

# Determinants of Variation in Natal Dispersal Distances amongst North American Birds

by

Jonathan Jo Jo Chu

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## **Abstract**

Dispersal is fundamental to many processes such as community connectivity, gene flow, and macroevolution. Natal dispersal, movement from birth site to breeding site, is usually the longest dispersal event among birds and thus the most influential to these processes. Recent work has suggested that the cost of transport may be an important factor for determining dispersal distance. I use large-scale mark-recovery data to estimate natal dispersal distances in North American birds and incorporate morphologically based flight efficiency proxies, ecological and behavioural factors into models that explain the variation of dispersal distances across species. Model inference techniques suggest that flight efficiency, population size and habitat are important for natal dispersal distance, the individual effects of which are difficult to disentangle. I suggest that since these parameters capture information about a species mobility, mobility is what determines natal dispersal distances in North American birds.

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# Using Wing Morphology to Determine Variation in Natal Dispersal Distances in North American Birds

## Introduction

Dispersal is an important aspect of ecology and evolutionary biology fundamental to many phenomena both at the broad spatio-temporal scale, such as biogeography, speciation, and macroevolution (Bohonak, 1999; Gaston, 2003; Hanski, 1998), as well as at smaller scales, including community and population dynamics (Bowler & Benton, 2005). Natal dispersal, defined as the movement of an animal from birth site to first breeding site, is usually the longest dispersal event among birds and thus it is influential to gene flow, population dynamics and metacommunity connectivity (Dawideit et al., 2009; Lester et al., 2007; Tingley et al., 2009). Understanding the determinants of natal dispersal distances will be crucial for understanding these key areas in ecology. As human impacts continue to depress population sizes understanding how these processes are fundamentally intertwined will be important (Rosenberg et al., 2019; Sutherland et al., 2013).

Evidently there exists variation in dispersal within species and across species. Philopatry can change with age and sex (Greenwood, 1980), and dispersal distances vary considerable among individuals, where most individuals disperse close to where they were born and few disperse far (Koenig et al., 1996; Paradis et al., 1998; Murray, 1967). Likewise, there can be variability in dispersal distances between species as well, some species can move great distances away from their natal site while some species are completely sedentary (Paradis et al., 1998; Wikelski et al., 2003). Most theories have framed dispersal as an adaptive strategy for the

settlement of individuals facing, competition, inbreeding, or resource scarcity (Clobert et al., 2009; Bowler and Benton 2005; Matthysen, 2012). In contrast there are arguments that dispersal is not an adaptive strategy, but a by-product of movements intended for short term activities such as foraging (Burgess et al., 2015). However empirical evidence to support these theories were lacking due to the multicausality of the dispersal process, lack of comparable dispersal distances and difficulty in estimating dispersal parameters (Matthysen, 2012). Although dispersal distances have been characterized for many species, the varying sampling methods, distance measuring techniques and geographies have made it problematic to do comparative analysis. In a landmark study, the distribution of dispersal distances for 75 British bird species were characterized using data from the ringing scheme of the British Trust for Ornithology (Paradis et al., 1998). The dispersal distances estimated by this study can be directly compared and have been used in many recent analyses of dispersal in birds (Claramunt, 2021; Dawideit et al., 2009; Garrard et al., 2012). Despite this, until recently there has been weak support for a key parameter that explains natal dispersal distances. Paradis et al. (1998) identified population size, geographic range size and migratory behaviour as important factors. Sutherland et al. (2000) found that body mass and diet accounted for a significant proportion of dispersal variation in juvenile birds, Garrard et al. (2012) preferred a model that included body mass, wingspan, sex and feeding guild. Dawideit et al. (2009) find their best model to explain variation in dispersal included Kipp's distance (distance between first secondary feather and longest primary feather when the wing is folded). The best models in the aforementioned studies explained 43% (Garrard et al., 2012) to 45% (Dawideit et al., 2009) of the variation in dispersal distances, and there has been no consensus on a unifying set of key parameters.

Physiological and physical efficiency of movement should be influential to dispersal ability (Bonte et al. 2012), so it is notable that in past analyses the consideration of the effect of the cost of transport and flight efficiency on natal dispersal is lacking. As the morphology of the flight apparatus, particularly the aspect ratio of the wings, is critical for flight efficiency, it is expected to be influential in determining natal dispersal distances (Pennycuik, 2008; Claramunt & Wright, 2017). Recent reanalysis of the British dataset suggested that the main driver of dispersal distance in birds is the cost of transport (Claramunt, 2021). Wing morphologies associated with flight efficiency were the best predictors of natal dispersal distances in British birds. Furthermore, in line with past analyses, migration and population size were correlated with natal dispersal distances suggesting that these factors may also be influential for natal dispersal in birds (Claramunt, 2021; Paradis et al., 1998; Dawideit et al., 2009; Garrard et al., 2012). It is postulated that the overall mobility of a species, estimated by flight efficiency, population, and migration, is what determines dispersal distance and not adaptations for dispersal itself (Claramunt, 2021).

Migratory behaviour has been shown to be a likely source of variation in dispersal distances. Some empirical evidence supports the idea that migratory behaviour/distance is important for determining dispersal distance (Claramunt 2021; Dawideit et al., 2009; Paradis et al., 1998). As both dispersal and migration depend on flight capacity, it is logical to assume that birds that migrate further will disperse further, and indeed there is a body of evidence that suggests key morphologies that correlate with the flight efficiency are correlated with migration distance. Wing pointedness has been found to be correlated with shorebird migration distance (Minias et al., 2015) and wing length has been found to be correlated with warbler migration

distance (Nowakowski et al., 2014). Furthermore, evidence suggests that wing morphology is adapted to increase the long-distance migration efficiency in birds, with species that have high-aspect ratio wings requiring less fuel accumulation (Vincze et al., 2019). Claramunt (2021) finds a relationship between migration and natal dispersal distance, though in this case the relationship is ambiguous. Claramunt (2021) described that the relationship could be driven by a few outliers, disregarding these species opens the possibility that migration has little effect on natal dispersal distances when considered alongside flight efficiency (Claramunt, 2021). In sum, it is reasonable to expect a relationship between migratory distance/behaviour and dispersal distance because flight efficiency is a primary determinant of both. However strong empirical evidence is lacking to corroborate this thinking.

Population size and density have been considered in theoretical models explaining dispersal, and it is thought that in general dispersal will have important impacts on population sizes (Tilman, 1994). Some models suggest that population size and dispersal distance should be positively correlated as a result of competition and inbreeding (Matthysen, 2005; Matthysen, 2012). Interestingly, population size is negatively correlated with dispersal distances among British birds (Claramunt, 2021; Paradis et al., 1998). Indeed some argue that patterns expected by dispersal as an outcome of inbreeding avoidance cannot solely be attributed to inbreeding avoidance and can be explained by other ecological factors (Moore & Ali, 1984; Perrin & Mazalov, 1999). As an alternative, a negative relationship may be a result of a more nuanced relationship between dispersal distance and population size. It is possible for this pattern to emerge depending on the spatial structure of the population. If population density is uniform through space, long-distance dispersal will have little benefit even if absolute population sizes

are large (Claramunt, 2021). Population sizes may also capture information about territory size and overall mobility which maybe directly related to dispersal distances (Bowman, 2003; Stephens et al., 2019; Claramunt, 2021). As it stands, there is a negative relationship between population size and natal dispersal distance (Paradis et al., 1998; Claramunt, 2021), but the mechanisms that produce this pattern and the generality of this pattern are still unknown.

In this study, I plan to describe the relative importance of flight efficiency on natal dispersal distances in North American birds. There is a strong need to validate the recent findings on the determinants of natal dispersal distances in British birds (Claramunt, 2021). Lacking are comparable data and analyses on species outside the ones originally estimated by Paradis et al. (1998). Comparable dispersal distance estimates for species in other parts of the world are needed to reach generalizable conclusions. Natal dispersal estimates have only recently been estimated using banding data for some North American species (Martin & Fahrig, 2018). Here I replicate the methodology described in Paradis et al (1998) and Martin and Fahrig (2018) to estimate natal dispersal distances in North American birds using banding data. Using these methods, I estimated natal dispersal distances for 51 North American bird species spanning many taxonomic groups. I conduct comparative analyses and assess the role of three morphologically based flight efficiency proxies on bird natal dispersal distances (Claramunt & Wright, 2017). Using model selection, I address which morphological parameter best estimates natal dispersal distance. Additionally I incorporate behavioural and ecological traits, that have been theorized to influence dispersal distances (Garrard et al., 2012; Paradis et al., 1998; Ronce, 2007; Sutherland et al., 2000), into models with flight efficiency proxies. These models highlight the relative

importance of flight efficiency, behavioural and ecological variables on natal dispersal distances and illustrate what key factors explain differences in dispersal distances among birds.

## **Methods**

### *Estimation of natal dispersal distances for North American birds:*

To estimate natal dispersal distances, the methods of Paradis et al. (1998) were applied to mark-recapture bird records from the North American bird banding program. I obtained recovery records of birds banded as nestlings or fledglings to ensure that the banding site reflects the natal site. The distance between this point and the subsequent recovery location was taken as an estimate of the individual's natal dispersal distance. Only birds banded and recaptured during the species breeding season and within the species breeding range were considered, as movement outside this season or area will tend to be migratory. To determine breeding range limits the most extreme points on shapefiles of the species' distribution were set as latitude and longitude filters (BirdLife International 2019). Only birds recaptured as mature adults were considered to ensure that recapture location represent a probable breeding site. Location data must have been precise to 1' block. To limit spatial biases of recoveries, only birds found dead were used. The filtered banding and recovery data were plotted on maps of North America with connecting line segments to inspect if filters were successful in limiting spurious effects and recoveries along migratory routes. Distances were measured using R package 'geosphere' (Hijmans, 2019). The shortest distance between the banding and recapture locations according to the "Vincenty" (ellipsoid) method was used as the estimate of that individual's natal dispersal distance. This method measures the distance between two points on an ellipsoid approximating Earth's actual

shape and should be the most accurate estimation for the distance between the two points (Vincenty, 1975). Geometric means were calculated to obtain an average natal dispersal distance for each species. To complement these estimates I added estimates for additional species from Martin & Fahrig (2018).

*Predictor measurements:*

I collected and calculated three indices that are proxies for flight efficiency, aspect ratio, hand-wing index, and lift-to-drag ratio. Hand-wing index was developed as an estimation of aspect ratio that can be measured easily from round skins (Claramunt et al., 2012). As hand-wing indices have been measured for majority of bird species (Sheard et al., 2020), it is a powerful tool for characterizing and comparing flight efficiency across species. Hand-wing index is defined as:

$$100 \cdot \frac{(L_w - S_1)}{L_w}$$

where  $L_w$  is the distance between the carpal joint and the tip of the longest primary feather and  $S_1$  is the distance between the carpal joint and the tip of the first secondary feather. The difference of which is equivalent to Kipp's distance. Hand-wing indices for all species were obtained from Sheard et al. (2020).

