al., 2020) and genomic techniques (Chua et al., 2017), but comparative studies of dispersal using these approaches remain limited to a few species. As a result, to overcome the logistical and financial challenges of direct characterization of dispersal distance, many ornithologists have turned to morphological indicators of dispersal ability as a means to indirectly study dispersal (Claramunt & Wright, 2017; Sheard et al., 2020).

In theory, bird dispersal ability can be determined by flight efficiency, which, in turn, can be inferred from wing morphology. In particular, one of the most important morphological determinants of long-distance flight efficiency (energy expended per unit distance) is the aspect ratio of the wings: higher aspect ratio wings result in a higher lift-to-drag ratio and lower cost of transport (Evans, 2021; Norberg, 1990; Pennycuick, 2008; Taylor & Thomas, 2014; Vágási et al., 2016). Other aspects of wing design, such as planform and camber, can affect flight performance in aircraft, and may be relevant to birds with particular flight styles or speeds. However, high aspect ratio is likely to have wider relevance, theoretically increasing long distance flight efficiency across flying styles, including flapping and gliding flight (Norberg, 1990; Pennycuick, 2008).

High aspect ratio is derived from greater elongation of the wing, generally achieved through lengthened wing bones (humerus, radius, ulna) or outer primary feathers, producing a more slender and pointed wing. In the case of round-tipped wings, a higher aspect ratio is achieved by a narrowing of the wing overall. The most accessible metric of wing elongation is the hand-wing index (HWI; Kipp, 1958; Lockwood et al., 1998), which—unlike the wing aspect ratio can be measured from preserved museum specimens (Claramunt & Wright, 2017). HWI therefore provides a useful of estimate dispersal ability across a wide range of study systems and timescales (Claramunt et al., 2012; Kennedy et al., 2016, 2017; Weeks & Claramunt, 2014; Weeks, Claramunt, et al., 2016; Weeks, Gregory, et al., 2016), particularly as the relevant data are now openly available for all extant birds (Sheard et al., 2020; Tobias et al., 2022).

The connection between HWI and flight efficiency is predicted by theory and supported by empirical studies. For example, it has been shown in one species (*Catharus ustulatus*) that individual birds with high wing-pointedness have lower heart rates in migratory flight (Bowlin & Wikelski, 2008) in line with the expected relationship between elongated wing shape and flight energetics (see Supporting Information). The pointedness of the outer wing is not the same as HWI but, all else being equal, higher wingtip pointedness is likely correlated with higher HWI (Sheard et al., 2020). In addition, dispersal-challenge experiments on a small sample of tropical species (Moore et al., 2008) show that bird species with higher HWI (Claramunt et al., 2012). These observations suggest that HWI captures elements of avian dispersal ability linked to flight efficiency.

HWI and the related measurement called Kipp's distance are highly correlated (Figure S1) and are both strongly related to migration in birds (Dawideit et al., 2009; Sheard et al., 2020). While this relationship between dispersal ability and long-distance flight is intuitive, the mechanistic link between flight efficiency and natal dispersal distance is less apparent. While the dispersal distances of many tropical residents may indeed be limited by their flight capacities (Moore et al., 2008), many species can travel much further than their average natal dispersal distance. For example, an Arctic tern Sterna paradisea typically circumnavigates the globe before returning to breed at the natal colony within metres of where it was born. Conversely, some non-migratory bird species undertake relatively large movements before settling to breed (Dawideit et al., 2009). Natal dispersal distance is therefore only weakly connected to migration (Winkler, 2005) suggesting that other mechanisms are involved.

One hypothesized link between flight efficiency and natal dispersal distance involves flight behaviour. Specifically, higher aspect ratio bird wings may be an adaptation not only to long-distance migration, but also to a more aerial lifestyle (Claramunt, 2021; Sheard et al., 2020). Regardless of migratory distance, HWI is predicted to correlate with the degree to which a species relies on flight during daily routines (Claramunt, 2021; Evans, 2021; Sheard et al., 2020). Thus, species with lifestyles dependent on frequent flight, for example because of an aerial foraging behaviour or daily movements between foraging and roosting areas (Table 1), may evolve elongated wings with increased flight efficiency. These species are likely to be more mobile, and better able to cross unsuitable terrain, potentially resulting in longer average natal dispersal distances.

