RESEARCH ARTICLE

Standardised empirical dispersal kernels emphasise the pervasiveness of long-distance dispersal in European birds

Guillermo Fandos[1,2] | Matthew Talluto[3] | Wolfgang Fiedler[4] |
Robert A. Robinson[5,6] | Kasper Thorup[7,8] | Damaris Zurell[1,2]

[1]Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany; [2]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany; [3]Department of Ecology, University of Innsbruck, Innsbruck, Austria; [4]Department of Biology, Max Planck Institute of Animal Behavior, University of Konstanz, Radolfzell, Germany; [5]British Trust for Ornithology, Thetford, Norfolk, UK; [6]European Union for Bird Ringing c/o British Trust for Ornithology, Norfolk, UK; [7]Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, Copenhagen, Denmark and [8]Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

Correspondence
Guillermo Fandos
Email: gfandos@hotmail.com

Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: ZU 361/1-1.

Handling Editor: Jean-Michel Gaillard

Abstract

1. Dispersal is a key life-history trait for most species and is essential to ensure connectivity and gene flow between populations and facilitate population viability in variable environments. Despite the increasing importance of range shifts due to global change, dispersal has proved difficult to quantify, limiting empirical understanding of this phenotypic trait and wider synthesis.

2. Here, we introduce a statistical framework to estimate standardised dispersal kernels from biased data. Based on this, we compare empirical dispersal kernels for European breeding birds considering age (average dispersal; natal, before first breeding; and breeding dispersal, between subsequent breeding attempts) and sex (females and males) and test whether different dispersal properties are phylogenetically conserved.

3. We standardised and analysed data from an extensive volunteer-based bird ring-recoveries database in Europe (EURING) by accounting for biases related to different censoring thresholds in reporting between countries and to migratory movements. Then, we fitted four widely used probability density functions in a Bayesian framework to compare and provide the best statistical descriptions of the different age and sex-specific dispersal kernels for each bird species.

4. The dispersal movements of the 234 European bird species analysed were statistically best explained by heavy-tailed kernels, meaning that while most individuals disperse over short distances, long-distance dispersal is a prevalent phenomenon in almost all bird species. The phylogenetic signal in both median and long dispersal distances estimated from the best-fitted kernel was low (Pagel's $\lambda < 0.25$), while it reached high values (Pagel's $\lambda > 0.7$) when comparing dispersal distance estimates for fat-tailed dispersal kernels. As expected in birds,

natal dispersal was on average 5 km greater than breeding dispersal, but sex-biased dispersal was not detected.

5. Our robust analytical framework allows sound use of widely available mark-recapture data in standardised dispersal estimates. We found strong evidence that long-distance dispersal is common among European breeding bird species and across life stages. The dispersal estimates offer a first guide to selecting appropriate dispersal kernels in range expansion studies and provide new avenues to improve our understanding of the mechanisms and rules underlying dispersal events.

KEYWORDS
birds, dispersal distance kernel, Europe, gamma, half-Cauchy, negative exponential, ring-recovery, weibull

1 | INTRODUCTION

Animal dispersal describes the movement from birth to breeding patch (natal dispersal) or between successive breeding patches (breeding dispersal) and is a fundamental biological process in ecology and evolution (Greenwood, 1980). Dispersal is a crucial determinant for different ecological processes at a wide range of spatial and temporal scales. At a macro scale, dispersal plays a key role in determining evolutionary patterns of speciation and extinction and the geographical distribution of species (Bowler & Benton, 2005; Kisel & Barraclough, 2010). Within populations, dispersal plays a key role in the genetic structure of populations and meta-population dynamics through its direct contribution to gene flow (Bonte & Dahirel, 2017; Hallatschek & Fisher, 2014; Venail et al., 2008) and in maintaining local populations (Millon et al., 2019; Schaub & Ullrich, 2021). Improved understanding of dispersal across many species is becoming increasingly important, given the need to predict how populations will respond to global change (Barbet-Massin et al., 2012; Zurell, 2017). Despite this broad relevance, however, we still have a limited understanding of this phenotypic trait as standardised empirical data on animal dispersal are largely missing, hampering wider synthesis of mechanisms and underlying drivers (Bullock et al., 2017).

Quantifying how far and how often animals move across the landscape is extremely challenging (Nathan, 2001). More recently, the understanding of movement processes has advanced through the implementation of new molecular tools (Hobson, 2005; Woltmann et al., 2012) and the use of cutting-edge biotelemetry (Kays et al., 2020; Kranstauber et al., 2011). Still, empirical dispersal measurements on vertebrates are scarce, mostly constrained to few organisms, and geographically limited (Paradis et al., 1998). As a consequence of these challenges, comparative dispersal analyses across species have relied on standardised biometric indices as proxies to quantify dispersal ability (Dawideit et al., 2009; Sheard et al., 2020), or imputation methods that fill information gaps based on phylogenetic relatedness between species (Barbet-Massin et al., 2012).

Syntheses of field movement and dispersal data provide a promising avenue for overcoming empirical data limitations for many vertebrate species and large spatial extents (Tucker et al., 2018). For example, two decades ago, Paradis et al. (1998) estimated average natal and breeding dispersal distances for 75 British bird species based on nearly 100 years of ringing data. Their analysis explored how dispersal distances vary according to certain life-history traits (e.g. migratory behaviour, range size, habitat) and dispersal type (breeding or natal dispersal). The estimates have subsequently been used to project bird dispersal and range dynamics under climate change (Barbet-Massin et al., 2012). However, the original dispersal estimates by Paradis et al. (1998) were constrained to Great Britain, to only a subset of European breeding birds, and summarised only average dispersal distances rather than explicitly estimating dispersal kernels and analysing their shapes. Dispersal kernels, which represent the density of dispersing individuals at certain distances from the source, provide a better understanding of the mechanisms and rules underlying dispersal events and are a prerequisite for modelling spatial population dynamics for scenarios of global change (Bullock et al., 2017; Nathan et al., 2012; Paradis et al., 2002). Yet, building a large dataset of empirical dispersal kernels for a wide range of species in large areas is challenging due to different biases and uncertainties in the field observations (Nathan et al., 2012).

Different studies have implemented a variety of functions to represent the frequency distribution of the dispersal distances (e.g. exponential, Gamma, Van Houtan et al., 2007; Nathan et al., 2012; half-Cauchy distribution, Paradis et al., 2002; Weibull, Nathan et al., 2012). These functions differ in the shape of the dispersal kernel and thus in the relative probability of different dispersal distances with consequent implications for predicting range change. Functions like the exponential kernel are popular as they have an underlying theoretical basis that represents movement in a random direction with a time or distance-dependent settlement rate (Bullock et al., 2017; Nathan et al., 2012). By contrast, heavy-tailed kernels such as the half-Cauchy, Gamma and Weibull

distribution assume a combination of local and distant selective pressures and they expect that a few individuals fly long distances (Viswanathan et al., 1996). To date, only a few studies compared different dispersal kernel functions for birds (Nathan et al., 2012; Paradis et al., 2002; Van Houtan et al., 2007, 2010). These indicated that simple summary statistics of empirically measured dispersal distances (rather than estimating dispersal kernels based on probability distributions) underestimate the species' dispersal ability and that heavy-tailed kernels may best explain empirical dispersal patterns (Paradis et al., 2002; Van Houtan et al., 2007). Comparing the performance of alternative empirical dispersal kernels for large numbers of species will improve our ecological understanding of relevant dispersal processes and their proximate and ultimate causes (Stevens et al., 2014).