Aspect ratio is important especially for long-distance flight (Pennycuick 2008). It is calculated as:

$$\frac{B^2}{A_{tot}}$$

Here  $B$  is the wingspan of the bird, and  $A_{tot}$  is the total area of both wings and the root box (segment of body in between the wings). To obtain species estimates for  $A_{tot}$ , I followed this formula (Figure 8.5 from (Claramunt & Wright, 2017)):

$$A_{tot} = 2A_w + C_r \cdot (B - 2E)$$

in which  $A_w$  is the area of a single wing,  $C_r$  is the width of wing as the base known as the root chord and  $E$  is the wing extent, measured as the distance of the tip of the longest primary feather perpendicular to the  $C_r$ .

Lift-to-drag ratio is the ratio of the lift force (that counteracts the body weight) to the drag forces required for horizontal steady flight, and it is given by the formula:

$$\frac{mgV}{P}$$

where  $m$  is body mass,  $g$  is the gravitational acceleration,  $V$  is the forward velocity, and  $P$  is the power required for flight.  $P$  can be estimated from aerodynamic models and morphological variables (Pennycuick, 2008). The three main components of the mechanical power required needs three morphological measurements: wingspan, wing area and body mass. Body masses were obtained from Tobias & Pigot (2009), which were based on Dunning (2007). As empirical field measurements of flight velocity are not available for most species, I estimated the maximum lift-to-drag ratio for each species by maximizing it with respect to velocity using function *optim* in R 4.0 (R Core Team 2020). This approach is based on evidence suggesting that birds tend to fly at maximum range velocities (velocity that maximizes the lift-to-drag ratio) during migration or commuting (Bruderer and Boldt 2001, Pennycuick et al. 2013, Pennycuick 1997). I used a number of other constants and parameters, induced power factor = 1, body drag coefficient = 0.1, and estimated the body's frontal area as 0.01 m<sup>2</sup>, following Pennycuick (2008), Pennycuick *et al.* (2013), and Claramunt and Wright (2017).



Flight efficiency measurements were either taken from spread wings photographed at the Royal Ontario Museum, from the Wings Database (Pennicuik, 2008) included in the Flight 1.25 software (<https://booksite.elsevier.com/9780123742995/?ISBN=9780123742995>), or from a digital collection of spread wing images available online from the Slater Museum of Natural History (<https://digitalcollections.pugetsound.edu/digital/collection/slaterwing>). Some specimens had missing primary feathers or excess tertiary feathers that artificially elongated the root chord, these images were adjusted by cloning primary feathers or removing excess tertiaries. Wings Database measurements included sufficient measurements to directly measure flight efficiency proxies per specimen, however wingspans were not recorded for most of the wing images, so adult wingspans were taken from museum specimen records in VertNet ([vertnet.org](http://vertnet.org)) to use in calculations of flight efficiency based on species averages.

I used ImageJ v.1.52 (Schneider et al., 2012) to process and measure wing images using the following steps: 1) set the scale to mm using the scale bars included in the images; 2) transform the image into a binary image using the thresholding tool; 3) measure the area of the wing using the tool Analyze Particles ( $A_w$ , mm<sup>2</sup>); 4) measure distance between the shoulder joint and the trailing edge of the wing (root chord,  $C_r$ , mm); 5) measure distance from and perpendicular to the root chord to the tip of the wing (wing extent,  $E$ , mm).

Migratory distances were estimated using range shape files (BirdLife International 2019). Shape files were analysed using QGIS v.3.14 (QGIS Development Team 2020). Centroids for breeding ranges and wintering ranges were obtained, and the shortest distance between the points

according to the “Vincenty” (ellipsoid) method was used as an estimate of the species migratory distance.

Ecological variables were habitat, diet, foraging behaviour and population size. Habitat, diet and foraging behaviour information was obtained from Billerman et al. (2020). Habitat was divided into four categories, woodlands, open, wetlands and coasts. Species that live in dry habitats were split between woodlands and open depending on the amount of canopy in their habitat. Species that inhabit aquatic ecosystems were split between wetland and coasts, depending on whether their habitat consists of interior lakes, wetlands, and rivers (wetland) or beaches, marine coastlines or open ocean (coasts). Diet was divided into four categories: herbivores, species that primarily feed on plants; carnivores, species that primarily feed on vertebrates; insectivores, species that primarily feed on insects and other invertebrates; and omnivores, species that feed on both plants and animals. Foraging behaviour was categorized into five groups that correspond to a continuum of the amount of flight required to forage. The first group, surface foraging, includes species that primarily forage while walking, wading, or floating so flight is not needed for prey detection and capture (e.g. Mourning Dove, *Zenaida macroura*). The second level, tree foraging, refers to species that forage in elevated vegetation like arboreal insect gleaners and tree climbers, that need to fly from branch to branch or from tree to tree during foraging, for example the Red-cockaded Woodpecker, *Dryobates borealis*. The third level, sallying, refers to species that take off from perches to pursue prey after which they shortly return to a perch, for example the Least Flycatcher, *Empidonax minimus*. The fourth level, aerial search, refers to species that search for prey in flight but dive down to capture prey on the ground or in the water, for example the Turkey Vulture, *Cathartes aura*. The fifth level,

aerial capture, refers to species that search for, capture and ingest prey on the wing, for example the Purple Martin, *Progne subis*. Population sizes were taken from Rosenburg et al. (2019) with data originally published by Partners in Flight (Stanton et al. 2019). Population sizes represent breeding population size in the United States and Canada estimated from the North American Breeding Bird Survey (Sauer et al. 2017).

#### *Statistical analysis:*

Relationships between predictors and natal dispersal distance were assessed using phylogenetic generalized least squares models (PGLS) to account for phylogenetic non-independence (Freckleton et al., 2002). PGLS models were fit by maximum likelihood with the *pgls* function in the R package ‘caper’ (Orme et al., 2018). Phylogenetic non-independence is incorporated into the error term of PGLS models by specifying an error-covariance matrix, the structure of which is specified by a maximum clade credibility tree computed using TreeAnnotator (Bouckaert et al., 2014) from a sample of 1000 phylogenetic trees of the study species obtained from Birdtree.org (Jetz et al., 2012), using the Hackett et al. (2010) backbone topology. Continuous variables were log-transformed to increase homoscedasticity in the case of natal dispersal distances (Faraway, 2005), and to improve likelihood values and the distribution of residuals for flight efficiency, migration distance and population size predictors.

I explored all predictors individually in single predictor models. I compared single predictor models consisting of flight efficiency predictors to assess the best morphology-based flight efficiency proxy to estimate natal dispersal distance. Then, I constructed multi-predictor models with main effects and second-order effects (interactions) between continuous predictors

and binary predictors. I did not consider models with more than five variables and greater than second-order effects. Three sets of models were built based on the inclusion of one of the three flight efficiency parameters. Models were assessed using model selection and multi-model inferences techniques (Burnham & Anderson, 2002). The Akaike information criterion (AICc) was calculated, and relative model likelihoods and model probabilities were obtained. Predictors were standardized before analyses. Model fit and proportion of variance explained by the models were assessed by calculating coefficients of determination:

$$R^2 = 1 - \frac{RSS_{\text{model}}}{SS_{\text{null}}}$$

in which  $RSS_{\text{model}}$  is the residual sum of squares of the full model and  $SS_{\text{null}}$  is the sum of squares for the response in the null model, as calculated by the ‘pgls’ function. The null model included only the intercept but used the same correlation structure as the full model. Additionally, to assess variable importance, I calculated the sum of model probabilities containing each variable (Burnham & Anderson, 2002). Finally, I estimated model-averaged coefficients and confidence intervals and built 95% confidence model sets by retaining models with a cumulative probability up to 0.95. Models were built using R package ‘MumIn’ with function *dredge*, and *model.avg* for computing model-averaged estimates (Bartón, 2018).

Predictors were assessed for multicollinearity using generalized variance inflation factors (GVIF). To allow for comparisons of categorical variables with multiple levels, I calculated a dimensionality correction (Fox and Monnette 1992):

$$GVIF^{\frac{1}{(2*DF)}}$$

where GVIF is generalized variance inflation factors, and DF is degrees of freedom of the predictor (number of categories – 1). The square of this result can be evaluated using the VIFs thresholds (< 2: no collinearity, > 5 high collinearity).

## Results

Natal dispersal distances were obtained for 103 species (Table S1). As standard errors increased exponentially for species with <5 dispersal estimates, only 51 species with a sample size >4 were retained for further analyses. As the final list was low in small species such as passerines and hummingbirds, I added estimates of natal dispersal distances from Martin & Fahrig (2018) for *Cardinalis cardinalis*, *Archilochus colubris*, *Dumetella carolinensis*, *Passerina cyanea*, *Thryothorus ludovicianus*, and *Zenaida asiatica*.

Of 57 species with natal dispersal estimates, 50 species had sufficient material to calculate mean aspect ratio and lift-to-drag ratio (Table S2). For 18 species I used specimen measurements from the Wings database (Pennycuick, 2008). The remaining 34 species had wing morphologies estimated from single wing specimens' images retrieved from Slater Museum of Natural History (2008), or personally photographed at the Royal Ontario Museum (Table S3). One species was dropped due to insufficient population size information. In total, 50 species were used to generate comparative models.

All three flight efficiency variables were positively and significantly correlated with natal dispersal distances, with aspect ratio being the best predictor followed by lift-to-drag ratio, and hand-wing index (Table 1, Figure 2 B-D). Flight efficiency predictors constituted the two

best single predictor models, aspect ratio and lift-to-drag ratio were able to explain 23% and 21% of the variability respectively, for other predictors, model probability was low. Migration was a poor predictor for natal dispersal distances (Table 1). Migration distance was positively correlated with natal dispersal distance but non-significantly. Migration behaviour (a binary variable denoting residents vs. migrants) was a slightly better predictor than migratory distance but still nonsignificant (Table 1). It is possible that the relationship between migration distance and natal dispersal distance is mainly driven by the difference in migration distances between residents and migrants (Figure 1F). Furthermore, I modeled natal dispersal distance using migration distances excluding resident species. The relationship of which shifted from positively non-significant to negatively non-significant once residents were excluded. Suggesting that migration distance has little effect on natal dispersal distance, and the shift in positive to negative may suggest the relationship is driven by migrants vs. non-migrants. Based on these observations only migratory behaviour was included in multi-predictor models.

Habitat was the best ecological variable amongst single predictor models and explained the highest proportion of variance (Table 1). Population size was negatively and significantly correlated with natal dispersal distances, in other words species with large populations showed shorter dispersal distances (Figure 1E, Table 1). Foraging behaviour had a significant relationship with natal dispersal distance and explained 20% of the variance but had low model probability (Figure 1J, Table 1). Foraging groups 2-4, tree foraging to aerial search, follow the expected trend that increased reliance on flight during daily life would be correlated with increasing dispersal distance. However foraging groups 1 and 5 do not follow this trend, surface foragers in fact had the highest natal dispersal distances. Diet was a non-significant predictor,

had low model probability and explained 10% of variance in natal dispersal distances (Figure 1I, Table 1).