Previous studies provide evidence that flight efficiency predicts natal dispersal distance in birds, but only for a small number of species occurring in the British Isles (Claramunt, 2021; Dawideit et al., 2009). Whether this pattern holds more generally is uncertain, particularly because many ecological processes (e.g. the strength of competition; Dobzhansky, 1950) are thought to vary across climatic or latitudinal gradients, potentially altering the relative importance of mechanisms shaping dispersal behaviours. However, the relationship between flight efficiency and natal dispersal distance remains largely untested in other species or regions, while the extent to which this association is related to aerial lifestyles is unknown.

Here, we compile a global dataset of published direct estimates of natal dispersal distances for birds, supplemented with banding recovery data. Our dataset includes 123 estimates of mean dispersal distances for 114 species occurring in both temperate and tropical regions, and breeding on every continent in the world, excluding Antarctica (Figure 1). Our sample is also phylogenetically diverse, spanning 37 families of birds across both passerines (46.5%) and non-passerines (53.5%). Natal dispersal distance estimates are based on a range of techniques, including banding, radiotag and gps methods (Table S1). We then use comprehensive HWI data (Sheard et al., 2020) and an index of flight behaviour (Table 1) to test (a) whether morphology-determined flight efficiency predicts natal dispersal distance across this global dataset, and (b) the degree to which this relationship reflects aerial lifestyles. By understanding how aerial lifestyles relate to HWI, we can better understand the coevolution of morphology and a complex suite of intrinsic and extrinsic selective pressures, and their impacts on dispersal distance.

2 | MATERIALS AND METHODS

2.1 | Natal dispersal distance

We merged two datasets on natal dispersal distance for birds (Paradis et al., 1998; Sutherland et al., 2000), and then expanded and updated the information by conducting a systematic review of the literature. To find as many natal dispersal distance estimates as possible, we searched Google Scholar for "(bird OR avian) AND ('natal dispersal' OR dispersal)". We read the titles and abstracts of the first 50 search results for each year, sorted by relevance, going back to 1970 to identify relevant papers for further review. When papers included compendia of data derived from studies conducted prior to 1970, those original references were included in our analyses.

Relevant papers were then read in detail to determine whether they included direct estimates of species mean natal dispersal distance(s). The resultant dataset showed a strong bias towards studies in the Northern Hemisphere.

To increase the representation of data from the Southern Hemisphere, we also estimated dispersal distances directly using mark-recapture data from the South African Bird Ringing Unit (http://safring.birdmap.africa) by replicating the methods used in Paradis et al. (1998). To obtain records of bird movement that would be representative of natal dispersal, we filtered the data as follows: (a) only records of birds banded as nestlings were used, to ensure banding locations were representative of the bird's natal location; (b) only birds recovered as mature adults were used, to ensure recovery locations represent potential breeding sites; (c) only birds banded and recovered during their breeding season were used; and (d) only birds banded and recovered within their breeding ranges were used, to minimize recaptures of migrating individuals. To estimate natal dispersal distances, we used the package 'GEOSPHERE' (Hijmans, 2019) in R (R Core Team, 2018) and calculated the distance between banding and recovery locations according to the 'Vincenty' (ellipsoid) method, a method that measures the distance between two points on an ellipsoid approximating Earth's actual shape (Vincenty, 1975). Geometric means were calculated for all species for which we were able to obtain dispersal distance estimates from more than five individuals, as mean estimates for species with data from fewer than five individuals had high variance in the dispersal estimate. When multiple studies estimated dispersal distance for the same species, we took the mean dispersal distance estimate across studies; if different estimates for male and female dispersal were given, we used the mean distance: and if multiple methods were used to estimate dispersal distance for a single species, we used banding-based estimates, as this was the most common method for estimating dispersal distance in our dataset.

