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Flight efficiency explains differences in natal dispersal distances in birds

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Abstract. The factors responsible for variation in dispersal distances across species remain poorly understood. Previous comparative studies found differing results and equivocal support for theoretical predictions. Here I re-examine factors that influence natal dispersal distances in British birds while taking into account the cost of transport as estimated from proxies of long-distance flight efficiency. First, I show that flight efficiency, as estimated by the hand-wing index, the aspect ratio, or the lift-to-drag ratio, is a strong predictor of dispersal distances among resident species. Most migratory species showed a similar pattern, but a group of species with relatively low aerodynamic efficiency showed longer-than-expected dispersal distances, making the overall trend independent of flight efficiency. Ecological, behavioral, and life history factors had a small or nil influence on dispersal distances, with most of their influence likely mediated by adaptations for the use of space reflected in flight efficiency. This suggests that dispersal distances in birds are not determined by adaptive strategies for dispersal per se, but are predominantly influenced by the energetic cost of movement.

Key words: aerodynamic efficiency; birds; cost of transport; ecomorphology; flight performance; functional traits; migration; natal dispersal distance; species traits; wing shape.

Introduction

Dispersal is a fundamental process that plays key roles in ecology and evolution (Bohonak 1999, Gaston 2003, Clobert et al. 2004, Bowler and Benton 2005). It has multiple facets depending on the organisms and temporal, geographic, and taxonomic scales considered, and it can be divided into three stages—departure, movement, and settlement—with different characteristics and influential factors (Clobert et al. 2004, Bowler and Benton 2005, Matthysen 2012). Theory on dispersal has focused mostly on adaptive strategies regarding departure and settlement of individuals depending on factors such as competition, inbreeding avoidance, opportunities for reproduction, or for dealing with spatially and temporally heterogeneous resources (Bowler and Benton 2005, Clobert et al. 2009, Matthysen 2012). However, contrasting theory with empirical data has been difficult, and the causes of variation in dispersal tendencies across species remain poorly understood (Paradis et al. 1998, Ronce 2007, Matthysen 2012, Duputié and Massol 2013). This state of affairs has been attributed to the multicausality of dispersal and the difficulties in quantifying the relevant parameters (Ronce 2007, Matthysen 2012, Duputié and Massol 2013) Alternatively, the dispersal process may be largely independent from life-history traits (Bonte and Dahirel 2017) and instead may be a by-product of movement conducted for different purposes (Burgess et al. 2015).

Previous comparative studies have exposed the complexities of estimating, analyzing, and interpreting dispersal distances in birds. Early studies of dispersal movement focused on local populations are difficult to compare across species, as distance estimates depend on the particularities of the sampling design and detection efforts that typically underestimate dispersal distances (Koenig et al. 1996, Tittler et al. 2009). In a groundbreaking study, Paradis et al. (1998) succeeded in estimating dispersal distances for 75 bird species in a standardized way by using data from the bird-ringing program of the British Trust for Ornithology. After analyzing a wide array of potentially influential factors, they found that only population size, geographic range size, and migratory behavior were consistently associated with differences in dispersal distances. However, other analyses, some using the same dispersal estimates, found different influential factors, including body mass, relative wingspan, feeding guild (Garrard et al. 2012), wing shape, bill depth, tail graduation, migration (Dawideit et al. 2009), and body mass, but only for carnivorous birds (Sutherland et al. 2000). Together, these studies do not suggest a unifying set of factors that explain variation in dispersal distances across birds, and hardly provide support for particular theoretical models.

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One aspect that has received little attention is the influence of the energetic cost of movement on patterns of dispersal (Bonte et al. 2012). The efficiency of organisms for moving across the landscape should have a strong influence on dispersal and this prediction can be tested in a comparative framework: species with energetically costly locomotion should disperse with less frequency and/or over shorter distances; conversely, species with energetically efficient locomotion should disperse more frequently and/or over longer distances. Birds are ideal organisms in which to test this prediction. Because most birds disperse by flying, our basic knowledge about the aerodynamics of avian flight can be used to quantify the relative energetic efficiency of flight across species (Rayner 1988, Norberg 1990, Taylor and Thomas 2014). In particular, because long-distance flight efficiency depends critically on the morphology of the wings, it can be assessed using measurements of the flying apparatus (Pennycuick 2008, Claramunt and Wright 2017).

Here I conducted a comparative analysis in order to evaluate the potential role of flight efficiency in explaining patterns of dispersal distances in birds. I revisited the Paradis et al. (1998) data set of British birds' natal dispersal distances and evaluated the predictive power of the energetic cost of movement by using morphological proxies for aerodynamic flight efficiency. I also re-evaluated the potential effect of behavioral, ecological, and life history traits that are prominent in theoretical models and empirical studies of dispersal (Greenwood and Harvey 1982, Paradis et al. 1998, Sutherland et al. 2000, Clobert et al. 2004, Ronce 2007, Garrard et al. 2012, Matthysen 2012, Duputié and Massol 2013).

Methods

Dispersal data

I used estimates of natal dispersal distances for 75 species of British birds derived from nearly a century of banding and recovery data from the British Trust for Ornithology ringing scheme (Paradis et al. 1998). I focused on natal dispersal distances because they are usually greater than subsequent dispersal distances and potentially more consequential for ecological and evolutionary dynamics (Greenwood and Harvey 1982, Paradis et al. 1998). Natal dispersal distances were estimated as the geographic distance between the banding site of a nestling or fledgling and the recovery site of the bird found dead at breeding age, in breeding grounds, and during the species breeding season. The focus on dead birds helps alleviate the bias produced by observations and recaptures in research sites (Koenig et al. 1996). Although the recovery site is not guaranteed to be a breeding site, the method is not expected to introduce strong biases in the estimated distances. Finally, the direction of dispersal distances was examined to filter out the effect of migratory movements (see Paradis et al. [1998] for further details regarding the derivation of the estimates). Restricting the study to birds banded in the British Isles ensures that all species included experienced a similar geographic setting with similar barriers and other factors that may affect dispersal. In addition, the British avifauna is probably the best-known avifauna in the world, and a rich body of information is available about its morphology, life history, behavior, and ecology (e.g., Wernham et al. 2002, Crick et al. 2003, Baker et al. 2006).