Multi-predictor models had low model probability and 95% confidence model sets contained many models (Table 2), revealing considerable model uncertainty. Between model sets containing aspect ratio or lift-to-drag ratio, all models within 5 AIC units of the best model, contained flight efficiency and population size (Table 2). Habitat also occurred frequently in these model sets; it was within all lift-to-drag models with  $\Delta AIC < 5$ . Hand-wing index was not included in the best model within its model set, population and habitat again occurred at high frequency, contained in all models within 5 AIC units of the best model. The other ecological variables occurred in the best models inconsistently. The top model in the lift-to-drag ratio model set and the aspect ratio set are the two best models overall with similar  $R^2$  values (Table 2). Both models contained, in addition to the flight efficiency parameter, population and habitat (Table 2). Most habitat categories were significantly different from the reference level (coast) in these best models (Tables S3, S4). To test the variables overall significance in the model I conducted a likelihood ratio test between models that include or remove habitat and found for both top models, habitat was a significant variable (lift-to-drag model,  $p\text{-value} = 0.011$ ; aspect ratio model,  $p\text{-value} = 0.010$ ). The residual phylogenetic inertia was  $\lambda = 0.51$  and  $0.16$  for these two models, respectively. However, there is much model uncertainty: many models fall within 5 AIC units from these two models and model likelihoods decreased gradually.

Variable importance indicated that aspect ratio, lift-to-drag ratio, and population were highly important (Figure 2). In the aspect ratio model set, aspect ratio and population size had high variable importance (0.98 and 0.91) (Figure 2A). In contrast, although appearing in the best model, habitat had lower importance in this set (0.71) (Figure 2A). In the lift-to-drag ratio model set, lift-to-drag ratio, habitat, and population size had high variable importance (0.98, 0.90 and 0.88) (Figure 2B). In the hand-wing index model set, only population and habitat had high importance (1.00 and 0.93), hand-wing index itself had low importance (0.43) (Figure 2C). Remaining predictors attained low importance across model sets. Variable importance was also calculated for model sets generated with no second-order effects to ensure equal representation of all variables within the models. Variable importance calculated this way were similar to the variable importance from the main models: flight efficiency and population had high variable importance while habitat had reduced importance in the aspect ratio model set excluding interactions (0.98, 0.91, 0.65, Figure S1A). Similarly in lift-to-drag model set excluding interactions, flight efficiency, habitat, and population have high variable importance (0.96, 0.93, 0.90, Figure S1B). Likewise, the hand-wing index model set excluding interactions resembles the main model set: only population and habitat have high variable importance (1.00, 0.94, Figure S1C).

Most model-averaged estimates have wide confidence intervals that include zero (Tables S5, S6, S7). Habitat categories in the lift-to-drag ratio and hand-wing index model set have estimates with narrower confidence intervals that exclude zero (Tables S6, S7).



A pairs plot show that there are no bivariate colinear relationships between independent variables except for between the wing morphologies, which are never included in the same model at the same time (Figure S2). Generalized variance inflation factors (GVIF) suggest that there is moderate multicollinearity among the variables. Hand-wing index shows moderate multicollinearity,  $(GVIF^{1/(2*DF)})^2 = 3.82$  (Table S8), aspect ratio shows moderate collinearity,  $(GVIF^{1/(2*DF)})^2 = 4.89$  (Table S9), and lift-to-drag ratio shows high collinearity,  $(GVIF^{1/(2*DF)})^2 = 7.62$  (Table S10). In addition, population sizes, habitat and foraging behaviour show moderate multicollinearity  $(GVIF^{1/(2*DF)})^2 > 2$  (Tables S8, S9, S10). Diet, mass, and migratory behaviour show little multicollinearity,  $(GVIF^{1/(2*DF)})^2 < 2$  (Tables S8, S9, S10).

## Discussion

My results suggest that flight efficiency, population size, and habitat may influence natal dispersal distance in North American birds. The most parsimonious models for natal dispersal distance included flight efficiency, as approximated by either aspect ratio or lift-to-drag ratio, population size and habitat (Figure 3). These factors consistently appear in the best models and had high variable importance. On the other hand, model-averaged parameter estimates had wide confidence intervals and only some habitat categories had confidence intervals that excluded zero (Tables, S6, S7). Confidence intervals overlapping zero do not support a role of flight efficiency and population size in determining natal dispersal distance. However, this uncertainty could be explained by moderate levels of multicollinearity present in key parameters, which increase variance in parameter estimates and widen confidence intervals. More generally, correlations among parameters make it difficult to tease apart the individual effect of each

parameter. The multicollinearity in key parameters could suggest that natal dispersal distance is mediated by an aspect of a bird's ecology that is correlated strongly with the key parameters in my models. As flight efficiency, population size and habitat all capture information about the mobility of the species, in this discussion I explore the possibility that mobility is what determines how far a bird will disperse and explains the interconnections between the key variables.

I found that flight efficiency, as estimated by wing morphology, may be an important factor influencing natal dispersal distances among North American birds. Natal dispersal distance and flight efficiency are positively correlated, and this supports the idea that the energetic cost of transport is influential in determining dispersal distances within or between species (Bonte et al., 2012; Matthysen et al., 2012; Claramunt, 2021). Aerodynamically efficient flight morphologies confer the ability for species to fly farther and for longer, allowing larger dispersal distances. I also found that the more precise descriptors of flight efficiency, aspect ratio and lift-to-drag ratio, were better predictors of dispersal distances than a simpler descriptor, the hand-wing index. Flight efficiency parameters have moderate to high multicollinearity, particularly lift-to-drag ratio, with the other variables. This result is not entirely unexpected given the multitude of ecological functions wings serve. Wing morphology is associated with foraging behaviour, and thus by extension, to diet and habitat (Raynor, 1988, Norberg, 1990. Sherry, 2016). In agreement with these ideas, in the present analysis it is evident that flight efficiency and habitat are correlated to each other in addition to natal dispersal distance (Figure 3). Forest dwelling birds have invariably low flight efficiency, while coastal birds have high flight efficiency (Figure 3). Perhaps this relationship is maintained because both variables

contain information about how the species can navigate its environment, in other words its mobility, and therefore the relationship between flight efficiency and natal dispersal distance is explained by the effect of the overall species' mobility.

My results provide more evidence that flight efficiency, as estimated by wing morphology, is an important factor in determining natal dispersal distances in birds (Claramunt, 2021; O'Brien et al., in review). These finding supports the already prominent usage of wing morphology as a proxy for dispersal ability (Claramunt et al., 2012; Sheard et al. 2020; Tobias et al., 2020). I found that more precise estimates of flight efficiency, such as the aspect ratio and lift-to-drag ratio, result in more predictive power regarding dispersal distance. Importantly, while the hand-wing index is already providing insights on ecological and evolutionary patterns of dispersal (Sheard et al., 2020; O'Brien et al., in review), using aspect ratio and lift-to-drag ratio may be beneficial as they are better proxies for dispersal ability (see also Claramunt 2021). I also show that even rough estimates of aspect ratio and lift-to-drag ratio taken from species averages are highly predictive of dispersal distance. In the absence of good specimen data this may be crucial. However, this also highlights the need for good specimens and accurate estimates of key morphologies such as the wingspan and wing area.

I also found support for a negative relationship between population size and natal dispersal distance: species with larger populations exhibited shorter dispersal distances. This result reveals that this curious pattern is not unique to British birds and that it may be more general (Paradis, 1998, Claramunt, 2021). This finding goes against models that suggest competition and inbreeding avoidance would necessitate that large or dense populations exhibit

longer dispersal movements (Matthysen, 2005; Matthysen, 2012). However, although inbreeding avoidance predicts patterns of dispersal in organisms. The same dispersal patterns can be explained by other ecological factors, thus it is unclear how significant the effect of inbreeding avoidance is on dispersal (Moore & Ali, 1984; Perrin & Mazalov, 1999). It is important to consider the fact that my measure of population size is the continental breeding population. This broad scale measurement may hide spatial population patterns that would explain a negative relationship. For example, if population densities are uniform across space, or closely matched to resources, there is little benefit to be gained for a far dispersing individual as similar population densities and resource availability will be found no matter how far the individual travels. Thus, it may be possible that in this dataset some species with large populations have relatively short dispersal distance because of population density dynamics. Furthermore if population density is high, selection for dispersal may be weak because many individuals in close proximity limit the negative effects of kin competition and inbreeding (Kisdi, 2016). Additionally, birds inhabiting prime habitat that confer high fitness, may occur abundantly in the area, and may not need to disperse far as suitable habitat is located in close proximity to natal sites (Paradis et al., 1998). Finally, high densities may also incite territorial birds to settle sooner as prolonging habitat search risks suitable habitats being taken up by territorial competitors (Greenwood, 1980; Greenwood et al., 1978; Nilsson, 1989).

In addition, population sizes may be negatively related to dispersal distance because of an indirect effect of a relationship between dispersal distance, territory size and mobility (Bowman 2003, Claramunt 2021). The “vacant territory hypothesis” (Bowman, 2003), describes how occupied territories present unsuitable habitat for settlement to a dispersing individual and thus

larger territories may require an individual to disperse further to find unclaimed suitable habitat. Species that do not congregate and maintain large territories show low population densities and have to disperse longer distances. Another explanation refers to the “vagility hypothesis” (Bowman, 2003; Stephens et al., 2019). Some species, such as raptors, have long daily commutes as the resources they use occur sparsely through space. Other species commute far because foraging grounds are far from breeding/roosting grounds, which is the case for gulls (Sherry, 2016). In the same vein as with the “vacant territory hypothesis”, small population sizes can be a characteristic of a species that is highly vagile, for example raptors. These species have flight efficient morphologies to accommodate the mobility required for daily life (Raynor, 1988; Norberg, 1990). Both these hypotheses predict that the covariation between population size and dispersal distance is a result of the relationship among flight efficiency, mobility and home range (Claramunt, 2021).

The “vagility hypothesis” predicts that species that inhabit large open areas with scarce resources are adapted for a mobile life which in turn is reflected by their natal dispersal distances. In agreement, I found that habitat was an important predictor along with flight efficiency and population size. Although when considered along with all parameters it was not consistently important, when considered as a single predictor it was the best ecological variable and was a significant predictor in the best models (Tables S3, S4). Model-averaged estimates of habitat categories were also significant for lift-to-drag ratio and hand-wing index model sets. It is expected that as habitat openness increase, dispersal distances increase. Supporting this pattern, coasts and open habitats had the longest dispersal distances while woodlands had the shortest (Figure 1H). However, it is possible the relationship is driven mainly by the difference in

woodland species' dispersal distance in comparison to the other three habitat types, which seem relatively similar in dispersal distance. Nevertheless, this result is in agreement with the “vagility hypothesis”: habitats characterized by large unsuitable areas between habitable environments or scarcity in resources promote species to have mobile lives, which will be reflected in dispersal distances.