2.2 | Morphological and ecological traits

To estimate variation in flight efficiency across species, we compiled HWI estimates from a comprehensive global dataset (Sheard

TABLE 1 Aerial Lifestyle Index. Species are scored from literature based on the degree to which flight is integral to foraging behaviour or daily routines. It is possible for species to be relatively sedentary (i.e. not move long distances) but still spend much of their daily life in the air (e.g. tropical swallows and hummingbirds)

| Score | Attributes |
|------------------------|--|
| 1. Infrequent flier | Flies rarely if ever, or flights are short, routinely in the order of 1–50 m. Does not fly as part of its foraging behaviour (ignoring brief sallies to catch prey on substrates) |
| 2. Moderate flier | Undertakes occasional longer flights (e.g. between foraging areas), sometimes over moderate distance, but usually below 1 km. May use shorter flights much more often (e.g. relatively brief aerial display flights, or foraging in sallies to catch insects or animal prey, but flying from one perch to another rather than airborne for long periods) |
| 3. Frequent flier | Flight is a regular and integral part of its daily routine. Flies long distances (often several km multiple times a day in search of food, or travelling to roost sites etc.). Includes species that search for food by gliding, soaring or in extended flight |

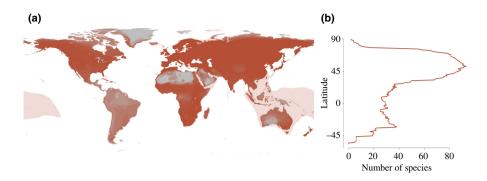


FIGURE 1 The geographical distributions of breeding and resident ranges for 114 species sampled for natal dispersal distance estimates. More intense red colour on the map (a) indicates a higher number of overlapping breeding and resident ranges. Our sample of study species spans all continents except Antarctica, with a bias towards species that breed in the Northern Hemisphere (b)

et al., 2020). This source calculated HWI as $100 \times \text{Kipp's distance}/\text{wing length}$, where Kipp's distance is the length of the distance between the tip of the first secondary feather and the tip of the longest primary feather on a folded wing, and wing length is the distance from the carpal joint to the tip of the longest primary feather (Claramunt & Wright, 2017).

Study species were then classified as either migratory or nonmigratory, following Sheard et al. (2020). Platalea alba, the only species in our dataset scored as a nomadic or local migrant, was grouped with the non-migratory species for the purposes of our analyses. We incorporated the potential effects of ecological factors by including habitat and diet for each species in our models. Primary habitat was characterized as open, semi-open or closed habitat, with these categories referring to the density of vegetation from deserts and grasslands (open) to forests and other thick vegetation (closed) (Pigot & Tobias, 2015). Each species was also assigned to one of three dietary categories based on their trophic level (carnivore, herbivore and omnivore; Pigot et al., 2020). Similar to work in other systems (e.g. Evans, 2021), we categorized species using an ordinal 'aerial lifestyle' index based on its primary lifestyle (Tobias et al., 2022) and foraging behaviour (Table 1). Given that this index is potentially biased by the availability of information, we scored each species for the level of uncertainty in our classification; aerial lifestyle was classified with high certainty for almost all species in our sample because they tend to be common and very well known (Supporting Information).

2.3 | Modelling the relationship between HWI and dispersal distance

We modelled mean dispersal distance estimates for each species as a function of its mean HWI (Sheard et al., 2020), controlling for migratory strategy, the interaction between migratory strategy and HWI, the method of measuring dispersal distance (band data vs. radiotag/gps), habitat type and trophic niche (see Table S1 for additional detail on species categorizations). Prior to fitting the model, we log transformed dispersal distance to reduce heteroscedasticity in the residual error, and we scaled HWI by subtracting the mean and dividing by twice the standard deviation (resulting in a variable with a mean of 0 and a standard deviation of 0.5) so that the model coefficient for HWI would be comparable to the coefficients of the categorical variables (Gelman, 2008).

Relationships were modelled using phylogenetic generalized least squares in the R package 'NLME' (Pinherio et al., 2013). Phylogenetic relationships were characterized using 1,000 trees from a comprehensive phylogeny of all birds (Jetz et al., 2012) based on a backbone tree from Hackett et al. (2008) to construct a 50% majority rule consensus phylogeny. Branch lengths were estimated using the SumTrees function in DendroPy to adjust the mean branch lengths such that the node ages in the phylogeny are consistent with the median ages of the corresponding nodes in the distribution of trees used as the basis of the majority rule consensus (Rubolini et al., 2015; Sukumaran & Holder, 2010). The phylogeny was incorporated into the models as a correlation structure derived with Pagel's lambda (Pagel, 1999) using the corPagel function from the ape package (Paradis et al., 2004) in R.