Predictors

Flight efficiency was characterized using three proxies: the hand-wing index, the wing aspect ratio, and the lift-to-drag ratio (Claramunt and Wright 2017). The hand-wing index was calculated using the distance from the carpal joint to the tip of the longest primary feather in the closed wing (W, the traditional wing length measurement) and the distance from the carpal joint to the tip of the most external secondary feather (S, the one originating near the carpal joint [Claramunt et al. 2012]). Then, the hand-wing index is calculated as $100(W - S)/W$. This index is nearly equivalent to Kipp's index (Kipp 1959) and reflects the relationship between the length and the width of the hand portion of the wing, and is thus related to the wing's aspect ratio (Lockwood et al. 1998, Claramunt et al. 2012, Claramunt and Wright 2017). I measured W and S for an average of 3.9 individuals per species at the Royal Ontario Museum (ROM), the Louisiana State University Museum of Natural Science (LSUMZ), and the University of Washington Burke Museum (UWBM, Data S1). Most specimens were from the British Isles or identified as the same subspecies that inhabit the isles.

The aspect ratio of the wing is probably the single most important morphological predictor of the efficiency of long-distance flight (Rayner 1988, Norberg 1990, Pennycuick 2008, Taylor and Thomas 2014). The aspect ratio is estimated as B^2/A_{tot}, in which B is the wingspan and A_{tot} is total wing area, including not only the area of both wings but also the area of the section of the body between the wings. I compiled wingspan and wing area data from published sources, mostly from the Wings Database (Pennycuick 2008) and Vágási et al. (2016), and from my own measurements of museum specimens (Data S1). These data consist of measurements of wingspan and wing area estimated directly from individual birds using the standards described by Pennycuick (2008). For museum specimens, I photographed spread wing specimens including a reference scale and estimated the area of a single wing using the program ImageJ (U.S. National Institutes of Health, Bethesda, Maryland) and the area of the body from measurements of wing extent, wing width, and wingspan, as described in Pennycuick (2008, see also Claramunt and Wright [2017]). For a few species, I obtained data from other sources as detailed in Data S1.

The lift-to-drag ratio is a fundamental quantity in aerodynamics that determines the efficiency of horizontal flight and is the reciprocal of the aerodynamic cost of transport (Videler 2005, Pennycuick 2008). The lift-to-drag ratio is the ratio of the weight to the forces required for sustaining flight; more precisely, lift-to-drag ratio = mgV/P, in which m is the bird's body mass, g is the gravitational acceleration, V is the forward velocity, and P is the power required for flying horizontally at speed V. The latter quantity can be estimated from aerodynamic models of avian flight and a few morphological variables. Here I used the Pennycuick (2008) model to estimate the three main components of the mechanical power (induced, parasite, and profile powers), which requires a minimum of three basic measurements: wingspan, wing area, and body mass. The lift-to-drag ratio varies with flying velocity because V appears in the numerator of the formula and in the estimators of induced and profile power. It shows an inverted-U-shape relationship with flying velocity in which the maximum lift-to-drag ratio is attained at a characteristic velocity called the *maximum range velocity*. Instead of using empirical field estimates of flying speeds, which are not available for most species and vary in accuracy and applicability, I estimated the maximum lift-to-drag ratio for each species by maximizing it with respect to flying velocity using the function *optim* in R 4.0 (R Development Core Team 2020). This approach is justified, given empirical evidence indicating that birds tend to fly at speeds around the maximum range velocity during migration or commuting (Bruderer and Boldt [2001, Pennycuick et al. [2013]; see also Pennycuick [1997] for a theoretical justification). For a discussion of values for other parameters and constants used in the calculations, see Pennycuick (2008), Pennycuick et al. (2013), and Claramunt and Wright (2017). In particular, I used an induced power factor = 1, a body's drag coefficient = 0.1, and estimated the body's frontal area as $0.01m^{2/3}$. Functions in the R language (R Development Core Team 2020) for calculating the different power components and the maximum lift-to-drag ratio are provided in Data S1.

Migratory behavior was modeled as a binary factor separating migratory vs. nonmigratory species. The migratory status of each species was determined for the British breeding population based on Wernham et al. (2002), as some species change their migratory status across their distribution (many species are year-round residents in the British Isles but migratory in central Europe). Species that are partial migrants in the British Isles (only part of the population migrates) were treated as residents if the partial migration involved a minority of the populations or occurred mostly within the British Isles. In a supplemental analysis, I used an ordinal variable that combined migratory behavior and migration distances: (0) year-round residents in the British Isles; (1) short-distance migrants wintering within the British Isles or in neighboring regions of France and the Low Countries; (2) migrants wintering in the Mediterranean region; (3) migrants crossing the Sahara and wintering in Western Africa, mainly in the Sahel region; (4) migrants wintering in tropical central Africa; and (5) migrants wintering in southern Africa. Wintering grounds for British breeding populations were based on Wernham et al. (2002). For species that fitted more than one category, I used the average of the applicable categories. In particular, partial migrants were assigned 0.5 (resident and short migration) or 1 (resident and wintering in the Mediterranean region).

Ecological variables were habitat, diet, and population size. Data on habitat and diet were obtained from Paradis et al. (1998), with few minor modifications. Habitat was scored as four broad categories combining habitat tridimensional structure type (closed vs. open) and dominance of water (land vs. water): (1) land habitats with closed vegetation including forests, and woodlands; (2) swamps and marshes with dense vegetation; (3) open uplands including grasslands, prairies, and steppes; and (4) open waters, including seas, lakes, and open waters in marshes and rivers. For diet, species were classified as herbivores if feeding mostly on plants, fruit, or grain; insectivores if feeding mostly on insects and other invertebrates; carnivores if feeding mostly on vertebrates; and omnivores if feeding on both plants and animals. Population sizes ware taken from Baker et al. (2006: Table 1) and refer to the estimated total number of breeding individuals in Great Britain and Northern Ireland. Numbers given in units of pairs or breeding territories in Baker et al. (2006: Table 1) were multiplied by two. Because it is measured for a fixed area, the population size is also a measure of overall density across the British Isles, although species are not uniformly distributed across this territory and may experience higher or lower local densities.