Foraging behaviour contains information about the foraging movements of species. When considered as a single predictor it was a significant predictor for dispersal distance but in multi-predictor models it had very low variable importance, suggesting its effect may be completely mediated by wing morphology (Figure 2). Foraging behaviours did not exhibit the expected pattern of increased dispersal distances with increased amount of flight required for foraging (Figure 1J). The category that required the least amount of flight on my foraging spectrum describes primarily surface foraging and showed unexpectedly high dispersal distances. I suspect this is because although some birds exhibit no flight proximate to prey capture, such as waterfowl and seabirds that float on the water and dive or dip-feed, they exhibit more mobility to reach these foraging grounds prior to prey capture, again suggesting that overall mobility is what is influencing natal dispersal distances. These results suggest that foraging behaviour alone cannot predict natal dispersal distance and is just one aspect of the overall mobility of a species, which may already be better captured by flight efficiency. A metric that considers the overall mobility exhibited by a species may be better in explaining dispersal distance.

In contrast to the idea that overall mobility influences dispersal distance, I found that migratory distance/behaviour is poor predictor of dispersal distance (Table 1). Past

investigations have pointed towards migratory behaviour as a key aspect in determining dispersal distance (Claramunt 2021; Dawideit et al., 2009; Paradis et al., 1998). Furthermore, both theory and empirical evidence suggest migratory behaviour/distance is affected by flight efficiency as estimated from wing morphology (Norberg, 1990; Minias et al., 2015; Nowakowski et al., 2014; Vágási et al., 2016). As I outlined above, the overall mobility exhibited by a bird may be influential to their dispersal distances, which would suggest migration would be a key determinant. Yet, I find that migration distance is not significantly correlated with natal dispersal distance, nor is it an influential parameter in multi-predictor models. To explain this apparent contradiction, I considered the fact that many birds migrate much further in a single season than they will ever disperse in their lifetime, thus birds are capable of flying much further than how far they disperse. Suggesting that dispersal distance is not predicated on migratory flight ability and that dispersal and migratory distances are dissociated (O'Brien et al. in review). In British birds, migration showed a complex interaction with dispersal distances (Claramunt, 2021). Among migrants, dispersal distances were not explained by flight efficiency, suggesting that for migrants, flight efficiency is dissociated from dispersal distances. However, this dissociation was driven by a few migrant species whose estimated dispersal distances were larger than what their flight morphology would predict. The remaining migrants exhibited a similar pattern between dispersal distance and flight efficiency to residents, thus in agreement with my analysis suggesting that migration is not important to natal dispersal distances. It is unclear if these species are outliers whose dispersal distance estimates were biased, or if these species are a true reflection of a different relationship between dispersal distance and flight efficiency among migrants. The latter explanation is possible as migrants possess characteristics that are absent in residents. Unique physiologies and philopatric tendencies are some characteristics that may

complicate the relationship between flight efficiency and dispersal distances within migrants (Winkler et al., 2016; Butler, 2016; Pennycuick, 2008). However, based on the present analysis, I agree with the idea that migration has little to no influence on natal dispersal distances. It is possible that philopatric tendencies remove the variation in settlement distance introduced by migration thus leaving the effects of other movements to determine natal dispersal distance. Once at the breeding grounds, dispersal distance reflects the overall flight efficiency and vagility of the species.

## **Conclusion**

I estimated natal dispersal distance for 103 species North American bird species (Table S1), 51 of which had a sample size of at least five, using an easily replicable method based on bird banding data. The estimates generated here should be comparable to the ones estimated by Paradis et al. (1998) or likewise with any generated from banding data. This is important as global comparative studies on the differences in dispersal distances are lacking. Here I use these data to show that dispersal distance may be predicted by flight efficiency, population and habitat. However, the relative effect of each was difficult to disentangle. There is theoretical basis, through the “vagility hypothesis”, that these parameters are inherently connected to a bird’s mobility which in turn determines dispersal movements. The interconnection between dispersal, mobility and these key parameters might explain why it is difficult to tease apart their relative effects. I suggest that the strong influence of flight efficiency, population and habitat on dispersal distance is explained by this relationship between the overall mobility exhibited by the species and its dispersal distance. For these reasons, I agree with Burgess et al. (2015) as my results suggest that dispersal is not necessarily an adaptive strategy but a by-product of mobility.



I highlight the importance of flight efficiency as a determinant of dispersal distance in volant birds and find support for the use of wing morphology as way to infer dispersal ability in birds. The effects of dispersal are far-reaching for phenomena in ecology and evolution. Flight efficiency presents a way to estimate dispersal ability. Using wing morphology as a proxy for dispersal ability will be key in assessing targets for conservation as climate and habitat use is expected to continually change (Dawideit et al., 2009; Lester et al., 2007; Martin & Fahrig, 2018; Parmesan & Yohe, 2003; Rosenberg et al., 2019; Tingley et al., 2009). Thus, further elucidating the relationship between dispersal flight efficiency and mobility, will provide a framework to answer many key questions in ecology and evolutionary biology, advancing our understanding of nature as whole (Bohonak, 1999; Gaston, 2003; Hanski, 1998).

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## Tables

Table 1.

Single-predictor PGLS models of the relationship between natal dispersal distance and indicated parameters. Flight efficiency parameters, population size, and mass were log-transformed.

Asterisks denote level of significance of a given coefficient; \* =  $p < 0.05$ , \*\* =  $p < 0.005$ , \*\*\* =  $p < 0.0005$ .  $\lambda$  estimates phylogenetic non-independence in residuals in a scale from 0 to 1,

Log(Lik) is the log-likelihood,  $\Delta AICc$  is the difference between the AICc of the best model and the given model,  $P_{model}$  is the model probability, and  $R^2$  is the coefficient of determination.

Model	Intercept	Coefficient	df	$\lambda$	Log(Lik)	AICc	$\Delta AICc$	$P_{model}$	$R^2$
aspect ratio	-1.25	2.36***	2	0.35	-68.6	141.4	0	0.71	0.23
lift-to-drag ratio	-2.23	2.01***	2	0.30	-69.6	143.4	1.96	0.27	0.21
habitat	4.24***	+**	4	0.41	-70.1	149.1	7.68	0.02	0.32
population	5.30***	-0.14*	2	0.39	-73.2	150.6	9.18	0.01	0.10
mass	1.73**	0.28**	2	0.35	-76.2	156.7	15.32	0	0.16
hand-wing index	-1.04	1.19*	2	0.45	-77.2	158.6	17.25	0	0.11
foraging behaviour	3.78***	+	5	0.45	-74.4	160.0	18.59	0	0.20
diet	3.84***	+	4	0.48	-77.4	163.5	22.15	0	0.11
migration behaviour	3.47***	+	2	0.51	-79.7	163.7	22.28	0	0.03

Table 2.

Multi-predictor PGLS models describing relationship between flight efficiency, ecological and behavioural variables with natal dispersal distance. Three model sets are listed each differ in which flight efficiency variable was used. Only models within the 95% confidence model set are shown. \* indicate interaction terms and main effects. Log(Lik) is the log-likelihood,  $\Delta\text{AICc}$  is the difference between the AICc of the best model, listed at the top, and the given model,  $P_{\text{model}}$  is the model probability, and  $R^2$  is the coefficient of determination.

Model	df	Log(Lik)	AICc	$\Delta\text{AICc}$	$P_{\text{model}}$	$R^2$
aspect ratio + population + habitat	6	-52.4	118.8	0.00	0.18	0.45
aspect ratio + population + mass	4	-55.7	120.2	1.42	0.09	0.44
aspect ratio + population + habitat + mass	7	-51.9	120.5	1.70	0.08	0.47
aspect ratio * population + habitat	7	-52.0	120.6	1.84	0.07	0.46
aspect ratio * population + mass	5	-54.8	120.9	2.12	0.06	0.47
aspect ratio + population + habitat + migration	7	-52.4	121.5	2.70	0.05	0.45
aspect ratio * migration + population + mass	6	-54.0	122.0	3.16	0.04	0.49
aspect ratio * migration + population + habitat	8	-51.3	122.2	3.39	0.03	0.47
aspect ratio * population + habitat + mass	8	-51.4	122.2	3.44	0.03	0.49
aspect ratio + population + migration + mass	5	-55.6	122.5	3.72	0.03	0.44
aspect ratio + population	3	-58.1	122.8	3.97	0.02	0.35
aspect ratio * population	4	-57.1	123.2	4.38	0.02	0.38
aspect ratio + population * migration + habitat	8	-51.9	123.3	4.47	0.02	0.46
aspect ratio + population + habitat + mass + migration	8	-51.9	123.3	4.49	0.02	0.47
aspect ratio * population + mass + migration	6	-54.7	123.4	4.63	0.02	0.47
aspect ratio * population + habitat + migration	8	-52.0	123.5	4.68	0.02	0.46
aspect ratio + population * migration + mass	6	-55.0	123.9	5.11	0.01	0.45
aspect ratio + habitat	5	-56.4	124.1	5.34	0.01	0.39
aspect ratio * migration + population	5	-56.5	124.4	5.62	0.01	0.40
aspect ratio + population + mass + diet	7	-53.9	124.4	5.64	0.01	0.50
aspect ratio * population + diet + mass	8	-52.6	124.7	5.89	0.01	0.55

aspect ratio + population + migration	4	-58.0	124.9	6.14	0.01	0.36
aspect ratio + habitat + mass	6	-55.6	125.1	6.35	0.01	0.41
aspect ratio + population + foraging behaviour	7	-54.3	125.3	6.51	0.01	0.43
aspect ratio * population + migration	5	-57.1	125.6	6.77	0.01	0.39
aspect ratio + mass	3	-59.6	125.6	6.84	0.01	0.37
aspect ratio + population + habitat + diet	9	-51.6	125.7	6.87	0.01	0.47
population + habitat	5	-57.2	125.8	6.97	0.01	0.39
aspect ratio + population + diet	6	-55.9	125.8	7.04	0.01	0.41
aspect ratio + population + habitat	10	-50.2	125.9	7.15	0.01	0.50
aspect ratio + population + diet + foraging behaviour	10	-50.2	126.0	7.17	0.01	0.59
aspect ratio + habitat + foraging behaviour	9	-51.9	126.1	7.31	0.00	0.49
aspect ratio * population + diet + foraging behaviour	11	-48.6	126.1	7.33	0.00	0.62
population + habitat + mass	6	-56.2	126.3	7.51	0.00	0.42
aspect ratio * (population + migration)	6	-56.2	126.3	7.52	0.00	0.41
aspect ratio * population + diet	7	-54.8	126.4	7.57	0.00	0.47
aspect ratio * population + mass	8	-53.6	126.6	7.84	0.00	0.46
aspect ratio * migration + mass	5	-57.6	126.6	7.84	0.00	0.42
aspect ratio + habitat + migration	6	-56.4	126.7	7.91	0.00	0.39
aspect ratio + population * migration	5	-57.7	126.7	7.96	0.00	0.36
aspect ratio * migration + habitat	7	-55.1	126.9	8.09	0.00	0.41
aspect ratio * population + foraging behaviour	8	-53.7	126.9	8.10	0.00	0.45
aspect ratio * migration * population	6	-56.5	127.0	8.16	0.00	0.40
aspect ratio + population + migration + mass + diet	8	-53.8	127.1	8.34	0.00	0.51
aspect ratio + diet + foraging behaviour	9	-52.6	127.6	8.78	0.00	0.57
aspect ratio + foraging behaviour	6	-56.9	127.7	8.87	0.00	0.39
aspect ratio * population + habitat + diet	10	-51.0	127.7	8.87	0.00	0.49