Here, we aim to quantify empirical dispersal kernels of breeding birds across Europe, compare the dispersal characteristics of natal and breeding dispersal, explore dispersal differences between sexes, and test for phylogenetic signal in dispersal metrics. We use data on marked birds from EURING—The European Union for Bird Ringing database—that holds several million records of European bird movements (Du Feu et al., 2016). Although a uniquely rich data source on bird movements, analysis of dispersal distance based on EURING data are challenging because dispersing and migrating birds are not separated, and sampling effort is heterogeneous (Korner-Nievergelt et al., 2010; Paradis et al., 1998). Therefore, we develop a methodological framework that addresses these potential biases. Based on this, we first estimate dispersal kernel parameters for average dispersal (pooling all age and sex stages), for breeding and natal dispersal (pooling sex stages) and for female and male dispersal (pooling all age stages) using four different probability density functions and assess the best-fitting one. Then, we calculate multiple descriptors of dispersal (e.g. median and maximum dispersal distances) and quantify the phylogenetic signal in these descriptors. Our study is to a large extent exploratory as we compare the statistical support for different dispersal kernel functions. Based on the literature, we predict that natal dispersal distances are generally larger than breeding dispersal ones (Greenwood & Harvey, 1982; Paradis et al., 1998) and that female dispersal is larger than male dispersal (Li & Kokko, 2019). At last, we explore phylogenetic signals in multiple dispersal descriptors as we expect that short- versus long-distance dispersal patterns are associated with different selective pressures (e.g. long-distance flight efficiency depends critically on the morphology of the wings; Claramunt, 2021; Sheard et al., 2020).

2 | METHODS

2.1 | Ringing data

Raw data on dispersal distances were obtained from the EURING database (Du Feu et al., 2016). The data were requested following an approach that allowed us to keep only the reliable observations and test for different sampling biases. Therefore, for the present study, we included distances between the ringing and re-encounter locations of birds ringed and subsequently re-encountered between April and July (which encompasses the core breeding season for most species; also see supplemental material 3 for further refinement of core breeding season times) from 1979 until 2018 from almost all ringing schemes in Europe (see supplemental material 1). Re-encounters within the same breeding season as ringing were excluded, thus reducing the impact of non-dispersive movements. When multiple subsequent encounters at the same coordinates as the previous encounter were available, only the first one was considered. We re-classified the field codes for the condition of the reencountered birds into two classes, dead (EURING code: 1–3) and alive (code: 4–8), and defined two age classes with respect to the age of the birds when ringed: juvenile for birds ringed in their year of birth (age code 1 and 3), and adult for birds ringed later than the first year of birth (age code 4+). Finally, the sex code is defined in three classes (Male, Female and Unknown). No live animals were involved in this study, precluding the need for ethical approval.

Because sampling effort varies across schemes and species, we selected a balanced dataset in terms of sample size across Europe for all species, age groups (nestling or adult), and types of recovery (dead or alive) that allowed us to estimate dispersal and tackle the uneven spatial coverage and heterogeneous sampling associated with different types of re-encounter. In particular, we used a stratified random sampling by 5° grid cell to select ringing site locations across Europe, then chose a minimum of 20 records and a maximum of 100 records per 5° grid cell with c. 60% dead recoveries and 40% alive recoveries where possible. Only recoveries where the location of the encounter was known to a precision of ±5 km were included. The data were further screened following the procedure described in Paradis et al. (1998) to remove spurious effects and heterogeneity as far as possible (birds in poor condition, ringing or recovered events in uncommon circumstances, and lack of accuracy on the dates and places of ringing and/or recovery). The ringing data obtained from EURING consisted of 602,703 ringings and re-encountered events from 273 species.

2.2 | Potential bias analysis

Ringing databases hold dispersal information that could not be acquired using alternative techniques. Ring-recovery data are available in large quantities for many species and are not constrained by sampling being restricted to particular locations (Tellería et al., 2012). However, drawing conclusions on dispersal from raw data can be misleading because re-encounters, and hence dispersal distances, are the result of a heterogeneous observation process and subject to strong sample biases (Fandos & Tellería, 2018; Korner-Nievergelt et al., 2010; Naef-Daenzer et al., 2017; Thorup et al., 2014). Here, we used different approaches to exclude data that can lead to potential biases in calculating dispersal for the different species. In particular, those biases related to (i) different recovery rates between types of

recovery, (ii) migratory movements and (iii) the minimum number of cases used to infer robust dispersal estimates:

(i) Although a large variation in ringing and recovery effort could potentially bias the spatial and temporal distributions of ringing data (Figure S9.1), we expect that the large spatial scale of our study, which covers a high proportion of the range extent of most species considered, should minimise the biases associated with the heterogeneous recovery rates. Nevertheless, dead and alive re-encounters may be affected by different biases related to catching effort by ringers and reporting probability (Paradis et al., 1998). For instance, the spatial distribution of birds recaptured alive is likely to differ from dead recoveries as the former depends on the spatial and temporal efforts in field ornithologist activities (more recoveries at places with active research/ ringing stations; Tellería et al., 2014), while the latter are mostly reported by the general public and so are more evenly distributed. At the same time, the cause of death can be an important source of bias since intentionally killed birds are related to differential spatial and temporal hunting patterns and persecution across Europe (Potvin et al., 2017). Therefore, in an exploratory analysis, we compared the dispersal estimates obtained from using different recovery types. The results indicated that all dead recoveries (from a bird that was killed intentionally by humans or by other means) and alive recaptures (but excluding live resightings) showed similar dispersal patterns (see supplemental material 2).

(ii) The dispersal analysis of migratory or partial migratory species is particularly challenging because of variation in migration phenology between individuals and populations across Europe (Lehikoinen et al., 2019). Because migratory movements may lead to overestimation of dispersal distances, we aimed to exclude individuals captured or recovered during migration in the late or early breeding season, using a two-step approach. First, we estimated the potential core breeding period for each species and each spatial (5°) grid cell in Europe to account for the breeding time variation across space. For this, we used generalised additive models (GAMs) to regress dispersal distance against a smoothed function of the time of the year and used the second derivative to distinguish peak migratory periods with sudden increases in dispersal distances from the core breeding season with comparably stable dispersal distances. Second, we used the 95% quantile of the distances observed in the core breeding period as a conservative cut-off distance to distinguish between dispersal events and migratory movements (Supplemental material 3). By this analysis, we potentially identify migrating individuals and exclude them from subsequent analyses, but at the same time, we try to be conservative and avoid excluding potential long-distance dispersal movements.

(iii) Finally, we ran an exploratory analysis, where we used different subsets of ring-recoveries to assess how the number of events would affect the dispersal estimation. We concluded that a minimum of 20 individuals per analysis was sufficient to ensure robust dispersal estimates (ensuring a minimum sample size of $n = 10$ per parameter in two-parameter dispersal kernels).

2.3 | Statistical modelling of dispersal distance kernels

For each species, we fitted an average dispersal kernel (not distinguishing natal and breeding dispersal), and if enough data were available, we additionally fitted natal/breeding dispersal kernels and male/female dispersal kernels. We used a Bayesian approach to fit four commonly used dispersal kernel functions in their one-dimensional form (i.e. probability density functions) directly to the distribution of dispersal distances (Table 1). We selected these four 1- or 2-parameter probability density functions since those have been commonly used in analysing bird dispersal data (Nathan et al., 2012). Overall, because of sample size issues, we fitted average dispersal kernels for 234 species, natal dispersal kernels and breeding dispersal kernels were fitted only for 113 and 122 species, respectively; female and male (average) dispersal kernels were fitted for 141 species; thus, we estimated 3004 dispersal kernels for the combinations of species x four dispersal functions x average/natal/ breeding x female/male dispersal events.

One of the main challenges of fitting dispersal kernels to the EURING database for dispersal analysis is that different schemes have different procedures for reporting birds ringed and subsequently encountered again (Du Feu et al., 2016). For example, some schemes have minimum distances before a bird's re-encounter will be deemed reportable. This means that recaptures below a specific distance from the ringing location are not always reported, and this lower threshold of reporting a recovery varies between schemes. The resulting bias of omitting short dispersal events is problematic because it affects the dispersal kernel's shape. To overcome this problem, we defined two kinds of observation. When the dispersal distance is 0 m, we specified the observation as potentially *censored*. When the observation is precisely known and greater than 0 m, we defined it as *accurate*. Preliminary analyses showed that France had a particularly high threshold for reporting recoveries, but the thresholds for the other schemes also seemed variable. To avoid any arbitrary choices for the censoring thresholds, we decided to infer these from the model.