Life history variables included age at first breeding, reproductive output, and body mass. Age at first breeding was taken from Paradis et al. (1998). Annual reproductive output was estimated by multiplying the number of broods per year by the average clutch size; both variables were taken from the British Trust for Ornithology species summaries, which are based on the UK Nest Records Scheme (Crick et al. 2003). Finally, body mass was included as a variable that may be correlated with multiple life history traits. Body mass data were the same as used for estimating the lift-to-drag ratio. The data matrix compiling all variables used for analyses is provided in Data S1.

Statistical modeling

I evaluated the relationships between predictors and natal dispersal distance using phylogenetic generalized least-squares models (PGLS [Freckleton et al. 2002]) in combination with model selection and model averaging techniques (Burnham and Anderson 2002) using R 4.0 (R Development Core Team 2020). Phylogenetic

TABLE 1. Single-predictor phylogenetic GLS models of natal dispersal distances among 75 species of birds in the British Isles.

Model	Intercept	Coefficient	df	λ	Log(Lik)	AIC_c	ΔAIC_c	R^2
Population size	**4.89**	**−0.18**	2	0.59	−73.5	151.2	0	0.23
Lift-to-drag ratio	**−1.60**	**1.63**	2	0.43	−76.6	157.4	6.2	0.18
Aspect ratio	**−1.41**	**2.23**	2	0.66	−76.7	157.6	6.4	0.16
Migratory behavior	**2.73**	+	2	0.48	−77.5	159.2	8.0	0.15
Migration distance	**2.72**	**0.22**	2	0.47	−77.6	159.3	8.1	0.15
Hand-wing index	**−0.77**	**1.00**	2	0.55	−77.8	159.8	8.6	0.14
Diet	**2.26**	+	4	0.30	−77.0	162.6	11.4	0.19
Habitat	**2.46**	+	4	0.59	−78.7	166.0	14.8	0.12
Reproductive output	**3.29**	−0.07	2	0.51	−81.5	167.2	16.0	0.05
Age at first breeding	**2.43**	0.25	2	0.60	−81.9	167.9	16.7	0.04
Intercept	**2.88**		1	0.64	−83.3	168.6	17.4	0.00
Body mass	**2.94**	0.06	2	0.63	−83.1	170.3	19.1	0.01

Notes: λ is the degree of phylogenetic nonindependence in residuals, Log(Lik) is the log-likelihood, ΔAIC_c is the difference between the AIC_c of a model and the AICc of the best model, and R^2 is the coefficient of determination. Regression coefficients in bold are significantly different from zero at $P < 0.001$. + indicates the presence of more than one coefficient (not shown) for multicategory discrete variables. Flight efficiency variables, population size, and body mass were log-transformed.

nonindependence among species was incorporated in the error covariance in which a parameter λ modulates the degree of phylogenetic covariation (Freckleton et al. 2002). If λ = 1, phylogenetic covariation is proportional to the extent of shared evolutionary history between species, whereas if λ = 0, phylogenetic covariation is absent. PGLS models were fit by maximum likelihood with function *pgls* in the package *caper* (Orme et al. 2018). λ was estimated simultaneously with other parameters in the model. A sample of 1,000 phylogenetic trees of the 75 species was obtained from the "sequenced data set" in BirdTree.org (Jetz et al. 2012), using the Hackett et al. (2008) backbone topology. As there were few topological differences across trees, trees were summarized into a single maximum clade credibility tree using *TreeAnnotator* (Bouckaert et al. 2014). Natal dispersal values were log-transformed to improve homoscedasticity, a transformation confirmed using the Cox–Box method (Faraway 2005). Flight efficiency predictors, body mass, and population size—all strongly right-skewed—were also log-transformed to improve model fit and the distribution of residuals. Absolute model fit and proportion of variance explained were assessed using the coefficient of determination $R^2 = 1 - RSS_{model}/SS_{null}$, where RSS_{model} is the residual sum of squares of the full model and SS_{null} is the sum of squares for the response in the null model (i.e., an intercept-only model fitted using the same phylogenetic correlation structure as the full model [Orme et al. 2018]).

In addition to analyzing single-predictor models, I evaluated multipredictor models including main effects and second-order interactions between continuous and binary predictors. I did not explore models with more than five variables. I built three sets of models, one set for each flight efficiency proxy—hand-wing index, aspect ratio, and lift-to-drag ratio. Numerical variables were centered and divided by two standard deviations to facilitate the comparison of standardized coefficients between categorical and continuous variables (Gelman 2008). Then I used information-theoretic model selection and multimodel inference techniques for identifying optimal models that balance fit and complexity (Burnham and Anderson 2002). I calculated the Akaike information criterion (AIC_c), relative model likelihoods, and model probabilities based on differences in AIC_c values (ΔAIC_c).

When confronted with model selection uncertainty (i.e., top models with similar probabilities), I used model averaging techniques (Burnham and Anderson 2002). I assessed variable importance across all models using two different methods. First, I estimated effect sizes using model-averaged standardized coefficients (Galipaud et al. 2017). Second, because of problems with interpreting model-averaged coefficient for models with categorical predictors and interactions (Gelman 2008, Schielzeth 2010, Banner and Higgs 2017), I also assessed variable importance as the sum of the probabilities of all models that contain the specific variable (Burnham and Anderson 2002). I used the *MuMIn* library (Bartón 2018) for building all models (function *dredge*) and computing model-averaged estimates (function *model.avg*).