lift-to-drag ratio + population + habitat	6	-52.6	119.1	0.00	0.30	0.44
lift-to-drag ratio * population + habitat	7	-52.0	120.7	1.55	0.14	0.45
lift-to-drag ratio + population + habitat + mass	7	-52.3	121.2	2.07	0.11	0.45
lift-to-drag ratio + population + habitat + migration	7	-52.6	121.8	2.63	0.08	0.44
lift-to-drag ratio * population + habitat + mass	8	-51.7	122.9	3.76	0.05	0.46
lift-to-drag ratio * population + habitat + migration	8	-52.0	123.5	4.35	0.03	0.46
lift-to-drag ratio + population * migration + habitat	8	-52.0	123.6	4.41	0.03	0.45
lift-to-drag ratio + population + habitat + mass + migration	8	-52.2	123.8	4.69	0.03	0.46

lift-to-drag ratio + habitat	5	-56.4	124.2	5.07	0.02	0.38
lift-to-drag ratio * migration + population + habitat	8	-52.4	124.3	5.17	0.02	0.44
lift-to-drag ratio + habitat + mass	6	-55.8	125.5	6.38	0.01	0.40
lift-to-drag ratio + population + habitat + diet	9	-51.6	125.7	6.59	0.01	0.47
population + habitat	5	-57.2	125.8	6.62	0.01	0.39
population + habitat + mass	6	-56.2	126.3	7.16	0.01	0.42
lift-to-drag ratio + population + mass	4	-58.8	126.4	7.26	0.01	0.43
lift-to-drag ratio + habitat + foraging behaviour	9	-52.2	126.7	7.57	0.01	0.49
lift-to-drag ratio + migration + habitat	6	-56.4	126.8	7.63	0.01	0.38
lift-to-drag ratio * population + mass	5	-57.7	126.9	7.72	0.01	0.45
lift-to-drag ratio + population + habitat + foraging behaviour	10	-50.7	127.0	7.88	0.01	0.50
lift-to-drag ratio + population	3	-60.3	127.1	7.95	0.01	0.30
lift-to-drag ratio * population + habitat + diet	10	-50.9	127.3	8.20	0.01	0.48
lift-to-drag ratio * population	4	-59.2	127.4	8.21	0.01	0.34
lift-to-drag ratio + population + foraging behaviour	7	-55.5	127.7	8.57	0.00	0.44
lift-to-drag ratio + population + migration + mass	5	-58.2	127.7	8.61	0.00	0.44
lift-to-drag ratio + migration + habitat + mass	7	-55.7	128.1	8.95	0.00	0.41
population + habitat + migration	6	-57.1	128.1	8.96	0.00	0.39
lift-to-drag ratio * population + foraging behaviour	8	-54.4	128.4	9.26	0.00	0.52
lift-to-drag ratio * population + migration + mass	6	-57.3	128.5	9.40	0.00	0.46
lift-to-drag ratio + foraging behaviour	6	-57.3	128.5	9.41	0.00	0.41
lift-to-drag ratio + population + migration + habitat + diet	10	-51.5	128.6	9.49	0.00	0.47
lift-to-drag ratio + population + migration	4	-59.9	128.7	9.56	0.00	0.32
lift-to-drag ratio + population + mass	10	-51.5	128.7	9.59	0.00	0.47
population + migration + mass	7	-56.1	128.7	9.61	0.00	0.43

population + habitat	5	-57.2	125.8	0.00	0.21	0.39
population + habitat + mass	6	-56.2	126.3	0.54	0.16	0.42
hand-wing index * population + habitat	7	-55.4	127.4	1.60	0.10	0.43
hand-wing index + population + habitat	6	-57.1	128.1	2.34	0.07	0.39
population + habitat + migration	6	-57.1	128.1	2.34	0.07	0.39
hand-wing index + population + habitat + mass	7	-55.8	128.2	2.41	0.06	0.43
hand-wing index * population + habitat + mass	8	-54.5	128.3	2.49	0.06	0.46
population + habitat + mass + migration	7	-56.1	128.7	2.99	0.05	0.43
hand-wing index * population + habitat + migration	8	-55.3	130.0	4.23	0.03	0.44

population * migration + habitat	7	-56.8	130.2	4.45	0.02	0.40
population * migration + habitat + mass	8	-55.5	130.4	4.62	0.02	0.44
hand-wing index + population + mass	4	-60.8	130.4	4.67	0.02	0.35
hand-wing index + population + habitat + migration	7	-57.1	130.7	4.92	0.02	0.39
hand-wing index + population + habitat + mass + migration	8	-55.8	131.0	5.19	0.02	0.43
hand-wing index * population + mass	5	-60.4	132.0	6.25	0.01	0.43
population + habitat + diet	8	-56.4	132.1	6.31	0.01	0.41
hand-wing index + population + mass + migration	5	-60.7	132.7	6.92	0.01	0.36
hand-wing index + population * migration + habitat	8	-56.8	133.0	7.22	0.01	0.40
hand-wing index * migration + population + habitat	8	-56.9	133.2	7.45	0.01	0.40
population + mass + migration	4	-62.2	133.2	7.47	0.01	0.39
population + mass	3	-63.4	133.3	7.53	0.00	0.36
population + habitat + foraging behaviour	9	-55.6	133.6	7.82	0.00	0.43

## Figures

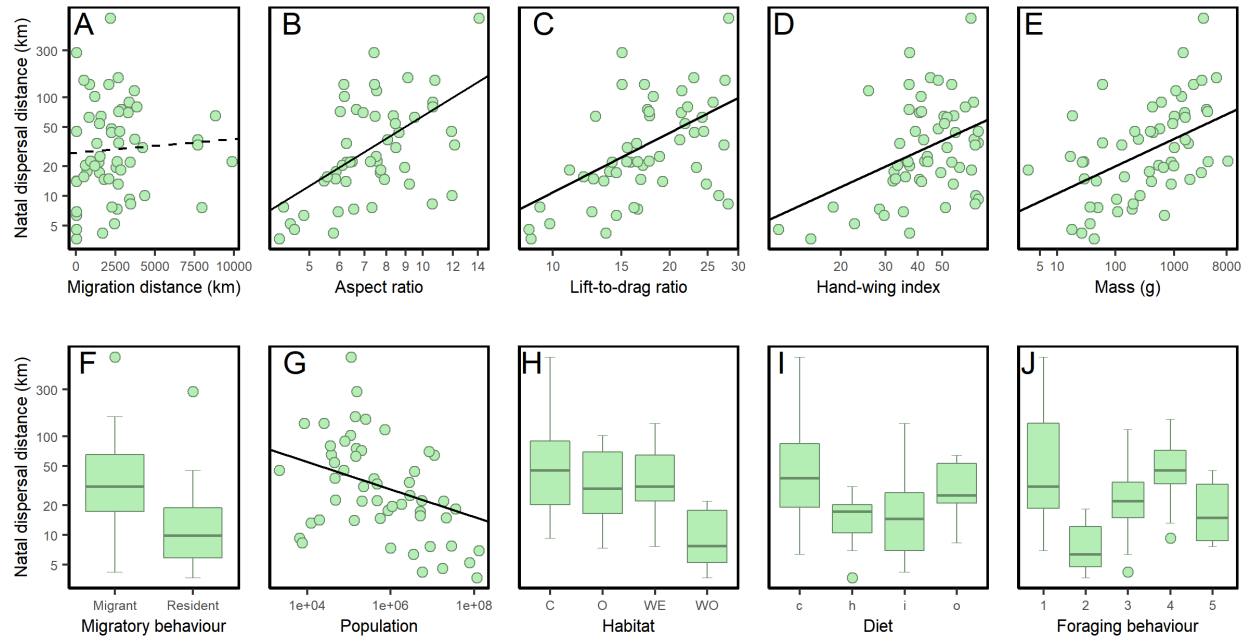


Figure 1.

Single predictor models of natal dispersal distance in 50 North American bird species. X-axes of panels B, C, D, E, G are in logarithmic scale in addition to the shared Y-axes. Lines corresponded to phylogenetic generalized least-squares models. Solid lines are models whose slopes were significantly different than 0. Habitat categories in H correspond as follows: coasts (C), open or uplands (O), wetlands (WE), and woodlands (WO). Diet categories in I correspond as follows: carnivores (c), herbivores (h), insectivores (i), and omnivores (o). Foraging behaviour categories are ranked in increasing flight requirements and are described in depth in Methods, in brief: surface foraging (1), tree foraging (2), sallying (3), aerial search (4), and aerial capture (5).



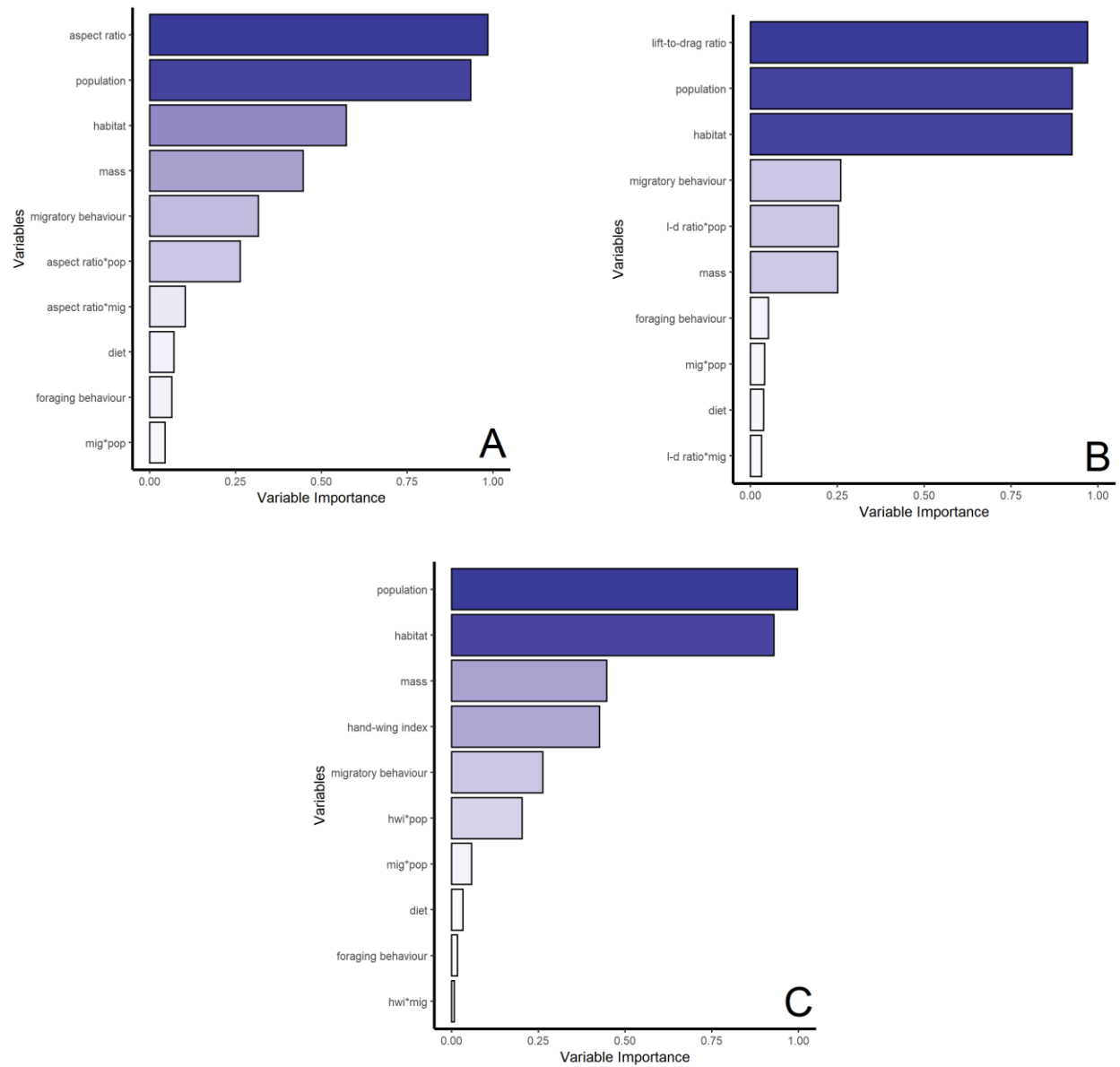


Figure 2.