In the following, we describe the steps to estimate the scheme-specific censoring thresholds and fit the four probability density functions (distributions) to our empirical data (Figure 1). The procedure was carried out separately for average dispersal (pooling all age and sex types; including species with unknown sex codes), breeding and natal dispersal (pooling sex types; including species with unknown sex codes), and male and female dispersal (pooling age dispersal). The Bayesian framework was implemented in STAN (Stan Development Team, 2021) and R version 4.0.5 (R Core Team, 2020) by using RSTAN R package (Stan Development Team, 2022), and code is available (see Data availability statement). All models were run with 4 chains and 2000 iterations, and convergence of the algorithms were checked by

TABLE 1 Alternative probability density functions to estimate dispersal kernels k for European birds. We provide the expressions of the one-dimensional dispersal distance kernels k_D as function of the distance d, as well as the parameters to estimate for each function. The frequency corresponds to the posterior model probabilities from the expected log posterior pointwise density divided by the number of species (frequency = 1 indicates the most likely distribution). The three bars represent the frequency with which each dispersal kernel best fitted the different dispersal types using the log posterior pointwise density (average: yellow, breeding: blue and natal: grey). [Correction added on 03 November 2022, after first online publication: table 1 has been revised]

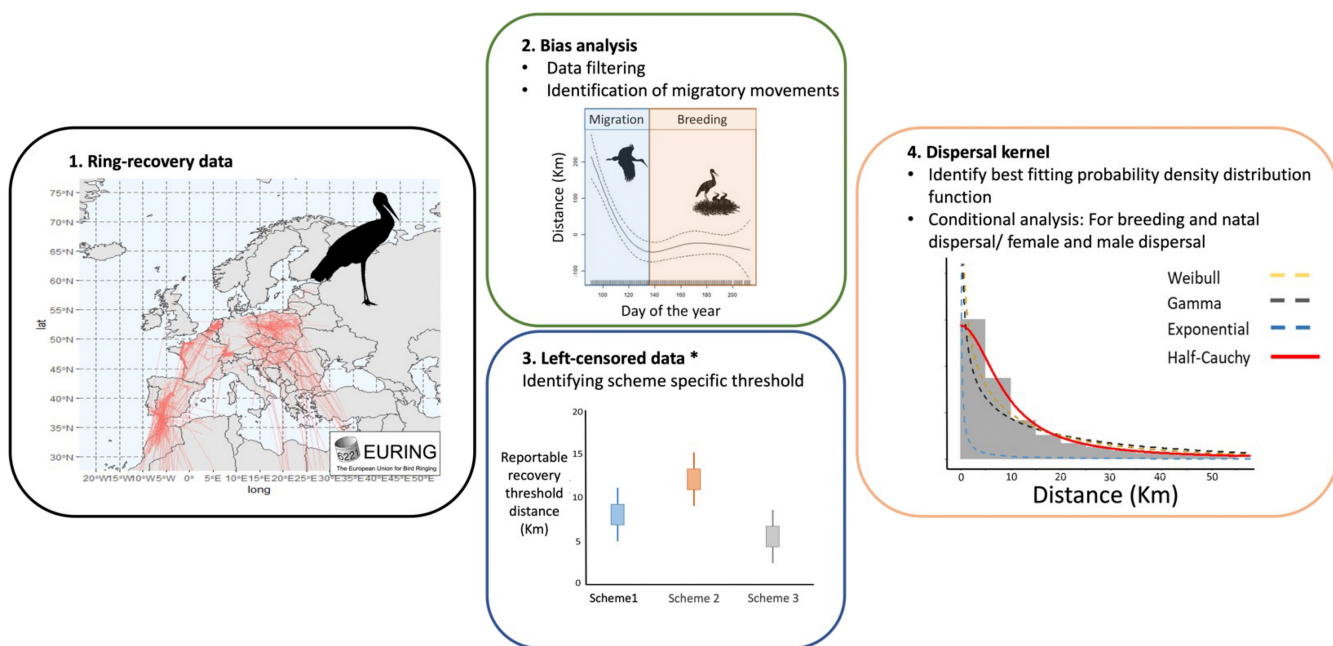| Kernel name	$k_D(d)$ expression	Parameter(s) (name)	Frequency
Exponential (EX)	$\lambda e^{-\lambda d}$	λ (rate)	
Weibull (WE)	$\beta / \delta \left(\frac{d}{\delta}\right)^{\beta-1} exp\left[-\left(\frac{d}{\delta}\right)^{\beta}\right]$	β (shape), δ (scale)	
Gamma (GA)	$\frac{\beta^{\alpha}}{\Gamma(\alpha)} \chi^{\alpha-1} e^{-\beta \chi}$	α (shape), β (rate)	
Half-Cauchy (HC)	$2\sigma / \Pi \left(\sigma^2 + d^2\right)$	σ (scale)	

FIGURE 1 Estimating specific dispersal parameters (White stork, *Ciconia ciconia* as an example). (1) A spatially balanced data set per species was requested from EURING. (2) Data screening included potential bias analysis accounting for the different recovery rates between recovery types (live recaptures, resightings and dead recoveries), and migratory movements. (3) Scheme-specific thresholds for the reported recovery threshold distance were estimated. Finally, (4) four different density distributions (Exponential, Gamma, Weibull and Half-Cauchy were fitted to all species, and the best fitting distribution was identified for each species.

the Rhat value. If Rhat is considerably greater than 1 (i.e. >1.1), the chains have not yet converged (Gelman & Rubin, 1992).

1. To make use of maximum information for identifying the scheme-specific censoring thresholds, we first fitted a separate dispersal kernel for each species, with a shared parameter describing the threshold for each scheme. We repeated this process for each dispersal function (exponential, Gamma, Weibull, half-Cauchy). We selected the best-fitting distribution by calculating the expected log posterior pointwise density (elppd) for each distribution

and compared them using the LOO package (Vehtari et al., 2022) to carry out Pareto smoothed importance-sampling leave-one-out cross-validation (PSIS-LOO). Better fitting distributions will have a higher log posterior pointwise density (Vehtari et al., 2017). Finally, we estimated the posterior distribution of the scheme-specific censoring threshold parameter using this best model.

2. We used the posterior distribution of the scheme-specific threshold parameter from the previous step as an informative prior in single-species models and for each dispersal function. The objective of these models was to estimate the dispersal kernels for each species, given the degree of left-censoring, and compute the posterior model probabilities from marginal likelihoods.

3. Assess which distribution is the "best" for each species using two different approaches for model comparison: (a) We use the marginal log-likelihood via bridge sampling (Gronau et al., 2020) by calculating a Bayes factor with the BRIDGERSAMPLER R package (Gronau et al., 2020). (b) We calculated the expected log posterior pointwise density (elppd) for each distribution and compared them using LOO package (Vehtari et al., 2022). In case of contrasting results between both model comparisons approaches, we used the log posterior pointwise density because it is a more robust measure than Bayes factors that are very sensitive to the model priors (Schad et al., 2022).

4. For all species and dispersal functions, we (a) extracted the dispersal kernel parameters (the mean and the credible interval of each parameter), (b) analytically derived the empirical median dispersal distance from the dispersal kernels (and the 95% credible interval for the median), and (c) derived long-distance dispersal measures, which we defined as the 95% percentile from a posterior predictive dispersal simulation with the estimated parameters.