RESULTS

In single-predictor models, flight efficiency proxies were all positively and significantly correlated with dispersal distances (Table 1, Fig. 1a–c). Among these, the lift-to-drag ratio was the best flight efficiency proxy, followed by the aspect ratio and the hand-wing index (Table 1). Migration, expressed either as a binary

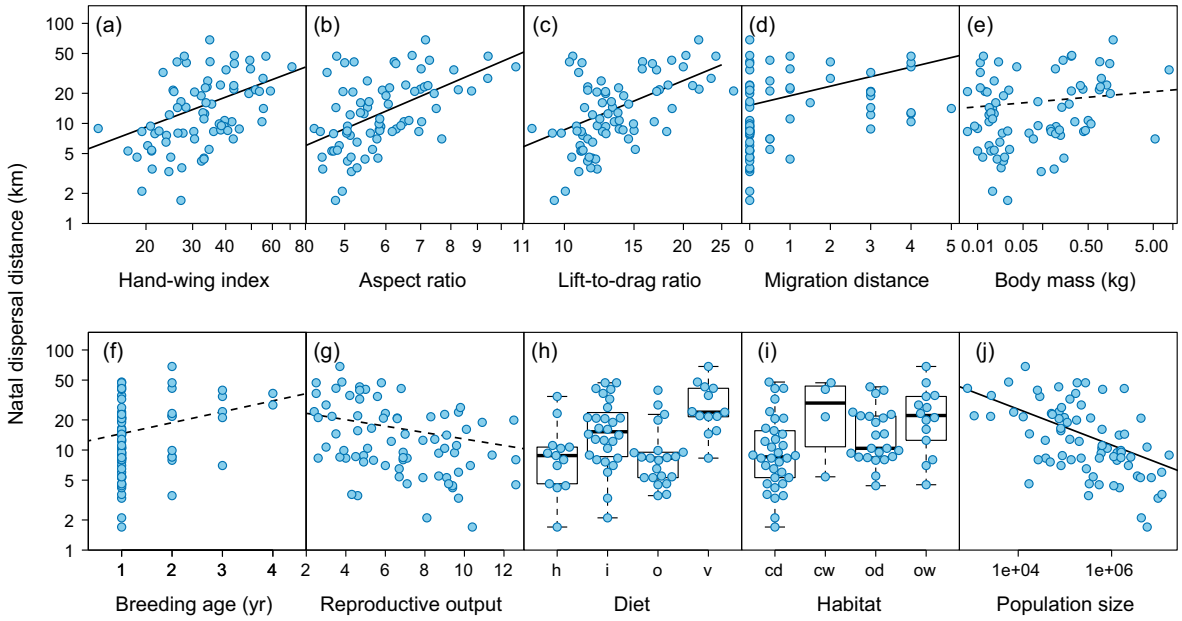

FIG. 1. Relationship between flight efficiency proxies, migration distance, body mass, life history traits, ecological factors, and natal dispersal distances among 75 bird species from the British Isles. *x*-axis in (a), (b), (c), (e), and (j) is in logarithmic scale. Lines correspond to phylogenetic generalized least-squares models (dashed lines indicate slopes not significantly different from 0). Migration distances (d) are numerical categories rather than physical distances and lines correspond to two regression models: one including both migratory and resident species and one for migratory species only (dashed line: not significantly different from 0). Reproductive output (g) is the total number of eggs laid in a year (i.e., the average clutch size multiplied by the average number of broods). Diet categories (h) are h, herbivore; i, insectivore; o, omnivore;v, vertivore. Habitat categories (i) are: cd, closed–dry; cw, closed–wet; od, open–dry; and ow, open–wet.

variable (residents vs. migrants) or as migration distance, performed slightly worse than the aspect ratio but better than the hand-wing index (Table 1). As expected, migrants showed greater dispersal distances (Table 1). The correlation between migratory distances and dispersal distances was driven by the difference between residents and migrants, as there was no correlation between migratory and dispersal distances among migrants (PGLS, *F*-statistic: 0.008 on 1 and 21 degrees of freedom, *P* value: 0.93; Fig. 1d).

Among ecological variables, population size attained the highest proportion of variance explained (Table 1). It showed a negative correlation in which abundant species tended to have shorter dispersal distances (Fig. 1j). Habitat and diet showed slightly lower performance than flight efficiency and migratory behavior but with some significant effects and more than 10% of variance explained. Finally, life-history traits—reproductive output, age at first breeding—and body mass showed poor performance, with coefficients not statistically significant and low levels of variance explained (Table 1).

The best multipredictor models all included flight efficiency (lift-to-drag ratio, aspect ratio, or the hand-wing index), migratory behavior, and their interaction (Table 2). Ecological and life-history variables were more inconsistent, with only population size and diet appearing in top-ranked models. The overall best model included the aspect ratio, migratory behavior, their interaction, population size, and diet, with a model probability of 0.47 and explaining 64% of the variance. However, model selection uncertainty was high, particularly for model sets including the hand-wing index and the lift-to-drag ratio, as several additional models were less than 5 AIC units apart from the best model and model probabilities decreased gradually. For all the best models, residual phylogenetic covariation was nil ($\lambda = 0$).

Model averaging and variable importance results showed that only flight efficiency proxies and migration were consistently important predictors of natal dispersal distances (Fig. 2). The aspect ratio and the lift-to-drag ratio showed very high importance (0.99 and 0.98, respectively), whereas the hand-wing index showed moderately high importance (89). The interaction between flight efficiency proxies and migration had a large effect size for all three proxies. Its variable importance was high when involving the aspect ratio (0.95) and the lift-to-drag ratio (0.93), but only moderate when involving the hand-wing index (0.73, Fig. 2). Population size was present in several of the best models, but its importance was high (0.97) only when combined with the lift-to-drag ratio as the flight efficiency proxy; the importance of population size was relatively low when using the aspect ratio (0.72) or the hand-wing index (0.65) (Fig. 2). Diet was also present in several of the top models involving the hand-wing index and aspect ratio, but

TABLE 2. Multipredictor phylogenetic GLS models of the relationship between flight efficiency, life history, ecological variables, and natal dispersal distances among British birds.