Variable importance for three multi-predictor PGLS model sets explaining natal dispersal distance. Each model set differs in which wing morphology parameter it includes as a proxy for flight efficiency. Panel A refers to variable importance in the model set constructed using aspect ratio. Panel B refers to variable importance in the model set constructed using lift-to-drag ratio. Panel C refers to variable importance in the model set constructed using hand-wing index.

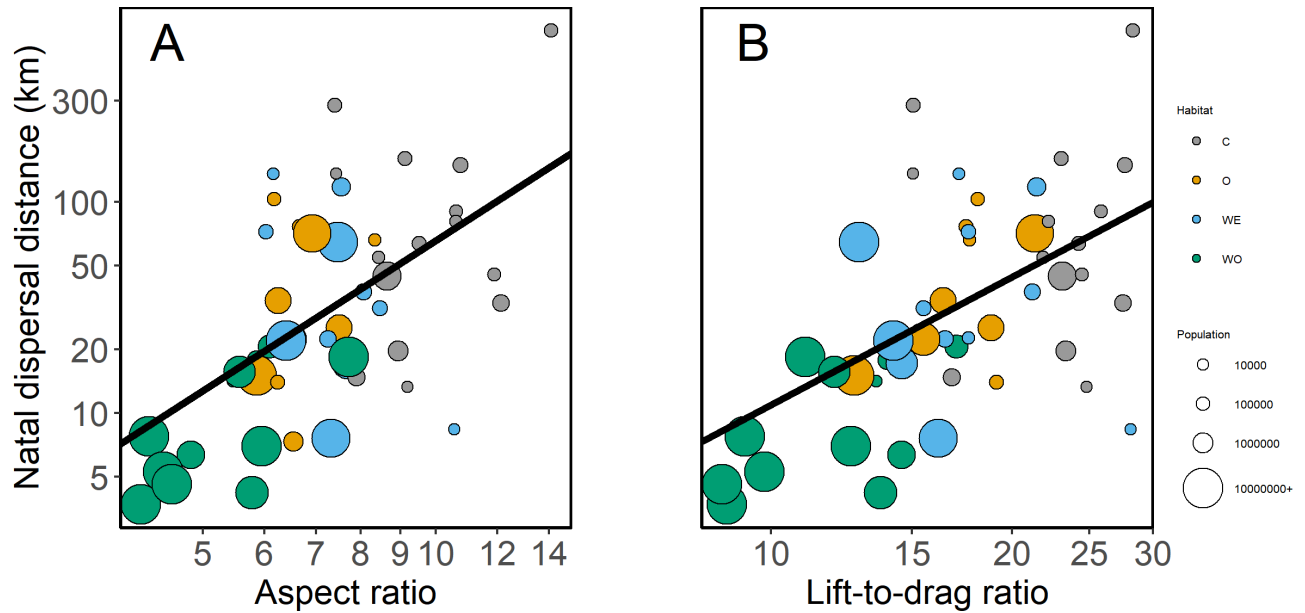


Figure 3.

Relationship between the three variables—flight efficiency, population size, and habitat— included in the best two overall models that explain natal dispersal distance. Panel A uses aspect ratio as the flight efficiency parameter. Panel B uses lift-to-drag ratio as the flight efficiency parameter. The size of the points is proportional to population size up to 100,000,000 individuals (species with greater populations are depicted with the same sized point). Colour of points refer to habitat categories; coasts (C) are gray, open and upland habitats (O) are yellow, wetlands (WE) are blue, and woodlands (WO) are green. Line represents single predictor model between each panel's flight efficiency variable and natal dispersal distance ( $\beta = 2.36$ ,  $p < 0.0005$ ;  $\beta = 2.01$ ,  $p < 0.0005$ ).

## Appendix 1 – Supplementary Figures

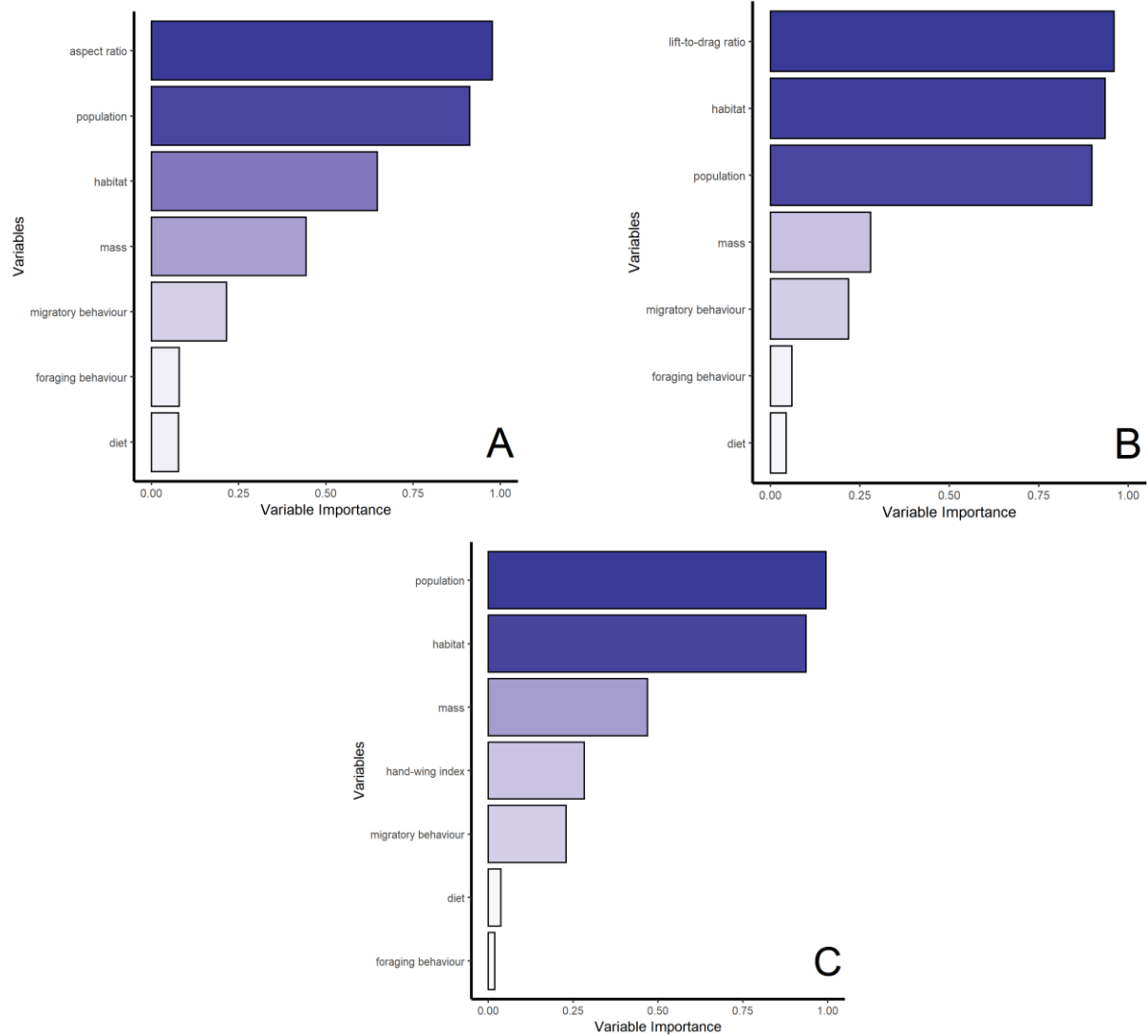


Figure S1.

Variable importance for three multi-predictor PGLS model sets explaining natal dispersal distance without second-order effects. Each model set differs in the flight efficiency proxy. Panel A refers to variable importance in the model set constructed using aspect ratio. Panel B refers to variable importance in the model set constructed using lift-to-drag ratio. Panel C refers to variable importance in the model set constructed using hand-wing index.



Figure S2.

Pairs plot of variables included into dispersal distance models. Three variables are categorical, diet, foraging (foraging behaviour), and habitat. The rest are continuous, dispersal (natal dispersal distance), AR (aspect ratio), HWI (hand-wing index), LD (lift-to-drag ratio), mass, mig distance (migratory distance) or binary, mig behaviour (migratory behaviour). All pairs of variables are plotted as scatterplots, both above and below the diagonal. Positive associations can be seen between wing morphology variables.

## Appendix 2 – Supplementary Tables

Table S1.

Natal dispersal distances estimated from North American bird banding data. n is the sample size, the number of records that satisfied filtering procedures.