2.4 | Phylogenetic signal in dispersal estimates

We used multivariate generalised linear mixed models (GLMMs) to estimate the phylogenetic dependency in both descriptors of dispersal ability, the median and the long-distance dispersal estimates (95% upper percentile of dispersal distances). Specifically, we estimated the phylogenetic dependency for both dispersal descriptors (median and 95% quantile) extracted from the best-fitted distribution (higher log posterior pointwise density of each species) and separately from each kernel function (e.g. phylogenetic signal in median dispersal estimates from the Weibull distribution). Dispersal estimates were log-transformed to satisfy assumptions of normality and linearity and scaled to have a mean of 0 and a variance of 1. We fitted separate multivariate Gaussian models for the median and the long-distance dispersal and included phylogenetic relatedness as a random effect. We fitted both models including no fixed effects and estimated the amount of variation in the dispersal estimates explained by shared ancestry between species (i.e. phylogenetic signal) by calculating Pagel's λ (Pagel, 1999). Pagel's λ values range between 0, implying no phylogenetic signal, and 1, when a trait evolves under Brownian motion (Pagel, 1999). Phylogenetic signal values were

tested for the null hypothesis of absence of signal (i.e. dispersal values are randomly distributed in the phylogeny) by likelihood ratio for λ using PHYLOSIGNAL R package (Keck et al., 2016), and based on a total of 10,000 permutations.

All GLMMs were implemented in a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling in the R package MCMCGLMM (Hadfield, 2010). We ran all models with three chains and 100,000 iterations, with a burn-in period of 1000 and a sampling interval of 50. The convergence of the models was confirmed by examining the effective sample size (>1000) and autocorrelation between samples (<0.10) for each chain, as well as the Gelman–Rubin statistics (Rhat < 1.1) among chains. Priors were initially set using inverse-Wishart priors for the phylogenetic and residual variance ($V = 1$, $\nu = 0.002$). Parameter estimates from models are reported as the posterior modes with 95% lower and upper credible intervals (CIs). All phylogenetic analyses were conducted on a sample of 100 trees obtained from the Hackett backbone of the global bird phylogeny (www.birdtree.org; Jetz et al., 2012).

2.5 | Dispersal differences between age (breeding and natal) and sex (female and male) classes

First, we tested dispersal differences between age groups by an ANOVA. Then, we explored the association between natal and breeding dispersal estimates (median and long-distance dispersal) for all species while accounting for the non-independence of species related to their joint evolutionary history by using a multivariate generalised linear mixed model (see above for details about priors and model fitting). We fitted two independent models using the median and the long-distance natal dispersal distance as response variables, the median and the long-distance breeding dispersal distance respectively as a fixed effect and phylogeny as a random effect. We fitted both models for the subset of 108 species where all measures were available.

Second, we tested dispersal differences between sexes by an ANOVA. Then we explored the association between female and male dispersal estimates (median and long-distance dispersal). In this case, we fitted two independent models using the median and the long-distance female distance as the response variable, the median and the long-distance male dispersal distance, respectively as a fixed effect and phylogeny as a random effect. We fitted both models for the subset of 137 species where all measures were available.

Third, we ran the same models to estimate the association between the mean dispersal distances reported in Paradis et al. (1998) and our median dispersal estimates (from the best-fitting distribution) for the subset of 75 species where both measures were available. Finally, we also explored the relationship between median versus long-distance dispersal by fitting multivariate generalised linear mixed models, with the median dispersal distance as a response variable, the long-distance estimate as a fixed effect and the phylogenetic relatedness as a random effect.

For the analyses of dispersal differences related to age and sex, we used the Weibull distribution for all dispersal estimates to make

fair comparisons. All estimates were log-transformed to satisfy assumptions of normality and linearity and then scaled to have a mean of 0 and a variance of 1.

3 | RESULTS

We analysed a total of 563,276 capture-recapture events from 234 species (median capture-recapture event per species n = 419, max = 27,837, min = 21), covering 55 bird families. The four probability density functions converged for all species. The Weibull distribution was the best-fitting function for 88 out of 234 species (38%, Figure 2; Table 1). The half-Cauchy distribution was the best one for 78 species (33%), the Gamma for 47 species (20%) and the exponential for 21 species (9%). We analysed a total of 122 species for natal dispersal, and the half-Cauchy distribution and Weibull were the best-fitting function for the majority of the species (51 and 42 respectively out of 122 species, equalling 42% and 35%). In the case of the breeding dispersal, the half-Cauchy was the best-fitting function for 53 out of 113 species (47%) analysed. Similarly, half-Cauchy and Weibull were the best-fitted functions for female (53 and 41 species respectively out of 140) and male dispersal (45 and 50 species respectively out of 140). We also found a relationship between the number of ring-recoveries used in the analysis and the best function fitted, with exponential and gamma distribution being the best fit for species with lower sample sizes (Table S10.1). However, the leave-one-out cross-validation indicated no strong difference in prediction accuracy of the different kernel functions (as reflected by the log posterior pointwise density). Reassuringly, the subset of species with large enough sample sizes to estimate breeding (n = 122) and natal dispersal (n = 113) reflected well the range of dispersal distances found over all species (n = 234; Figure S8.1).

The dispersal estimates (median and long-distance dispersal) varied between species and species orders (Figure 3; Figure S7.1),

and we found a general positive correlation between median and long-distance dispersal 0.872 (95% CI: 0.821–0.944; pMCMC < 0.01; Figure S11.1).

The phylogenetic signal of the median and long dispersal distances is summarised in Table 2. The phylogenetic signal was highly dependent on the fitted distribution to estimate dispersal (median λ range: 0.117–0.757; long λ range: 0.161–0.743), and was especially low when we used the best-fitted distribution for each species on both dispersal metrics or the Gamma distribution.

On average, median natal dispersal distances (mean: 7.74 km; sd: 10.49) were larger than median breeding dispersal distances (mean: 2.83 km; sd: 5.91; F-value = 20.4; p-value < 0.001; Figure 4a). Natal and breeding dispersal estimates from the Weibull distribution had a positive correlation for the median 0.668 (95% CI: 0.508–0.829; pMCMC < 0.001; Figure 4b) and long-distance dispersal 0.762 (95% CI: 0.624–0.892; pMCMC < 0.001; Figure S5.1). We also found positive correlations when we compared median natal and breeding dispersal estimates for the best-fitting kernels (see Figure S5.2).

In contrast, dispersal distance did not differ between sex on average (F-value = 0.127; p-value = 0.722; Figure S12.1). Female and male dispersal estimates from the Weibull distribution had a positive correlation for the median (r = 0.889; 95% CI: 0.823–0.975; pMCMC < 0.001; Figure S12.1b) and long-distance dispersal (r = 0.968; 95% CI: 0.912–1.039; pMCMC < 0.001).

Median dispersal estimates (from the best-fitting kernels) were also positively associated with mean dispersal distances reported for n = 75 species in Paradis et al. (1998) (Figure S6.1).

4 | DISCUSSION

While much theory has been developed around bird dispersal and their impacts on populations, few empirical studies have estimated and synthesised dispersal kernels for multiple species, although an
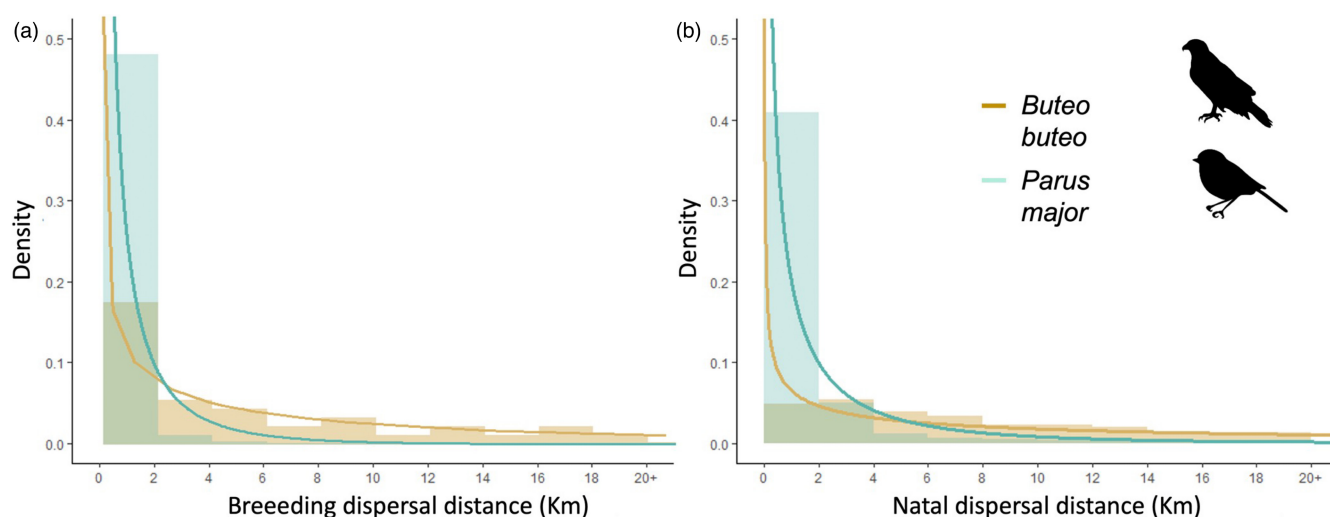