2.4 | Understanding the link between HWI and aerial lifestyle

To test whether HWI is linked to the aerial lifestyle index, we used two approaches: (a) a phylogenetic generalized least squares approach, following the modelling approach described above, but with HWI predicted by aerial lifestyle score; and (b) a maximum likelihood estimate of the polyserial correlation between HWI and aerial lifestyle score, implemented using the 'polyserial' function in the package 'POLYCOR' (Fox, 2019) in R. A *p*-value was calculated for the maximum likelihood-derived estimate of the polyserial correlation coefficient as: $2 \times$ the integral from $-\infty$ to the quartile defined by $-1 \times$ the absolute value of the parameter estimate/standard error in a normal probability distribution function with a mean of 0 and a standard deviation of 1.

3 | RESULTS

After removing one flightless penguin Spheniscus humboldti, our final dataset included 123 estimates of mean natal dispersal distance

for 114 bird species (Table S1). These species were from a range of latitudes and systems, though there is a bias towards the Northern Hemisphere (Figure 1). Of these, 64% of the dispersal estimates came from migratory species. The dispersal distances ranged from <1 to 935 km. Roughly half of the species (50.9%) are found in semiopen habitats, with 12.3% found in closed habitats and 36.8% found in open habitats. The species represent a range of trophic levels, with 17.5% being primary consumers, 59.6% being secondary/tertiary consumers and 22.8% being omnivores.

HWI was significantly positively associated with the logarithm of natal dispersal distance ($\beta = 0.86$, p = 0.008; Figure 2). No other variables in the model were significantly associated with dispersal distance (Table 2). Non-migratory species had lower dispersal distances than migratory species, but this effect was marginally nonsignificant ($\beta = -0.39$, p = 0.07), and primary consumers dispersed shorter distances than secondary/tertiary consumers, but this effect

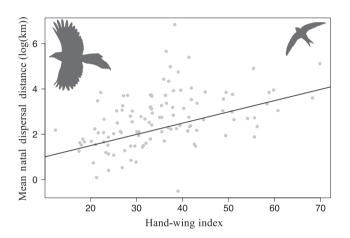


FIGURE 2 Hand-wing Index (HWI) is positively related to mean natal dispersal distance. Each point represents the mean HWI and dispersal distance for 114 species in the analyses; the model fitted is a pgls regression of log(dispersal distance) predicted by HWI. Note that negative logarithms of dispersal distance occur when dispersal distances are less than 1 km

was also marginally non-significant ($\beta = -0.64$, p = 0.07). The interaction between migration and HWI had a small effect size and was not significant ($\beta = 0.06$, p = 0.89).

HWI and aerial lifestyle score are significantly positively related. Based on the phylogenetic generalized least squares approach, in which the HWI of species with an aerial lifestyle score of 1 (infrequent flier) was the intercept (i.e. reference value), an aerial lifestyle score of 2 (moderate flier) was associated with significantly higher HWI values ($\beta = 0.3, p < 0.001$), and an aerial lifestyle score of 3 (frequent flier) was associated with an even larger significant increase in HWI ($\beta = 0.83, p < 0.001$). Similarly, based on the maximum likelihood polyserial correlation, the relationship between HWI and aerial lifestyle score is 0.84 and is significant (p < 0.01; Figure 3).

4 | DISCUSSION

Our analyses reveal that HWI is a significant predictor of mean natal dispersal distance, with higher values of HWI associated with longer dispersal distances, even after controlling for a range of ecological and life-history variables. While previous studies have shown a link between flight efficiency and natal dispersal distance in a limited sample of species from the British Isles (Claramunt, 2021; Dawideit et al., 2009), our findings indicate that the relationship between flight efficiency and natal dispersal distance is generalizable across the globe and in all biomes.