Model	df	Log(Lik)	AIC_c	ΔAIC_c	P_{model}	R^2
Aspect ratio * migration + population size + diet	8	−52.5	123.1	0	0.47	0.64
Aspect ratio * migration + diet + age at first breeding	8	−53.4	125.1	1.9	0.18	0.63
Aspect ratio * migration + population size + reproductive output	6	−57.0	127.2	4.1	0.06	0.59
Aspect ratio * migration + diet	7	−56.2	128.1	5.0	0.04	0.60
Aspect ratio * migration + population size	5	−58.6	128.1	5.0	0.04	0.57
Lift-to-drag ratio * migration + population size	5	−57.5	126.0	0	0.19	0.59
Lift-to-drag ratio * migration + population size + age at first breeding	6	−56.4	126.0	0.01	0.18	0.60
Lift-to-drag ratio * migration * population size	6	−56.8	126.8	0.8	0.12	0.59
Lift-to-drag ratio * migration + population size + habitat	8	−54.3	126.9	0.9	0.12	0.62
Lift-to-drag ratio * migration + population size + diet	8	−54.6	127.4	1.4	0.09	0.62
Migration * hand-wing index + population size + diet	8	−55.3	128.8	0	0.28	0.61
Migration * hand-wing index + diet + age at first breeding	8	−55.3	128.9	0.02	0.28	0.61
Migration * hand-wing index + population size + reproductive output	6	−59.9	133.1	4.2	0.03	0.56
Migration * hand-wing index * population size	6	−60.0	133.2	4.3	0.03	0.56
Migration * hand-wing index + population size + age at first breeding	6	−60.0	133.2	4.4	0.03	0.56

Notes: Log(Lik) is the log-likelihood, ΔAIC_c is the difference between the AIC_c of a model and the AIC_c of the best model, P_{model} is the model probability, and R^2 is the coefficient of determination. Flight efficiency variables and population size were log-transformed. Only the top five models are shown for each flight efficiency proxy. The asterisks indicate interaction terms between the corresponding variables in addition to main effects.

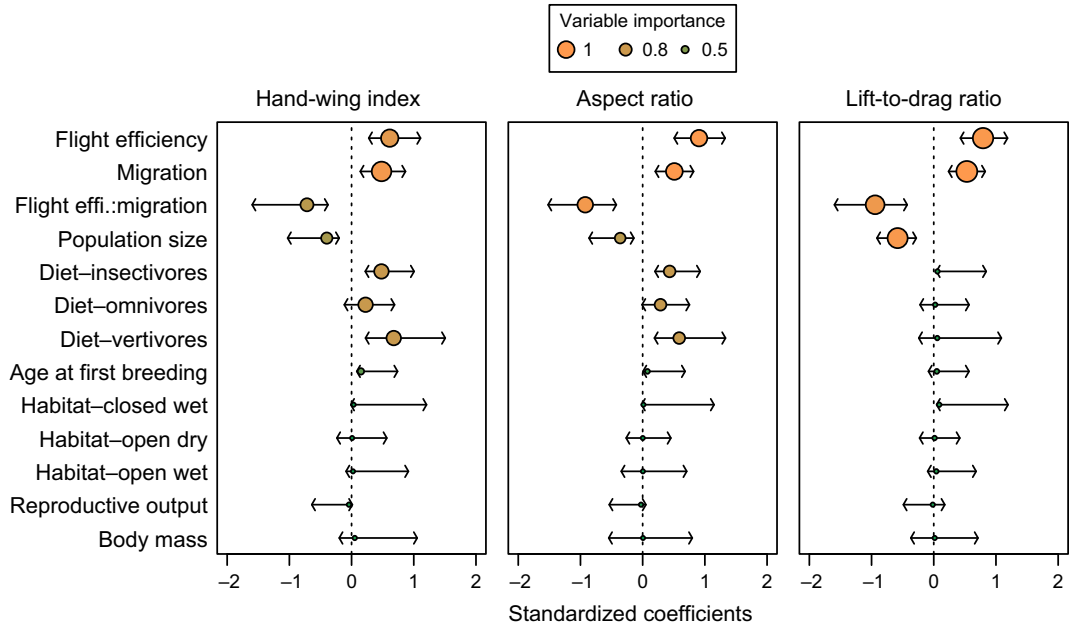

FIG. 2. Performance of predictors of natal dispersal distances among British birds based on model-averaged phylogenetic GLS models. Each panel corresponds to the use of a different proxy for flight efficiency: the hand-wing index, the aspect ratio, and the lift-to-drag ratio. Standardized coefficients and their 95% confidence intervals are model-averaged estimates. Variable importance based on model probabilities is indicated by the size and color of the dots. Interaction terms other than the ones involving flight efficiency and migration were not significantly different from zero, unimportant, and are not shown.

its overall relative importance was only moderate (~0.78). The remaining predictors and interaction terms received very low importance scores and model-averaged coefficients were not statistically different from zero (Fig. 2).

Models including only flight efficiency and migratory behavior—the two variables that were consistently important and significant across models—show the interrelationships among these variables (Table 3). For resident birds, dispersal distances increase exponentially

TABLE 3. Phylogenetic GLS models of the relationship between flight morphology, migration and natal dispersal distances among 75 species of birds in the British islands.

Model	β_0	β_{aero}	β_{migr}	β_{inter}	λ	df	Log(Lik)	R^2
Lift-to-drag ratio * migration	**−2.77**	**2.23**	**5.56**	**−2.17**	0.00	4	−65.08	0.49
Aspect ratio * migration	−2.68	**2.89**	**5.54**	**−2.80**	0.26	4	−65.80	0.40
Hand-wing index * migration	−1.37	**1.15**	**5.98**	**−1.54**	0.40	4	−69.54	0.32

Notes: β_0 regression intercept, β_{aero} is the coefficient of the aerodynamic parameter (hand-wing index, aspect ratio, or lift-to-drag ratio), β_{migr} is the migration factor, β_{inter} is the interaction term, λ is the degree of phylogenetic non-independence among residuals, Log(Lik) is the log-likelihood, and R^2 is the coefficient of determination. Regression coefficients in bold are significantly different from zero at $P < 0.01$. Flight efficiency variables were log-transformed.

with flight efficiency (linearly in the log-log space). The interaction between flight efficiency and migration was negative, and nearly of the same magnitude as the main effect of flight efficiency, resulting in no relationship between flight efficiency and dispersal distances among migrants. A scatterplot further reveals that most migratory species fall within the prediction interval of resident species (Fig. 3). Migrants with relatively low flight efficiency (lift-to-drag ratio <10, mostly passerines) tended to be above the regression line, but only four species were outside the 95% prediction interval (Fig. 3).