FIGURE 2 Breeding (a) and natal (b) dispersal kernels for two species: *Parus major* and *Buteo buteo*. Bars represent observed frequency distributions and lines the Weibull probability density curves.
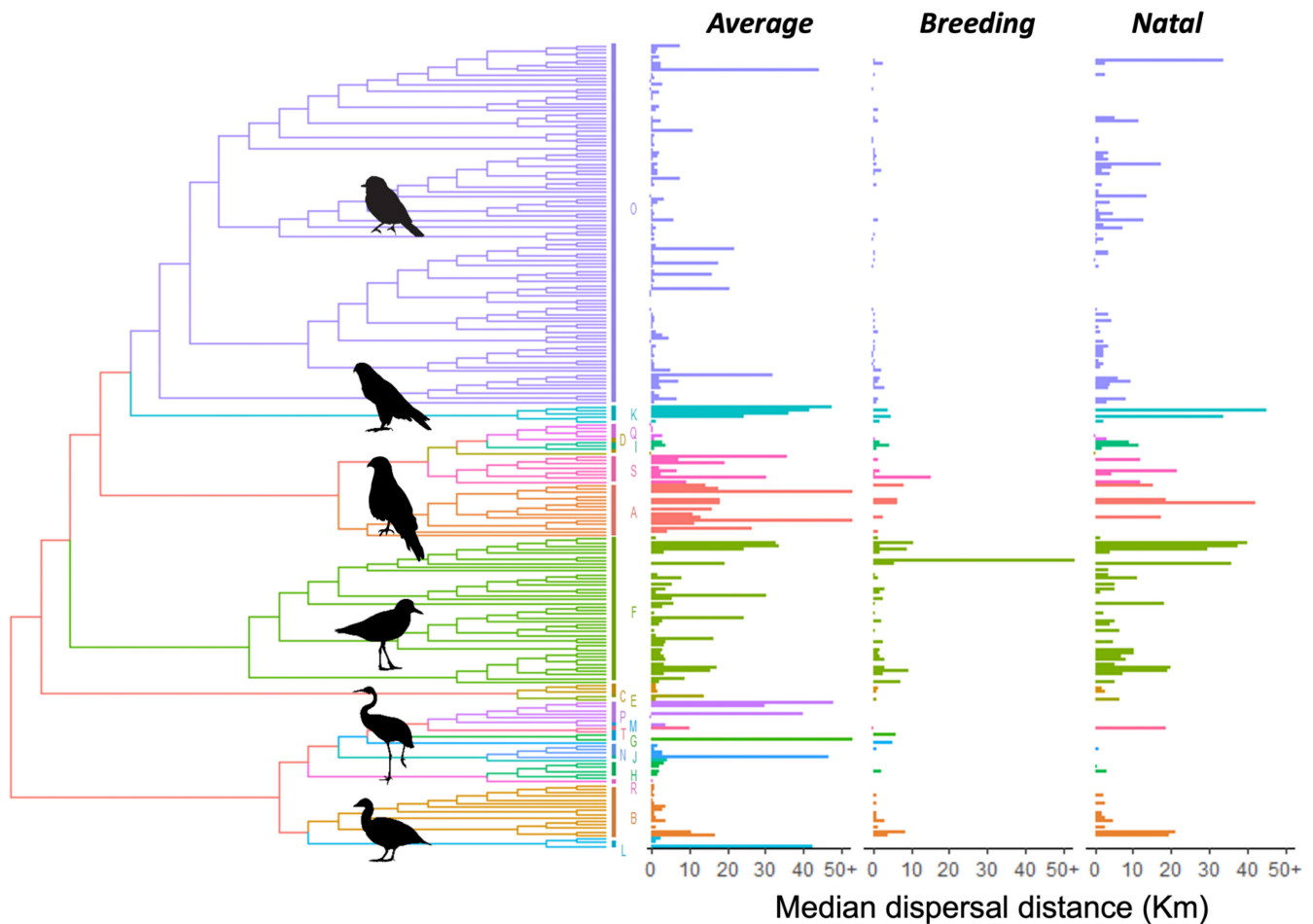
FIGURE 3 Median dispersal distance (km) from the best-fitting distribution along the bird phylogeny for the average (234 species), breeding (113 species) and natal dispersal (121 species). The dispersal distance is truncated at 50 km for visualisation purposes. Each colour and letter represent the same order in the phylogeny and the bar plots. A: Accipitiformes, B: Anseriformes, C: Apodiformes, D: Bucerotiformes, E: Caprimulgiformes, F: Charadriiformes, G: Ciconiiformes, H: Columbiformes, I: Coraciiformes, J: Cuculiformes, K: Falconiformes, L: Galliformes, M: Gaviformes, N: Gruiformes; O: Passeriformes, P: Pelecaniformes, Q: Piciformes, R: Podicipediformes, S: Strigiformes, T: Suliformes.

TABLE 2 Phylogenetic signal λ for the median and long-distance dispersal are estimated for each distribution and the best-fitted distribution (higher log posterior pointwise density) for each species (average dispersal kernels)

	Median dispersal			Long-distance dispersal		
	Lambda	CI		Lambda	CI	
Exponential	0.752***	0.572	0.893	0.732***	0.542	0.905
Weibull	0.758***	0.600	0.896	0.743***	0.585	0.897
Gamma	0.117	0.002	0.309	0.217	0.044	0.428
Hcauchy	0.755***	0.596	0.888	0.743***	0.573	0.886
Best-fitted	0.219	0.041	0.458	0.161	0.041	0.458

p-values are based on 10,000 permutations: ***$p < 0.001$. Constrained evolution relative to Brownian motion if Pagel's λ (0; 1) >0.5.