Natal dispersal involves the departure of individuals from their natal sites (Matthysen, 2005), the movement or 'transience' phase (Matthysen, 2012) and the ability of species to survive in the location to which they have dispersed. Each of these stages of dispersal may be influenced by various factors unrelated to flight efficiency, including species biology, biotic interactions and geographical barriers (Pearson & Dawson, 2003; Sexton et al., 2009; Weeks, Claramunt, et al., 2016). Nonetheless, flight is clearly a critical factor in bird dispersal. Our results suggest that species adapted for efficient flight disperse further, perhaps because they are more mobile and thus are

TABLE 2 Dispersal ability predicts natal dispersal distance. Hand-wing Index (HWI) was significantly and positively associated with natal dispersal distance; relationships of all other variables and interactions were non-significant. Categorical variables are presented as contrasts with migratory species, species in closed habitat and secondary/tertiary consumers as the references. Distance measurement method refers to data source (Not-band = either GPS or radiotracker). Habitat categories refer to vegetation (closed = forests; semi-open = shrubland, parkland and marsh vegetation; open = grassland, desert, coast and ocean). Significant parameters (p < 0.05) are in bold and noted with an *

| Parameter | Parameter estimate | Standard error | p-value |
|--|--------------------|----------------|---------|
| Hand-wing Index | 0.86* | 0.32 | 0.008 |
| Distance measurement method (Not-band) | -0.90 | 0.47 | 0.06 |
| Migration (No) | -0.39 | 0.22 | 0.07 |
| Habitat (Semi-open) | 0.32 | 0.31 | 0.30 |
| Habitat (Open) | 0.19 | 0.37 | 0.60 |
| Diet (Primary consumer) | -0.65 | 0.35 | 0.07 |
| Diet (Omnivore) | -0.03 | 0.28 | 0.93 |
| HWI:Migration | 0.06 | 0.41 | 0.89 |

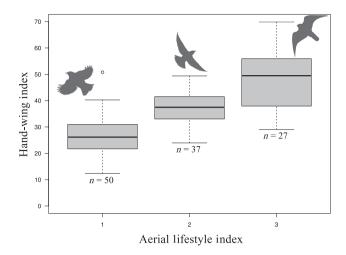


FIGURE 3 Hand-wing Index (HWI) is positively correlated with aerial lifestyle. The aerial lifestyle index reflects the degree to which flight is an important part of the daily routine or lifestyle of each species (Table 1; 1 = infrequent flier, 2 = moderate flier, 3 = frequent flier). The relationship between flight efficiency (estimated by HWI) and aerial lifestyle likely reflects morphological adaptation to behavioural strategies such that the energetic costs of movement are reduced in species relying on frequent or prolonged flight. Number of species for each category of the lifestyle index are shown. Images of representative species for each category were produced by Liftarn, Gareth Monger and Sharon Wegner-Larson under a creative commons license (https://creat ivecommons.org/licenses/by-sa/3.0/) and available from http:// phylopic.org

capable of crossing gaps in suitable habitat, which results in them travelling longer distances on average during the movement phase.

The role of flight efficiency in shaping patterns of natal dispersal aligns with similar findings in related contexts. Flight efficiency is associated with multiple dispersal-mediated patterns and processes, including variation in geographical range size (Lester et al., 2007; Sheard et al., 2020), gene flow (Chua et al., 2017), diversification (Claramunt et al., 2012; Weeks & Claramunt, 2014) and community assembly (Lasky et al., 2016). Although the impacts of dispersal ability and flight efficiency are pervasive, this still leaves major question marks over the mechanisms involved. In particular, the evidence that dispersal is associated with high mobility in migratory birds is equivocal.

Migratory species are slightly over-represented in our sample (64%), yet–somewhat surprisingly–do not have significantly longer dispersal distances than non-migratory species. Furthermore, the non-significant interaction (p = 0.89) between HWI and migratory strategy in our analysis, indicates that, as in British birds (Claramunt, 2021), the relationship between flight efficiency and dispersal distance at a global scale is similar for migratory and non-migratory species. These results reinforce the view that migration is not necessarily positively associated with dispersal distance or range expansion (Böhning-Gaese et al., 1998) largely because many migratory species are strongly philopatric, returning to the same or nearby territory in successive breeding seasons.