Common name	Scientific name	Geometric mean natal dispersal distance (km)	n
Canada Goose	<i>Branta canadensis</i>	17.30	940
Purple Martin	<i>Progne subis</i>	7.63	690
Turkey Vulture	<i>Cathartes aura</i>	70.59	435
Peregrine Falcon	<i>Falco peregrinus</i>	65.67	424
Roseate Tern	<i>Sterna dougallii</i>	9.29	377
Osprey	<i>Pandion haliaetus</i>	37.54	154
Caspian Tern	<i>Hydroprogne caspia</i>	90.05	130
Brown Pelican	<i>Pelecanus occidentalis</i>	149.54	128
Royal Tern	<i>Thalasseus maximus</i>	80.45	124
Double-crested Cormorant	<i>Phalacrocorax auritus</i>	14.80	120
Bald Eagle	<i>Haliaeetus leucocephalus</i>	72.14	109
Trumpeter Swan	<i>Cygnus buccinator</i>	22.64	106
American White Pelican	<i>Pelecanus erythrorhynchos</i>	160.21	92
Tree Swallow	<i>Tachycineta bicolor</i>	22.06	84
American Kestrel	<i>Falco sparverius</i>	25.45	77
Barn Owl	<i>Tyto alba</i>	14.07	75
Mourning Dove	<i>Zenaida macroura</i>	6.97	73

Black-footed Albatross	<i>Phoebastria nigripes</i>	644.17	68
Common Tern	<i>Sterna hirundo</i>	33.07	62
Sandwich Tern	<i>Thalasseus sandvicensis</i>	45.40	59
Herring Gull	<i>Larus argentatus</i>	13.27	50
Mallard	<i>Anas platyrhynchos</i>	64.38	46
Least Tern	<i>Sternula antillarum</i>	34.60	43
Eastern Bluebird	<i>Sialia sialis</i>	15.04	36
Wood Stork	<i>Mycteria americana</i>	136.08	25
American Oystercatcher	<i>Haematopus palliatus</i>	19.79	25
Mountain Bluebird	<i>Sialia currucoides</i>	22.44	22
Piping Plover	<i>Charadrius melodus</i>	136.00	21
Red-tailed Hawk	<i>Buteo jamaicensis</i>	34.22	20
Black Skimmer	<i>Rynchops niger</i>	10.17	18
Snail Kite	<i>Rostrhamus sociabilis</i>	45.54	18
Western Gull	<i>Larus occidentalis</i>	54.53	17
Brandt's Cormorant	<i>Phalacrocorax penicillatus</i>	285.52	15
Cooper's Hawk	<i>Accipiter cooperii</i>	17.81	15
Golden Eagle	<i>Aquila chrysaetos</i>	76.30	14
Burrowing Owl	<i>Athene cunicularia</i>	7.36	14
Great Egret	<i>Ardea alba</i>	117.36	13
Great Black-backed Gull	<i>Larus marinus</i>	63.44	12
Ring-billed Gull	<i>Larus delawarensis</i>	44.50	12
Red-cockaded Woodpecker	<i>Dryobates borealis</i>	14.21	12
California Gull	<i>Larus californicus</i>	19.64	10
Sandhill Crane	<i>Antigone canadensis</i>	22.43	10
Gull-billed Tern	<i>Gelochelidon nilotica</i>	8.37	8
Ferruginous Hawk	<i>Buteo regalis</i>	102.94	8
Western Bluebird	<i>Sialia mexicana</i>	4.21	8
Elegant Tern	<i>Thalasseus elegans</i>	37.70	7
Brant	<i>Branta bernicla</i>	31.34	7

Reddish Egret	<i>Egretta rufescens</i>	20.35	7
Northern Goshawk	<i>Accipiter gentilis</i>	22.03	7
Red-shouldered Hawk	<i>Buteo lineatus</i>	20.62	5
Barred Owl	<i>Strix varia</i>	6.35	5
Wood Duck	<i>Aix sponsa</i>	4.38	4
Spectacled Eider	<i>Somateria fischeri</i>	9.23	4
Snowy Plover	<i>Charadrius nivosus</i>	37.10	4
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	9.32	4
Common Loon	<i>Gavia immer</i>	10.43	3
Glossy Ibis	<i>Plegadis falcinellus</i>	203.36	3
Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>	6.29	3
American Woodcock	<i>Scolopax minor</i>	260.21	3
Snowy Owl	<i>Bubo scandiacus</i>	3.55	3
Barn Swallow	<i>Hirundo rustica</i>	16.96	3
Razorbill	<i>Alca torda</i>	477.46	2
Arctic Tern	<i>Sterna paradisaea</i>	44.51	2
Snow Goose	<i>Anser caerulescens</i>	511.42	2
Snowy Egret	<i>Egretta thula</i>	42.63	2
Swainson's Hawk	<i>Buteo swainsoni</i>	14.74	2
Prairie Falcon	<i>Falco mexicanus</i>	114.56	2
Merlin	<i>Falco columbarius</i>	10.37	2
Great Horned Owl	<i>Bubo virginianus</i>	10.25	2
Common Raven	<i>Corvus corax</i>	3.37	2
European Starling	<i>Sturnus vulgaris</i>	17.14	2
House Sparrow	<i>Passer domesticus</i>	2.78	2
Pigeon Guillemot	<i>Cepphus columba</i>	41.47	1
Common Murre	<i>Uria aalge</i>	19.11	1
Thick-billed Murre	<i>Uria lomvia</i>	1500.85	1
Black-legged Kittiwake	<i>Rissa tridactyla</i>	25.24	1
Laughing Gull	<i>Leucophaeus atricilla</i>	14.04	1

Forster's Tern	<i>Sterna forsteri</i>	552.67	1
Black Tern	<i>Chlidonias niger</i>	68.51	1
Fork-tailed Storm-Petrel	<i>Oceanodroma furcata</i>	5.64	1
Red-tailed Tropicbird	<i>Phaethon rubricauda</i>	1499.73	1
Brown Booby	<i>Sula leucogaster</i>	108.52	1
Northern Gannet	<i>Morus bassanus</i>	2715.28	1
Common Merganser	<i>Mergus merganser</i>	0.67	1
Mottled Duck	<i>Anas fulvigula</i>	57.86	1
Northern Pintail	<i>Anas acuta</i>	2.54	1
Lesser Scaup	<i>Aythya affinis</i>	0.70	1
Common Goldeneye	<i>Bucephala clangula</i>	1.17	1
King Eider	<i>Somateria spectabilis</i>	1.32	1
White-winged Scoter	<i>Melanitta deglandi</i>	10.81	1
Emperor Goose	<i>Anser canagicus</i>	810.11	1
White-faced Ibis	<i>Plegadis chihi</i>	789.34	1
American Avocet	<i>Recurvirostra americana</i>	353.97	1
Hudsonian Godwit	<i>Limosa haemastica</i>	21.42	1
Whimbrel	<i>Numenius phaeopus</i>	6.91	1
Wilson's Plover	<i>Charadrius wilsonia</i>	2.40	1
Black Oystercatcher	<i>Haematopus bachmani</i>	22.60	1
American Crow	<i>Corvus brachyrhynchos</i>	51.76	1
Black-capped Vireo	<i>Vireo atricapilla</i>	4.54	1
Cactus Wren	<i>Campylorhynchus brunneicapillus</i>	0.46	1
House Wren	<i>Troglodytes aedon</i>	147.43	1
Brown-headed Nuthatch	<i>Sitta pusilla</i>	3.53	1
Black-capped Chickadee	<i>Poecile atricapillus</i>	3.00	1



Table S2.

Parameter estimates for the 57 North American bird species with natal dispersal estimates. AR is aspect ratio, HWI is hand wing index, LD is lift-to-drag ratio.

Scientific name	Dispersal distance (km)	AR	HWI	LD	Mass	Diet	Foraging behaviour	Habitat	Population	Migratory behaviour	Migratory distance
<i>Accipiter cooperii</i>	17.81	5.87	32.26	13.97	373.10	c	3	WO	844899	Migrant	675.65
<i>Accipiter gentilis</i>	22.03	6.26	36.49	15.84	888.17	c	3	WO	205103	Migrant	1438.65
<i>Anas platyrhynchos</i>	64.38	7.46	50.78	12.88	1012.90	o	1	WE	11000000	Migrant	1567.15
<i>Aquila chrysaetos</i>	76.30	6.66	36.97	17.51	3629.16	c	4	O	146673	Migrant	2869.04
<i>Athene cunicularia</i>	7.36	6.54	28.33	16.51	189.18	c	3	O	987921	Migrant	2575.75
<i>Branta bernicla</i>	31.34	8.46	52.20	15.50	1008.61	h	1	WE	220000	Migrant	4207.51
<i>Branta canadensis</i>	17.30	7.69	49.37	14.54	2916.93	h	1	WE	5100000	Migrant	1481.86
<i>Buteo jamaicensis</i>	34.22	6.26	34.08	16.40	1738.97	c	3	O	2808115	Migrant	1299.47
<i>Buteo lineatus</i>	20.62	6.10	33.43	17.04	539.93	c	3	WO	1827010	Migrant	562.62
<i>Buteo regalis</i>	102.94	6.18	41.31	18.13	1332.46	c	3	O	109004	Migrant	1159.76
<i>Casmerodius albus</i>	117.36	7.54	25.70	21.45	1079.09	c	3	WE	712641	Migrant	3687.19
<i>Cathartes aura</i>	70.59	6.93	40.70	21.37	1520.55	c	4	O	8418387	Migrant	3272.85
<i>Charadrius melodus</i>	136.00	7.44	54.46	15.03	59.38	i	1	C	8400	Migrant	2077.75
<i>Cygnus buccinator</i>	22.64	7.54	42.69	17.64	8419.72	h	1	WE	47000	Migrant	905.56
<i>Egretta rufescens</i>	20.35	NA	37.19	NA	983.93	c	1	C	NA	Migrant	1183.20
<i>Falco peregrinus</i>	65.67	8.34	55.42	17.69	17.94	c	3	O	37000	Migrant	8831.71
<i>Falco sparverius</i>	25.45	7.50	43.68	18.81	16.55	o	3	O	2827776	Migrant	1485.96
<i>Grus canadensis</i>	22.43	7.25	43.74	16.50	3862.22	o	1	WE	469538	Migrant	9874.74
<i>Haematopus palliatus</i>	48.05	NA	48.05	NA	564.15	i	1	C	NA	Migrant	2221.20
<i>Haliaeetus leucocephalus</i>	72.14	6.04	41.38	17.64	3771.80	c	4	WE	200000	Migrant	2686.38
<i>Larus argentatus</i>	13.27	9.19	55.26	24.80	889.92	c	4	C	12000	Migrant	2656.38