important prerequisite for modelling species spatial dynamics (but see Paradis et al., 2002; Van Houtan et al., 2007). In this paper, we estimated average dispersal kernels for 234 bird species across Europe, natal and breeding dispersal kernels for a subset of 122 and 113 species, respectively, and female and male dispersal kernels for a subset of 140 species in both. This extensive analysis allows an improved understanding of interspecific variations in dispersal patterns and strategies in European birds. Specifically, we found that the dispersal of almost all bird species across age (natal and breeding dispersal) and sex (females and males) follows a heavy-tailed distribution, indicating a general tendency towards long-distance dispersal in birds. This result supports previous findings in active
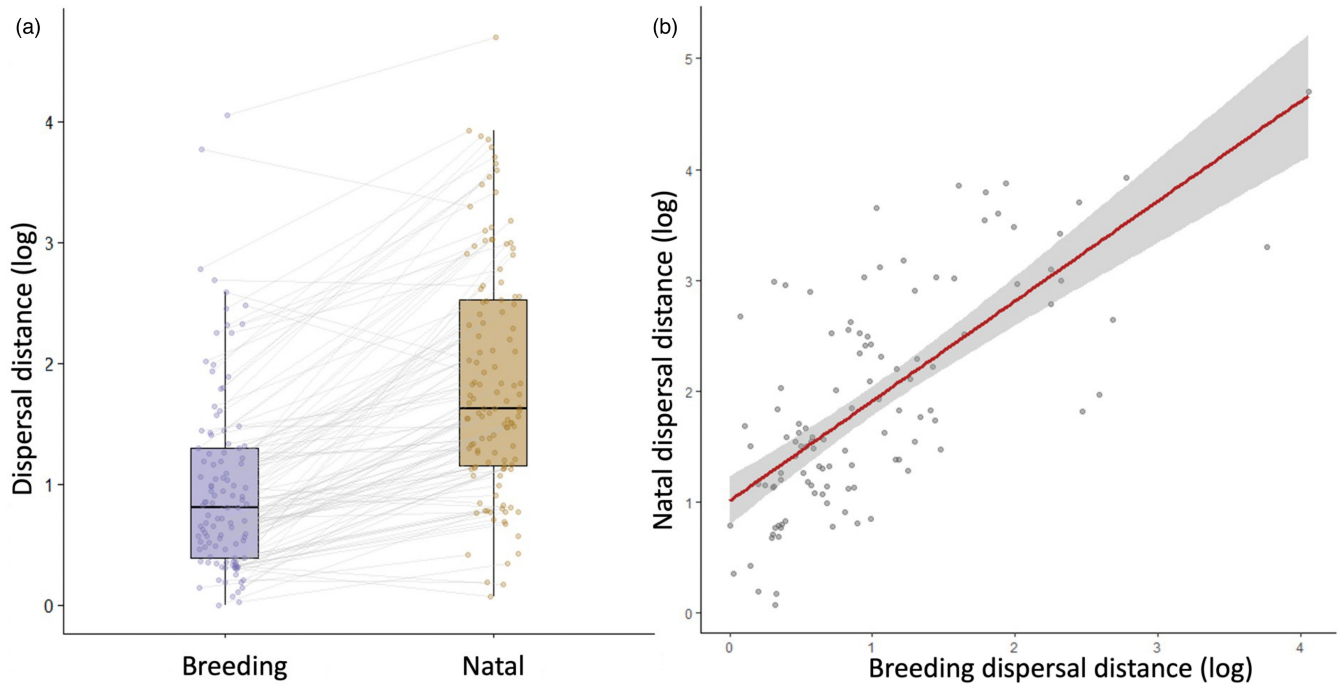
FIGURE 4 (a) Boxplot diagram for the log median dispersal distance (km) estimated from the Weibull distribution for natal and breeding dispersal. Lines connect the same species in both types of dispersal. (b) Linear relationship between breeding and natal dispersal distances (log) estimated from the Weibull distribution.

dispersers that although most individuals of most species do not move far, a small proportion of individuals can disperse long distances (Paradis et al., 2002; Van Houtan et al., 2007). However, in some species, the statistical support for different dispersal kernel functions was very similar indicating that they are generally simple statistical descriptions of the complex dispersal process (Bullock et al., 2017; Nathan et al., 2012). The standardised dispersal estimates from different underlying kernel functions will allow researchers to use kernels in combination and represent uncertainty in the dispersal estimates.

Long-distance dispersal events are extremely important for population dynamics and range colonisation across changing landscapes, but their low frequency and detectability make them hard to measure and quantify (Clobert et al., 2012; Travis et al., 2013). Empirical dispersal kernels are a fundamental tool to address many of the limitations for characterising dispersal patterns (Bullock et al., 2017; Nathan et al., 2012), in particular when direct measures of dispersal fail to capture the frequency of potential long-distance dispersal events (Koenig et al., 1996; Whitmee & Orme, 2013). The standardisation of dispersal kernels across a wide range of species should allow more realistic and representative forecasts of potential species distributions and better integration of dispersal in comparative life-history analysis (Bullock et al., 2017; Nathan et al., 2012; Stevens et al., 2012). Our analyses clearly showed that dispersal kernel functions that assume an underlying random walk are insufficient in explaining observed dispersal distances. Rather, heavy-tailed kernel functions received much higher support from our data. The heavy-tailed distributions probably result from the interplay or

overlap of multiple movement modes that widen dispersal kernels when considered simultaneously (Nathan, 2008). Dispersers may switch between movement modes based on the complex trade-offs between internal state, environmental context, motion capacity and navigational ability (Nathan, 2008). Future analyses will benefit from integrating detailed movement behaviour with improved analytical methods to understand how environmental context affects dispersal and consequently, eco-evolutionary dynamics in space (Bonte & Dahirel, 2017).

Phylogenetic information has been extensively used to infer dispersal distances for species without data (Barbet-Massin et al., 2012; Thomas, 2008). However, this approach neglects that dispersal can evolve rapidly by adaptive processes (Stevens et al., 2010), and that contrasting environmental conditions can generate variability in phenotypic dispersal patterns among individuals or populations (Beckman et al., 2018; Bonte & Dahirel, 2017; Clobert et al., 2009). Our results show that both long and median dispersal distances have a wide range of phylogenetic conservatism depending on the distribution fitted on each species (Table 2). When comparing dispersal estimates based on the same kernel function, the phylogenetic signal for long and median dispersal was significant for most distribution functions except the Gamma distribution. However, we found weak phylogenetic conservatism for median and long-distance dispersal when we used the best-fitted distribution for each species (Table 2), indicating that species exhibit distinct dispersal distances despite a common evolutionary history. Overall, the phylogenetic liability in bird dispersal suggests that evolutionary history should only be

used as a predictor of dispersal ability when data are scarce and should otherwise be used with caution.

Accurately measuring age or sex-specific dispersal differences for many species has typically been hampered by the low juvenile survival rates compared to adults, the impossibility of separating by sex based on the plumage in some species, and because dispersal distances often exceed study area boundaries (Greenwood & Harvey, 1982; Newton, 1998). Here, we take advantage of continent-wide ringing and recovery efforts to show, first, that natal dispersal of immature individuals that depart their natal range in search of new sites is generally more extensive and covers a wider geographical area than breeding dispersal (Greenwood & Harvey, 1982; Hollenbeck et al., 2018; Paradis et al., 1998). This considerable dispersal asymmetry between ages could arise from a range of selective pressures, such as inbreeding avoidance, competition among offspring, or simply finding suitable habitat (Clobert et al., 2012). In contrast, mature breeders have evolved comparably lower breeding dispersal rates favouring territories they already know from previous breeding attempts (Kokko & Lundberg, 2001). Second, although female-biased dispersal has been widely identified in many socially monogamous bird species (Greenwood, 1980; Li & Kokko, 2019), we found no evidence for widespread sex-biased dispersal patterns. Additional social or ecological factors might need to be considered to explain the lack of dispersal sex bias (Li & Kokko, 2019), such as the interaction between sex and age dispersal and the analysis of both dispersal frequency and dispersal distance, which measure different aspects of the dispersal process and have often been confounded (Mabry et al., 2013). Disentangling whether dispersal strategies are conditional on age and/or sex is essential to understanding how demography and fitness influence the overall dispersal process (Bonte et al., 2011).

Studies of marked individuals are essential for understanding life histories and population dynamics. The EURING database provides an unrivalled source of mark-recapture information at a continental scale that is of immense value to ecology and conservation (Du Feu et al., 2016) including, as we have shown here, for estimating empirical dispersal distributions. However, sampling effort and detection in ring-recovery data vary considerably over time, space, species, and recovery types (Figure S9.1; Naef-Daenzer et al., 2017; Perdeck, 1977; Thorup et al., 2014). If not corrected for, this typically results in unsubstantiated estimates of dispersal that can lead to biased results or, in the worst case, to wrong conclusions. Here, we identified sampling biases related to heterogeneous variation in ring and recapture activities (uneven spatial coverage, uneven sampling effort per type of recapture, heterogeneous reporting threshold between schemes) and biases related to the recoveries of birds on migration. We approached these biases by (1) using methods to exclude (filter) and standardise subsets of the data, keeping only the reliable observations (Geldmann et al., 2016) and (2) with an appropriate analytical approach to estimate dispersal for left-censored data using a Bayesian approach. This approach can be helpful for those working with large mark-recapture datasets from any taxa which cannot infer sampling effort or account for uneven detectability (using the provided code, see Data Accessibility). The filtering process and analysis could also be helpful to improve running monitoring programs or plan future ones.