DISCUSSION

Results suggest that only two factors are strongly and consistently associated with variation in natal dispersal

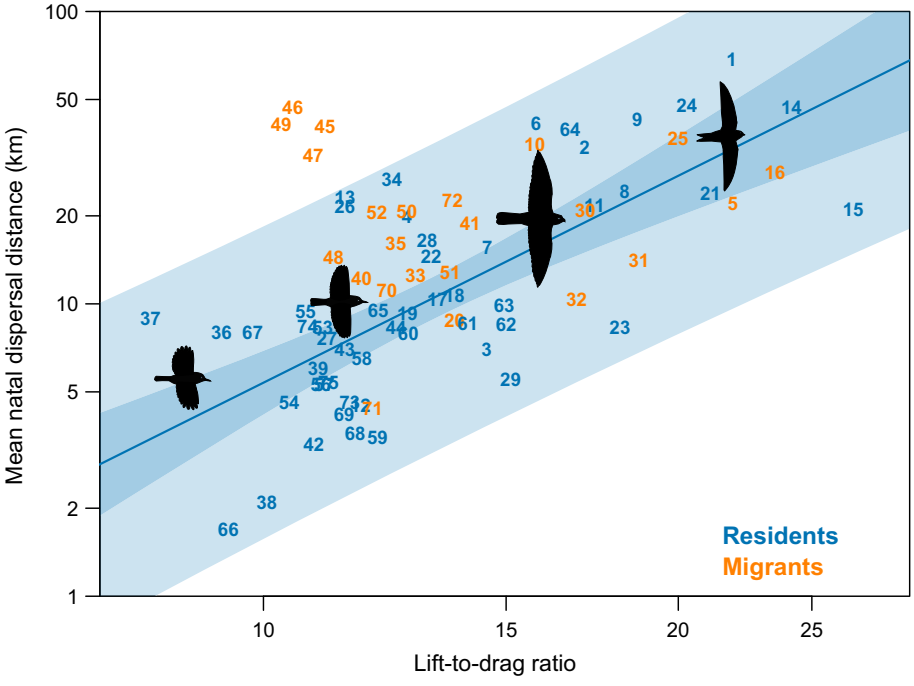

FIG. 3. Relationship between flight efficiency and natal dispersal distances among 75 species of birds in the British Isles. The regression line and 95% confidence region for slope (dark shade) and prediction (light shade) are from a model based on resident species only. Silhouettes represent examples of birds with different wing morphologies. Numbers correspond to species as follows: 1, *Ardea cinerea*; 2, *Cygnus olor*; 3, *Branta canadensis*; 4, *Anas platyrhynchos*; 5, *Circus cyaneus*; 6, *Accipiter gentilis*; 7, *Accipiter nisus*; 8, *Buteo buteo*; 9, *Falco tinnunculus*; 10, *Falco columbarius* (silhouette); 11, *Falco peregrinus*; 12, *Gallinula chloropus*; 13, *Fulica atra*; 14, *Larus ridibundus*; 15, *Larus canus*; 16, *Larus fuscus*; 17, *Columba oenas*; 18, *Columba palumbus*; 19, *Streptopelia decaocto*; 20, *Streptopelia turtur*; 21, *Tyto alba*; 22, *Athene noctua*; 23, *Strix aluco*; 24, *Asio otus*; 25, *Apus apus* (silhouette); 26, *Alcedo atthis*; 27, *Picus viridis*; 28, *Dendrocopos major*; 29, *Alauda arvensis*; 30, *Riparia riparia*; 31, *Hirundo rustica*; 32, *Delichon urbicum*; 33, *Motacilla flava*; 34, *Motacilla cinerea*; 35, *Motacilla alba*; 36, *Cinclus cinclus*; 37, *Troglodytes troglodytes* (silhouette); 38, *Prunella modularis*; 39, *Erithacus rubecula*; 40, *Phoenicurus phoenicurus*; 41, *Oenanthe oenanthe*; 42, *Turdus merula*; 43, *Turdus philomelos*; 44, *Turdus viscivorus*; 45, *Acrocephalus schoenobaenus*; 46, *Acrocephalus scirpaceus*; 47, *Sylvia curruca*; 48, *Sylvia communis* (silhouette); 49, *Sylvia atricapilla*; 50, *Phylloscopus trochilus*; 51, *Muscicapa striata*; 52, *Ficedula hypoleuca*; 53, *Aegithalos caudatus*; 54, *Poecile montanus*; 55, *Periparus ater*; 56, *Cyanistes caeruleus*; 57, *Parus major*; 58, *Sitta europaea*; 59, *Garrulus glandarius*; 60, *Pica pica*; 61, *Corvus monedula*; 62, *Corvus frugilegus*; 63, *Corvus corone*; 64, *Corvus corax*; 65, *Sturnus vulgaris*; 66, *Passer domesticus*; 67, *Passer montanus*; 68, *Fringilla coelebs*; 69, *Chloris chloris*; 70, *Carduelis carduelis*; 71, *Linnaria cannabina*; 72, *Acanthis flammea*; 73, *Pyrrhula pyrrhula*; 74, *Emberiza citrinella*; 75, *Emberiza schoeniclus*.

distances among British birds: flight efficiency and migratory behavior. Among resident species, dispersal distances increase exponentially with flight efficiency. The increase in dispersal distances with an increase in flight efficiency is consistent with the idea that the energetic cost of transport is a major determinant of dispersal distances (Bonte et al. 2012, Matthysen 2012). Species with aerodynamically efficient flight morphologies fly longer distances and for longer periods of time, dispersing farther away from their natal areas. As predicted under this hypothesis, more precise descriptors of flight efficiency—such as the wing aspect ratio and the lift-to-drag ratio—predicted natal dispersal distances better than simpler descriptors such as the hand-wing index.