<i>Larus californicus</i>	19.64	8.94	58.42	23.35	657.31	o	4	C	1065791	Migrant	2515.21
<i>Larus delawarensis</i>	44.50	8.64	56.25	23.10	437.89	o	4	C	3740458	Migrant	2232.08
<i>Larus marinus</i>	63.44	9.50	52.20	24.21	1565.58	o	4	C	145361	Migrant	819.05
<i>Larus occidentalis</i>	54.53	8.44	50.99	21.87	951.53	c	4	C	44003	Migrant	1465.75
<i>Mycteria americana</i>	136.08	6.17	37.02	17.16	2173.57	c	1	WE	25000	Migrant	846.51
<i>Pandion haliaetus</i>	37.54	8.06	42.16	21.20	1557.48	c	5	WE	399228	Migrant	7720.55
<i>Pelecanus erythrorhynchos</i>	160.21	9.11	44.90	23.02	5328.60	c	1	C	140000	Migrant	2651.51
<i>Pelecanus occidentalis</i>	149.54	10.75	48.10	27.65	2998.54	c	4	C	250000	Migrant	466.41
<i>Phalacrocorax auritus</i>	14.80	7.89	40.73	16.82	1868.33	c	1	C	557887	Migrant	1776.28
<i>Phalacrocorax penicillatus</i>	285.52	7.40	37.16	15.04	1432.75	c	1	C	151200	Resident	1.00
<i>Phoebeastria nigripes</i>	644.17	14.10	64.68	28.32	3190.54	c	1	C	110000	Migrant	2176.28
<i>Picoides borealis</i>	14.21	5.46	32.08	13.52	46.71	i	2	WO	19000	Resident	1.00
<i>Progne subis</i>	7.63	7.32	51.29	16.17	49.11	i	5	WE	8728591	Migrant	7980.92
<i>Rostrhamus sociabilis</i>	45.54	NA	39.07	NA	393.66	i	5	WE	2100	Resident	1.00
<i>Rynchops niger</i>	10.17	11.94	67.42	26.68	258.57	c	5	C	NA	Migrant	4345.37
<i>Sialia currucoides</i>	22.44	6.48	36.60	15.49	28.28	i	3	O	5568751	Migrant	2600.94
<i>Sialia mexicana</i>	4.21	5.78	37.24	13.68	25.85	i	3	WO	5661189	Migrant	1654.70
<i>Sialia sialis</i>	15.04	5.87	32.77	12.70	28.81	i	3	O	21439020	Migrant	2068.98
<i>Sterna antillarum</i>	34.60	NA	69.13	NA	59.37	c	4	C	NA	Migrant	2683.13
<i>Sterna caspia</i>	90.05	10.62	66.22	25.81	602.71	c	4	C	78325	Migrant	3340.05
<i>Sterna dougallii</i>	9.29	NA	69.12	NA	104.07	c	4	C	6400	Migrant	3371.83
<i>Sterna elegans</i>	37.70	NA	66.60	NA	242.07	c	4	C	45000	Migrant	3724.48
<i>Sterna hirundo</i>	33.07	12.15	67.26	27.54	126.06	c	4	C	468971	Migrant	7709.43
<i>Sterna maxima</i>	80.45	10.61	61.37	22.20	426.32	c	4	C	35206	Migrant	3839.26
<i>Sterna nilotica</i>	8.37	10.56	67.04	28.16	200.12	o	5	WE	7430	Migrant	3443.94
<i>Sterna sandvicensis</i>	45.40	11.89	69.23	24.42	213.12	c	4	C	75060	Migrant	2770.85
<i>Strix varia</i>	6.35	4.83	29.56	14.55	686.39	c	3	WO	3458782	Resident	1.00
<i>Tachycineta bicolor</i>	22.06	6.41	54.34	14.21	26.60	i	5	WE	18581775	Migrant	3429.38
<i>Tyto alba</i>	14.07	6.24	41.40	19.11	404.93	c	4	O	130751	Resident	1.00
<i>Zenaida macroura</i>	6.97	5.96	35.14	12.59	107.82	h	1	WO	1.33E+08	Resident	1.00

<i>Archilochus colubris</i>	18.43	7.72	65.01	11.02	3.15	h	2	WO	35777111	Migrant	2829.76
<i>Cardinalis cardinalis</i>	3.69	4.16	15.28	8.80	42.83	h	2	WO	1.18E+08	Resident	1.00
<i>Dumetella carolinensis</i>	7.78	4.26	18.65	9.27	36.15	i	2	WO	28700211	Migrant	2251.85
<i>Passerina cyanea</i>	5.28	4.44	22.62	9.81	36.16	i	2	WO	77494167	Migrant	2418.47
<i>Thryothorus ludovicianus</i>	4.61	4.56	11.40	8.68	17.53	i	2	WO	17733395	Resident	1.00
<i>Zenaida asiatica</i>	15.72	5.57	35.86	11.99	141.75	h	1	WO	5159586	Migrant	473.14

Table S3.

Coefficients for the best PGLS multi-predictor-model containing lift-to-drag ratio as the flight efficiency variable determined by model selection. Habitat category “coast” was set as the reference level for the habitat predictor.

	<b>β</b>	<b>Standard Error</b>	<b>t-value</b>	<b>p-value</b>
intercept	1.14	0.38	2.96	$4.9 \cdot 10^{-3}$
lift-to-drag ratio	-0.03	0.20	-0.13	0.90
population	-0.19	0.15	-1.29	0.21
habitat (open)	-1.01	0.42	-2.39	0.02
habitat (wetlands)	-1.03	0.36	-2.90	$5.8 \cdot 10^{-3}$
habitat (woodlands)	-1.97	0.48	-4.11	$1.7 \cdot 10^{-4}$

Table S4.

Coefficients for the best PGLS multi-predictor-model containing aspect ratio as the flight efficiency variable determined by model selection. Habitat category “coast” was set as the reference level for the habitat predictor.

	$\beta$	Standard Error	t-value	p-value
intercept	1.01	0.40	2.53	0.01
aspect ratio	0.12	0.20	0.59	0.56
population	-0.17	0.14	-1.24	0.22
habitat (open)	-0.85	0.45	-1.89	0.07
habitat (wetlands)	-0.92	0.38	-2.45	0.02
habitat (woodlands)	-1.72	0.51	-3.33	$1.7 \cdot 10^{-2}$

Table S5.

Model averaged estimates and 95% confidence interval bounds for variables in the aspect ratio model set.

<b>Variables</b>	<b>Estimate</b>	<b>Standard error</b>	<b>95% CI - Lower</b>	<b>95% CI - Upper</b>
intercept	0.63	0.53	-0.41	1.68
habitat (open)	-0.45	0.53	-1.50	0.59
habitat (wetland)	-0.50	0.53	-1.53	0.54
habitat (woodland)	-0.93	0.90	-2.70	0.85
population	-0.16	0.15	-0.46	0.14
aspect ratio	0.27	0.25	-0.22	0.77
mass	0.11	0.16	-0.20	0.42
aspect ratio:population	0.04	0.09	-0.14	0.22
migratory behaviour (resident)	0.05	0.31	-0.56	0.66
migratory behaviour (resident):aspect ratio	0.07	0.26	-0.44	0.59
migratory behaviour (resident):population	-0.01	0.08	-0.17	0.15
diet (herbivore)	-0.05	0.24	-0.51	0.41
diet (insectivore)	-0.02	0.14	-0.30	0.26
diet (omnivore)	-0.03	0.16	-0.34	0.27
foraging behaviour (tree foraging)	-0.03	0.19	-0.41	0.35
foraging behaviour (sallying)	-0.03	0.17	-0.37	0.31
foraging behaviour (aerial search)	-0.02	0.14	-0.30	0.26
foraging behaviour (aerial capture)	-0.08	0.33	-0.72	0.56

Table S6.

Model averaged estimates and 95% confidence interval bounds for variables in the lift-to-drag ratio model set.

<b>Variables</b>	<b>Estimate</b>	<b>Standard error</b>	<b>95% CI - Lower</b>	<b>95% CI - Upper</b>
intercept	1.06	0.44	0.21	1.92
habitat (open)	-0.97	0.43	-1.86	0.06
habitat (wetland)	-1.00	0.37	-1.79	-0.05
habitat (woodland)	-1.90	0.50	-3.12	-0.40
lift-to-drag ratio	-0.01	0.25	-0.48	0.47
population	-0.18	0.15	-0.46	0.13
lift-to-drag ratio:population	0.13	0.13	-0.13	0.20
mass	0.15	0.17	-0.17	0.24
migratory behaviour (resident)	-0.08	0.39	-0.42	0.38
migratory behaviour (resident):population	-0.26	0.28	-0.16	0.14
lift-to-drag ratio:migratory behaviour (resident)	0.18	0.38	-0.14	0.15
diet (herbivore)	-0.64	0.53	-0.33	0.28
diet (insectivore)	-0.45	0.45	-0.25	0.22
diet (omnivore)	-0.36	0.38	-0.21	0.18
foraging behaviour (tree foraging)	-0.34	0.64	-0.34	0.30
foraging behaviour (sallying)	-0.62	0.52	-0.38	0.32
foraging behaviour (aerial search)	-0.59	0.47	-0.36	0.30
foraging behaviour (aerial capture)	-1.39	0.57	-0.72	0.58

Table S7.

Model averaged estimates and 95% confidence interval bounds for variables in the hand-wing index model set.

<b>Variables</b>	<b>Estimate</b>	<b>Standard error</b>	<b>95% CI - Lower</b>	<b>95% CI – Upper</b>
intercept	0.92	0.44	0.06	1.78
habitat (open)	-0.77	0.47	-1.70	0.16
habitat (wetland)	-0.85	0.42	-1.68	-0.02
habitat (woodland)	-1.61	0.64	-2.86	-0.35
population	-0.11	0.14	-0.39	0.18
mass	0.11	0.16	-0.21	0.42
hand-wing index	0.01	0.15	-0.29	0.31
hand-wing index:population	0.04	0.10	-0.16	0.24
migratory behaviour (resident)	-0.03	0.18	-0.39	0.32
migratory behaviour (resident):population	-0.01	0.07	-0.15	0.13
diet (herbivore)	-0.02	0.12	-0.26	0.23
diet (insectivore)	-0.01	0.09	-0.19	0.17
diet (omnivore)	-0.01	0.08	-0.17	0.15
hand-wing index: migratory behaviour (resident)	0.00	0.03	-0.05	0.05
foraging behaviour (tree foraging)	0.00	0.09	-0.19	0.18
foraging behaviour (sallying)	0.00	0.07	-0.14	0.14
foraging behaviour (aerial search)	0.00	0.07	-0.13	0.12
foraging behaviour (aerial capture)	-0.01	0.13	-0.27	0.24



Table S8.

Generalized variance inflation factors (GVIF) for variables in the aspect ratio model set. Last column allows for comparison of GVIFs between categorical and continuous variables.

<b>Variables</b>	<b>df</b>	<b>GVIF</b>	<b><math>(GVIF^{1/(2*DF)})^2</math></b>
aspect ratio	1	4.89	4.89
population	1	1.96	1.96
habitat	3	19.04	2.67
foraging behaviour	4	17.01	2.03
mass	1	1.85	1.85
diet	3	4.80	1.69
migratory behaviour	1	1.62	1.62

Table S9.

Generalized variance inflation factors (GVIF) for variables in the lift-to-drag ratio model set. Last column allows for comparison of GVIFs between categorical and continuous variables.

<b>Variables</b>	<b>df</b>	<b>GVIF</b>	<b><math>(GVIF^{1/(2*DF)})^2</math></b>
lift-to-drag ratio	1	7.62	7.62
population	1	2.22	2.22
habitat	3	15.09	2.47
foraging behaviour	4	26.16	2.26
mass	1	1.93	1.93
diet	3	4.68	1.67
migratory behaviour	1	1.46	1.46

Table S10.

Generalized variance inflation factors (GVIF) for variables in the hand-wing index model set. Last column allows for comparison of GVIFs between categorical and continuous variables.

<b>Variables</b>	<b>df</b>	<b>GVIF</b>	<b><math>(GVIF^{1/(2*DF)})^2</math></b>
hand-wing index	1	3.82	3.82
population	1	2.14	2.14
habitat	3	13.64	2.39
foraging behaviour	4	23.27	2.20
mass	1	1.94	1.94
diet	3	4.47	1.65
migratory behaviour	1	1.83	1.83