The robust empirical characterisation of the avian dispersal kernels as presented in this study is crucial for conservation and management and for predicting potential future range changes. The estimated dispersal distances as well as the analytical tools designed here provide many avenues for future research. Outstanding questions include, among others, the assessment of dispersal syndromes to understand how dispersal kernels vary across species traits and explore covariation patterns between dispersal and other traits (Clobert et al., 2009; Ronce & Clobert, 2012) and the exploration of how dispersal processes respond to habitat fragmentation and climate change (Bowler & Benton, 2005; Travis et al., 2013). The presented study paves the road towards a new generation of more realistic modelling and comparative studies to evaluate the role of dispersal in several issues of population biology and their eco-evolutionary dynamics under global change.

AUTHOR CONTRIBUTIONS

Guillermo Fandos: Conceptualization (equal); Investigation (equal); Data request (lead); Formal analysis (lead); Methodology (lead); Writing—original draft (lead); Writing-review & editing (lead). Matthew Talluto: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing-review and editing (equal). Wolfgang Fiedler: Conceptualization (equal); Investigation (supporting); Data request (supporting); Writing—original draft (supporting); Writing-review & editing (equal). Robert A. Robinson: Conceptualization (equal); Investigation (supporting); Data request (supporting); Methodology (supporting); Writing-review and editing (equal). Kasper Thorup: Conceptualization (equal); Investigation (supporting); Data request (supporting); Writing-review and editing (equal). Damaris Zurell: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Data request (equal); Formal analysis (equal); Methodology (equal); Writing—original draft (equal), Writing-review & editing (equal).

ACKNOWLEDGEMENTS

FUNDING INFORMATION

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

ORCID

Guillermo Fandos https://orcid.org/0000-0003-1579-9444
Matthew Talluto https://orcid.org/0000-0001-5188-7332
Robert A. Robinson https://orcid.org/0000-0003-0504-9906
Kasper Thorup https://orcid.org/0000-0002-0320-0601
Damaris Zurell https://orcid.org/0000-0002-4628-3558

REFERENCES

Barbet-Massin, M., Thuiller, W., & Jiguet, F. (2012). The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology*, *18*(3), 881–890. https://doi.org/10.1111/j.1365-2486.2011.02552.x

Beckman, N. G., Bullock, J. M., & Salguero-Gómez, R. (2018). High dispersal ability is related to fast life-history strategies. *Journal of Ecology*, *106*(4), 1349–1362. https://doi.org/10.1111/1365-2745.12989

Bonte, D., & Dahirel, M. (2017). Dispersal: A central and independent trait in life history. *Oikos*, *126*(4), 472–479. https://doi.org/10.1111/oik.03801

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., ... Travis, J. M. J. (2011). Costs of dispersal. *Biological Reviews*, *87*(2), 290–312. https://doi.org/10.1111/j.1469-185x.2011.00201.x

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews*, *80*(2), 205–225. https://doi.org/10.1017/S1464793104006645

Bullock, J. M., Mallada González, L., Tamme, R., Götzenberger, L., White, S. M., Pärtel, M., & Hooftman, D. A. P. (2017). A synthesis of empirical plant dispersal kernels. *Journal of Ecology*, *105*(1), 6–19. https://doi.org/10.1111/1365-2745.12666

Claramunt, S. (2021). Flight efficiency explains differences in natal dispersal distances in birds. *Ecology*, *102*(9), e03442. https://doi.org/10.1002/ecy.3442

Clobert, J., Baguette, M., Benton, T. G., & Bullock, J. M. (2012). *Dispersal ecology and evolution*. Oxford University Press.

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, *12*(3), 197–209. https://doi.org/10.1111/j.1461-0248.2008.01267.x

Dawideit, B. A., Phillimore, A. B., Laube, I., Leisler, B., & Böhning-Gaese, K. (2009). Ecomorphological predictors of natal dispersal distances in birds. *Journal of Animal Ecology*, *78*(2), 388–395. https://doi.org/10.1111/j.1365-2656.2008.01504.x

Du Feu, C. R., Clark, J. A., Schaub, M., Fiedler, W., & Baillie, S. R. (2016). The EURING Data Bank – A critical tool for continental-scale studies of marked birds. *Ringing & Migration*, *31*(1), 1–18. https://doi.org/10.1080/03078698.2016.1195205

Fandos, G., Matthew, T., Fiedler, W., Robinson, R. A., Thorup, K., & Zurell, D. (2021). *European_bird_dispersal: V1.0.3-Edispersal. Zenodo*, https://doi.org/10.5281/zenodo.7191344

Fandos, G., & Tellería, J. L. (2018). Range compression of migratory passerines in wintering grounds of the Western Mediterranean: Conservation prospects. *Bird Conservation International*, *28*(3), 462–474. https://doi.org/10.1017/S0959270917000120

Geldmann, J., Heilmann-Clausen, J., Holm, T. E., Levinsky, I., Markussen, B., Olsen, K., Rahbek, C., & Tøttrup, A. P. (2016). What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Diversity and Distributions*, *22*(11), 1139–1149. https://doi.org/10.1111/ddi.12477

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–472.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*(4), 1140–1162. https://doi.org/10.1016/S0003-3472(80)80103-5

Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, *13*(1), 1–21. https://doi.org/10.1146/annurev.es.13.110182.000245

Gronau, Q. F., Singmann, H., & Wagenmakers, E.-J. (2020). Bridgesampling: An R package for estimating normalizing constants. *Journal of Statistical Software*, *92*(1), Article 1. https://doi.org/10.18637/jss.v092.i10

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22.

Hallatschek, O., & Fisher, D. S. (2014). Acceleration of evolutionary spread by long-range dispersal. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(46), E4911–E4919. https://doi.org/10.1073/pnas.1404663111

Hobson, K. A. (2005). Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions*, *11*(2), 157–164. https://doi.org/10.1111/j.1366-9516.2005.00149.x

Hollenbeck, J. P., Haig, S. M., Forsman, E. D., & Wiens, J. D. (2018). Geographic variation in natal dispersal of Northern Spotted Owls over 28 years. *The Condor*, *120*(3), 530–542. https://doi.org/10.1650/condor-17-164.1

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/nature11631

Kays, R., McShea, W. J., & Wikelski, M. (2020). Born-digital biodiversity data: Millions and billions. *Diversity and Distributions*, *26*(5), 644–648. https://doi.org/10.1111/ddi.12993

Keck, F., Rimet, F., Bouchez, A., & Franc, A. (2016). Phylosignal: An R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, *6*(9), 2774–2780. https://doi.org/10.1002/ece3.2051

Kisel, Y., & Barraclough, T. G. (2010). Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, *175*(3), 316–334. https://doi.org/10.1086/650369

Koenig, W. D., Van Vuren, D., & Hooge, P. N. (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution*, *11*(12), 514–517. https://doi.org/10.1016/S0169-5347(96)20074-6

Kokko, H., & Lundberg, P. (2001). Dispersal, migration, and offspring retention in saturated habitats. *The American Naturalist*, *157*(2), 188–202. https://doi.org/10.1086/318632

Korner-Nievergelt, F., Sauter, A., Atkinson, P. W., Guélat, J., Kania, W., Kéry, M., Köppen, U., Robinson, R. A., Schaub, M., Thorup, K., Van Der Jeugd, H., & Van Noordwijk, A. J. (2010). Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. *Journal of Avian Biology*, *41*(1), 8–17. https://doi.org/10.1111/j.1600-048X.2009.04907.x