Our analyses reveal that HWI is also strongly correlated with aerial lifestyle, pointing to a wider role for flight behaviour in shaping patterns of dispersal (Evans, 2021). We interpret the relationship between HWI and aerial lifestyle as reflecting the evolution of flight efficiency in species with lifestyles heavily dependent on flight. Efficient flight and aerial lifestyles coevolve, leading to a combination of phenotypic and behavioural adaptations that may increase natal dispersal distances. This coevolution of aerial behaviour and flight efficiency helps to explain the relationship between flight efficiency and dispersal distance, particularly given that better studied aspects of behaviour-including migration-fail to account for variation in dispersal distances across species. Thus, aerial lifestyle may have broad implications not only for understanding the determinants of dispersal distance (Burgess et al., 2016), but also for the use of flight efficiency as a predictor of dispersal distance. While flight efficiency may only indirectly control dispersal distances, morphological indicators of flight efficiency (e.g. HWI) are highly correlated with aerial lifestyles and thus are appropriate 'universal' predictors of dispersal distances.

Despite the presumed importance of ecological and life-history variables in determining the propensity of species to disperse, we do not find diet or habitat affinity to be important predictors of natal dispersal distance in this sample (Table 2). This is in line with previous regional-scale work that found habitat and diet add little to models of dispersal distance beyond what is contributed by morphological indicators of flight efficiency (Claramunt, 2021; Dawideit et al., 2009). However, the variables used in all cases are quite coarse, and it is possible that more nuanced ecological dynamics, such as temporal variation in food availability and sex-biased differences in dispersal, may play a role in determining natal dispersal distance. The variance left unexplained by our models could reflect this type of missing information, suggesting that important biotic or abiotic predictors of dispersal remain unidentified. Our results provide a foundation for the next phase of research based on wider sampling of ecological or environmental determinants, ideally coupled with improved accuracy of dispersal distance data.

Although we recover a strong relationship between HWI and dispersal distance, there are some limitations to our study. In our sample, ~95% of dispersal distances were based on banding data, with radio tags only accounting for ~5% of the values, and GPS <1%. This may be an issue if banding data tend to underestimate dispersal distances (Baker et al., 1995). When we tested for this pattern, we did not find a significant effect of the collection method on natal dispersal distance, although this may relate to weak statistical power because of limited radio tag and GPS data. Furthermore, the relatively small amount of dispersal data from tropical locations leaves us with a sample heavily biased towards Northern Hemisphere species. Dispersal in tropical regions is limited by both natural and anthropogenic barriers such as rivers, road building and habitat loss and degradation (Develey & Stouffer, 2001; Fernandes et al., 2014; Moore et al., 2008; Van Houtan et al., 2007), and the impacts of these barriers may be

particularly constraining to tropical species that have lower flight efficiency (Sheard et al., 2020).

5 | CONCLUSIONS

We find that HWI-a morphological determinant of flight efficiency-is a reliable predictor of natal dispersal distance across a global sample of bird species. We also show that flight efficiency is closely associated with the degree to which species rely on an aerial lifestyle, suggesting lower energetic constraints are correlated with a greater use of flight, along with increased dispersal or gap-crossing ability, and ultimately longer dispersal distances. As such, our findings provide a potential mechanistic basis for the positive relationship between flight efficiency and natal dispersal distance. They also support the use of HWI as an index of relative flight use and natal dispersal, with potential wide applications in phylogenetic comparative analyses (Menezes & Palaoro, 2022), biodiversity modelling (e.g. Weeks, Naeem, et al., 2022) and the calculation of dispersal buffers in models of geographical range shift under climate change scenarios (e.g. Stewart et al., 2022). As both natural and anthropogenic climate change and habitat destruction progress, understanding dispersal limitations will be increasingly important to inform conservation interventions.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest. J.A. Tobias is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

B.K.O. and B.C.W. conceived the study; J.A.T. developed the aerial lifestyle index; J.J.C. estimated the natal dispersal distances from South African Bird Ringing Unit data; B.C.W., B.K.O., J.J.C., S.C., C.S. and J.A.T. contributed to the analyses and manuscript development.

DATA AVAILABILITY STATEMENT

All data and code available from the Dryad Digital Repository https:// doi.org/10.5061/dryad.2ngf1vhqm (Weeks, O'Brien, et al., 2022).

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