Migration and dispersal distances

Migratory species tend to show greater dispersal distances compared to resident species (Paradis et al. 1998, Sutherland et al. 2000, Dawideit et al. 2009). This is not surprising, given that migration distances are much greater than average dispersal distances. But the present results revealed a complex interaction between migratory behavior, flight efficiency, and dispersal distances. Taken at face value, the statistical models suggest that, in contrast to resident species, dispersal distances among migrants do not depend significantly on their flight efficiency. There are multiple factors that can dissociate flight efficiency and dispersal distances among migrants. Prominent among them is philopatry, which may be a strong force constraining dispersal distances among migrants (Weatherhead and Forbes 1994, Winkler et al. 2016), a phenomenon that may be intrinsic to the evolution of migration (Winger et al. 2019). Moreover, migratory movements themselves may enhance the capacity of birds to return to their natal areas, for example, by allowing birds to acquire geographic information at large scales that can be used for navigating back to the natal areas (Winkler 2005). Migrants also have physiological adaptations that equip them with long-distance flight capabilities that go beyond what can be inferred from morphology alone (Pennycuick 2008, Butler 2016, Winkler et al. 2016). Finally, interactions between resource phenology and body condition may affect natal dispersal distances in ways that would be dissociated with flight efficiency (Studds et al. 2008).

On the other hand, most migratory species in the data set showed a pattern that is very similar to that of resident species, clustering around the regression line and within the confidence interval for a model fit to resident species (Fig. 3). Only four species of migratory passerines showed unusually long dispersal distances for their flight efficiency (Fig. 3). These species were warblers in the families Acrocephalidae and Sylviidae (*Acrocephalus schoenobaenus*, *Acrocephalus scirpaceus*, *Sylvia curruca*, and *Sylvia atricapilla*) and do not share any particular characteristic that set them apart from other similar passerines in the British avifauna. Other migratory warblers analyzed, including *Sylvia communis*, showed dispersal distances following the trend of resident species (Fig. 3). The possibility that the greater dispersal distances of these warblers are artifactual cannot be completely ruled out. Because distinguishing migratory from dispersal movement in band-recovery data is not straightforward, some dispersal distances may have been overestimated (Paradis et al. 1998). It is also plausible that migrants with relatively low aerodynamic efficiency —such as these warblers—may have a harder time dealing with hurdles during the spring migration, making the return to their natal areas more difficult, resulting in greater dispersal distances. This idea is supported by mounting evidence showing that small passerines are very sensitive to weather conditions during migration (Haest et al. 2020). In particular, migrants with less efficient wing morphologies are more susceptible to adverse weather conditions (Saino et al. 2010) and stop sooner after long over-water flights (Buler et al. 2017). These migrants may not have the energy or the time needed to seek their natal areas, settling farther away from them. All these factors would particularly affect young birds during their first migratory flights, making them even more relevant for natal dispersal distances. Further research is needed to determine if migrants with low aerodynamic efficiency tend to have greater dispersal distances in general, the potential causes of this, and how this may contribute to a lack of a relationship between flight efficiency and dispersal distances among migrants. If, on the other hand, the longer dispersal distances among these warblers end up being artifactual or exceptional, migratory birds would show a trend of increasing dispersal distances with flight efficiency very similar—if not identical—to that shown by resident species. This would suggest that the strong philopatric tendencies can completely override the potential effect of long migratory movements on dispersal distances among migrants.

Body mass and dispersal distances

Body mass is expected to be correlated with dispersal distances in actively dispersing animals because it is usually related to movement capacity and home range (Sutherland et al. 2000, Jenkins et al. 2007). However, body mass was found here to be unimportant in explaining natal dispersal distances in British birds. Using the same data set, Paradis et al. (1998) found equivocal evidence for an effect of body size, with the significance of the result depending on the phylogenetic tree used for the independent-contrasts method. Using an updated phylogeny and phylogenetic regression methods, I confirmed that the correlation between body mass and natal dispersal distances is low and not statistically significant (Table 1, Fig. 1e). The significant association found by Sutherland et al. (2000) needs re-evaluation using phylogenetic regressions methods. These findings may be

explained by a larger effect of wing shape over body size on the capacity of movement in birds. Indeed, the empirical negative relationship between the cost of transport and body mass in birds has been attributed to variation in wing shape, in which larger birds have also higher aspect ratios, rather than an intrinsic effect of body mass per se (Videler 2005, Pennycuick 2008). Both small and large birds can be either aerodynamically efficient (e.g., swifts, albatrosses) or nearly flightless (e.g., tapaculos, turkeys), decoupling the expected relationship between body mass and locomotor capacity.

Ecological factors and dispersal distances

Population size was the strongest single predictor of dispersal distances (Table 1; see also Paradis et al. [1998]). Species that dispersed farther showed reduced population sizes. This negative correlation is at odds with the idea that dispersal distances should increase with population size as a way of avoiding competition and inbreeding (Nilsson 1989, Matthysen 2005, 2012). However, if abundance is uniformly high or closely matches resource availability, dispersing longer distances would not be advantageous (Ronce 2007). Also, higher densities may dilute the potential negative effects of kin competition and inbreeding, resulting in no selection for dispersal (Kisdi 2016). Finally, other factors may select for reduced dispersal distances in larger populations. Birds that are abundant because they inhabit dominant habitats may find adequate breeding grounds near their natal sites, resulting in low dispersal distances (Paradis et al. 1998). Also, high densities may prompt territorial birds to settle sooner, resulting in shorter dispersal distances, because birds that prolong the search for a territory, thus potentially dispersing farther away, may find all suitable sites already occupied (Greenwood et al. 1979, Nilsson 1989).