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., & Kays, R. (2011). The Movebank data model for animal tracking. *Environmental Modelling & Software*, *26*(6), 834–835. https://doi.org/10.1016/j.envsoft.2010.12.005

Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T. L., Dunn, E. H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., Røer, J. E., Sharpe, C., Sokolov, L. V., Steinholtz, Å., Stervander, M., Tirri, I.-S., & Tjørnløv, R. S. (2019). Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators*, *101*, 985–991. https://doi.org/10.1016/j.ecolind.2019.01.083

Li, X.-Y., & Kokko, H. (2019). Sex-biased dispersal: A review of the theory. *Biological Reviews*, *94*(2), 721–736. https://doi.org/10.1111/brv.12475

Mabry, K. E., Shelley, E. L., Davis, K. E., Blumstein, D. T., & Vuren, D. H. V. (2013). Social mating system and sex-biased dispersal in mammals and birds: A phylogenetic analysis. *PLoS ONE*, *8*(3), e57980. https://doi.org/10.1371/journal.pone.0057980

Millon, A., Lambin, X., Devillard, S., & Schaub, M. (2019). Quantifying the contribution of immigration to population dynamics: A review of methods, evidence and perspectives in birds and mammals. *Biological Reviews*, *94*(6), 2049–2067. https://doi.org/10.1111/brv.12549

Naef-Daenzer, B., Korner-Nievergelt, F., Fiedler, W., & Grüebler, M. U. (2017). Bias in ring-recovery studies: Causes of mortality of little owls *Athene noctua* and implications for population assessment. *Journal of Avian Biology*, *48*(2), 266–274. https://doi.org/10.1111/jav.00947

Nathan, R. (2001). The challenges of studying dispersal. *Trends in Ecology & Evolution*, *16*(9), 481–483. https://doi.org/10.1016/S0169-5347(01)02272-8

Nathan, R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19050–19051. https://doi.org/10.1073/pnas.0808918105

Nathan, R., Klein, E., Robledo-Arnuncio, J. J., & Revilla, E. (2012). Dispersal kernels: Review 25.

Newton, I. (1998). *Population limitation in birds*. Academic Press.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–884. https://doi.org/10.1038/44766

Paradis, E., Baillie, S. R., & Sutherland, W. J. (2002). Modeling large-scale dispersal distances. *Ecological Modelling*, *151*(2), 279–292. https://doi.org/10.1016/S0304-3800(01)00487-2

Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, *67*(4), 518–536. https://doi.org/10.1046/j.1365-2656.1998.00215.x

Perdeck, A. C. (1977). The analysis of ringing data: Pitfalls and prospects. *Vogelwarte*, *29*, 33–44.

Potvin, D. A., Pavón-Jordán, D., & Lehikoinen, A. (2017). To filter or not to filter: Assessing the exclusion of hunting and persecution data in ringing recovery studies. *Ornis Fennica*, *94*, 17.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ronce, O., & Clobert, J. (2012). Dispersal syndromes. *Dispersal Ecology and Evolution*, *155*, 119–138.

Schad, D. J., Nicenboim, B., Bürkner, P.-C., Betancourt, M., & Vasishth, S. (2022). Workflow techniques for the robust use of bayes factors. *Psychological Methods*. https://doi.org/10.1037/met0000472

Schaub, M., & Ullrich, B. (2021). A drop in immigration results in the extinction of a local woodchat shrike population. *Animal Conservation*, *24*(3), 335–345. https://doi.org/10.1111/acv.12639

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, *11*(1), 2463. https://doi.org/10.1038/s41467-020-16313-6

Stan Development Team. (2021). Stan user's guide. https://mc-stan.org/docs/2_18/stan-users-guide/index.html

Stan Development Team. (2022). *RStan: The R interface to Stan*. R package version 2.21.7. https://mc-stan.org/

Stevens, V. M., Pavoine, S., & Baguette, M. (2010). Variation within and between closely related species uncovers high intra-specific variability in dispersal. *PLoS ONE*, *5*(6), e11123. https://doi.org/10.1371/journal.pone.0011123

Stevens, V. M., Trochet, A., Van Dyck, H., Clobert, J., & Baguette, M. (2012). How is dispersal integrated in life histories: A quantitative analysis using butterflies: Dispersal life-history correlates. *Ecology Letters*, *15*(1), 74–86. https://doi.org/10.1111/j.1461-0248.2011.01709.x

Stevens, V. M., Whitmee, S., Le Galliard, J.-F., Clobert, J., Böhning-Gaese, K., Bonte, D., Brändle, M., Matthias Dehling, D., Hof, C., Trochet, A., & Baguette, M. (2014). A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology Letters*, *17*(8), 1039–1052. https://doi.org/10.1111/ele.12303

Tellería, J. L., Fernández-López, J., & Fandos, G. (2014). Using ring records and field surveys to predict the winter distribution of a migratory passerine. *Bird Study*, *61*(4), 527–536. https://doi.org/10.1080/00063657.2014.953033

Tellería, J. L., Santos, T., Refoyo, P., & Muñoz, J. (2012). Use of ring recoveries to predict habitat suitability in small passerines. *Diversity and Distributions*, *18*(11), 1130–1138. https://doi.org/10.1111/j.1472-4642.2012.00900.x

Thomas, G. H. (2008). Phylogenetic distributions of British birds of conservation concern. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1647), 2077–2083. https://doi.org/10.1098/rspb.2008.0549

Thorup, K., Korner-Nievergelt, F., Cohen, E. B., & Baillie, S. R. (2014). Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: A review including methodological perspectives. *Methods in Ecology and Evolution*, *5*(12), 1337–1350. https://doi.org/10.1111/2041-210X.12258

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, *122*(11), 1532–1540. https://doi.org/10.1111/j.1600-0706.2013.00399.x

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. V., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., … Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466–469. https://doi.org/10.1126/science.aam9712

Van Houtan, K. S., Pimm, S. L., Halley, J. M., Bierregaard, R. O., Jr., & Lovejoy, T. E. (2007). Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters*, *10*(3), 219–229. https://doi.org/10.1111/j.1461-0248.2007.01004.x

Van Houtan, K. S. V., Bass, O. L., Lockwood, J., & Pimm, S. L. (2010). Importance of estimating dispersal for endangered bird management. *Conservation Letters*, *3*(4), 260–266. https://doi.org/10.1111/j.1755-263X.2010.00108.x

Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T., Gelman, A., Goodrich, B., Piironen, J., & Nicenboim, B. (2022). *Loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models* (2.5.1). https://CRAN.R-project.org/package=loo

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*(5), 1413–1432. https://doi.org/10.1007/s11222-016-9696-4

Venail, P. A., MacLean, R. C., Bouvier, T., Brockhurst, M. A., Hochberg, M. E., & Mouquet, N. (2008). Diversity and productivity peak at

intermediate dispersal rate in evolving metacommunities. *Nature*, *452*(7184), Article 7184. https://doi.org/10.1038/nature06554

Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A., & Stanley, H. E. (1996). Lévy flight search patterns of wandering albatrosses. *Nature*, *381*(6581), 413–415. https://doi.org/10.1038/381413a0

Whitmee, S., & Orme, C. D. L. (2013). Predicting dispersal distance in mammals: A trait-based approach. *Journal of Animal Ecology*, *82*(1), 211–221. https://doi.org/10.1111/j.1365-2656.2012.02030.x

Woltmann, S., Sherry, T. W., & Kreiser, B. R. (2012). A genetic approach to estimating natal dispersal distances and self-recruitment in resident rainforest birds. *Journal of Avian Biology*, *43*(1), 33–42. https://doi.org/10.1111/j.1600-048X.2011.05572.x

Zurell, D. (2017). Integrating demography, dispersal and interspecific interactions into bird distribution models. *Journal of Avian Biology*, *48*(12), 1505–1516. https://doi.org/10.1111/jav.01225

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.