Alternatively, the relationship between population size and dispersal distances may be indirect and emerge as a side effect of the relationship between home range or territory size and mobility. A strong correlation between home range or territory size and dispersal distance may arise for two reasons (Bowman 2003). First, territory size may determine dispersal distances if dispersing individuals have to travel across other birds' territories until they find a vacant plot (Greenwood and Harvey 1982; the "vacant territory hypothesis" of Bowman 2003). Second, a correlation between population density and home range may be a consequence of differences in mobility (the "vagility hypothesis" of Bowman 2003, Stephens et al. 2019). Species that use large areas daily do so because they exploit resources that are in low densities (e.g., raptors) or because they commute from roosting or breeding sites to foraging grounds (e.g., gulls; Schoener 1968, Sherry 2016). In both cases, these species are adapted to a mobile lifestyle by possessing efficient flight morphologies (Rayner 1988, Norberg 1990), which, in turn, result in greater dispersal distances, as shown in this study. Therefore, the correlation between population size and dispersal distances may be explained by the covariation between population size and flight efficiency mediated by home range and mobility. Two results of the present study are consistent with this hypothesis. First, all three flight efficiency variables showed a negative correlation with population size, and the correlation increased with the accuracy of the flight efficiency variable (Pearson's r, hand-wing index: -0.37, aspect ratio: -0.42, lift-to-drag ratio: -0.46). Second, the importance of population size as a predictor of dispersal distances dwindled in multivariate models including flight efficiency (Fig. 2). Therefore, the correlation between population size and dispersal distances may be largely produced by the relationship between home range, mobility, and flight efficiency.

Other ecological and life history factors analyzed were only weakly associated with dispersal distances and may be only indirectly related to dispersal (Greenwood and Harvey 1982, Paradis et al. 1998, Sutherland et al. 2000). For example, diet and habitat are related to foraging strategies, home range, population size, and population structure (Wiens 1989*a*, Sherry 2016) but because avian foraging strategies and home range are also associated with flight efficiency and the morphology of the flight apparatus (Rayner 1988, Norberg 1990), the effects of habitat and diet on dispersal distances may be partially or entirely mediated by flight efficiency.

One aspect of ecology not analyzed that may show a stronger association with dispersal distances is the spatial distribution of resources (Sutherland et al. 2000). As most of the movement that a bird performs on a daily basis is associated with coping with the spatial distribution of resources, from foraging maneuvers to commuting, the distribution of resources may determine overall levels of movement and ultimately dispersal distances. As foraging and commuting are one of the most obvious factors associated with locomotor adaptations in birds (Leisler and Winkler 1985, Rayner 1988, Norberg 1990, Hertel and Ballance 1999), the influence of the distribution of resources, foraging behavior, and flight efficiency on dispersal may be fundamentally intertwined. The study of the coevolution between the distribution of resources, foraging behavior, flight efficiency, and their effects on dispersal would be a fruitful avenue of research.

These results suggest that if ecological and life history characteristics play a role in determining dispersal distances, their influence is likely indirect and largely mediated by the efficiency of locomotion, which determines how far species disperse more directly. This is consistent with the idea that the energetic cost of movement has a strong effect on dispersal distances (Bonte et al. 2012), and suggests that dispersal distances are not the result of adaptive strategies for dispersal per se but emerge as a side effect of the mobility of species (Burgess et al. 2015). One potential exception to this conclusion is philopatry, which can be considered an adaptive strategy

for restricting dispersal and, as discussed in the previous section, may have a strong influence on dispersal among migratory birds (Winkler 2005, Winger et al. 2019).

Predicting dispersal distances from morphology

The results of this study can contribute to the development of predictors of dispersal distances in birds. Because the basic principles of bird flight apply to all birds, the relationship between flight efficiency and dispersal distances found here may be similar across all volant birds. The hand-wing index is already providing insights into a diverse array of ecological and evolutionary phenomena, including species coexistence (Pigot et al. 2018), range expansion and colonization (White 2016, Hosner et al. 2017), the macroecology of dispersal (Sheard et al. 2020), and the macroevolutionary dynamics of speciation (Claramunt et al. 2012, Weeks and Claramunt 2014). However, the present results suggest that the wings' aspect ratio and estimates of the lift-to-drag ratio may be better proxies of dispersal ability. To take advantage of these better predictors, accurate estimates of wingspan and wing area are required. An additional advantage of using the lift-to-drag ratio is that it can incorporate additional factors that may affect flight efficiency and dispersal ability. For example, data on flight speeds for each species can be estimated empirically (e.g., Bruderer and Boldt 2001, Pennycuick et al. 2013) and used instead of assuming that birds fly at optimal speeds; or differences in air density can be taken into account to evaluate dispersal abilities along elevational gradients. Finally, the use of wing morphology as a proxy for dispersal ability can be instrumental in assessing species vulnerability to habitat fragmentation and climate change (Sutherland et al. 2000, Garrard et al. 2012, Travis et al. 2013, MacLean and Beissinger 2017).

Conclusions

I found that flight efficiency is the most important factor explaining variation in natal dispersal distances among nonmigratory birds in the British Isles. Migratory behavior may also be important, but its effect and interaction with flight efficiency need to be further investigated, and strong philopatry may mute its potential effects on dispersal distances. Ecological and life history factors have a small or indirect influence on dispersal distances, and most of their influence is likely mediated by adaptations for the use of space and movement, which is reflected in flight efficiency. With the exception of philopatry among migratory birds, hypothesized adaptive strategies for dispersal do not seem to have much influence on patterns of dispersal. Instead, the results suggest that the energetic cost of movement, as reflected in flight efficiency, has a strong effect on dispersal distances.

Whether these conclusions apply to birds in other regions remains to be investigated. Given that the principles of flight and the adaptations for flight efficiency are similar across birds and geographies, it is plausible that a similar relationship between wing shape and dispersal distances exists for birds in other parts of the world. The need for further evaluating the generality of this conclusion is urgent, given the prominent use of wing morphology as a proxy for dispersal ability in avian macroecology and macroevolution (Claramunt et al. 2012, Sheard et al. 2020, Tobias et al. 2020). Moreover, the possibility of estimating dispersal ability based on morphology may have applications in conservation biology, as this can be instrumental in assessing species vulnerability to habitat fragmentation and climate change (Travis et al. 2013, MacLean and Beissinger 2017).

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Supporting Information

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