

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

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20

21 Abstract

22

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

28 2. Here we aim to estimate and compare empirical dispersal kernels for
29 European breeding birds considering average dispersal, natal (before first
30 breeding) and breeding dispersal (between subsequent breeding attempts),
31 and test whether different dispersal properties are phylogenetically conserved.

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

39 4. The dispersal movements of the 234 European bird species analysed were
40 statistically best explained by heavy-tailed kernels, meaning that while most
41 individuals disperse over short distances, long-distance dispersal is a feature
42 in almost all bird species. The overall phylogenetic signal in both median and
43 long dispersal distances was low (Pagel's $\lambda < 0.40$), implying a high degree of
44 taxonomic generality in our findings. As expected in birds, natal dispersal was

45 5 Km greater as an average than breeding dispersal for most species (88%
46 species analysed).

47 5. Our comprehensive analysis of empirical kernels indicates that long-distance
48 dispersal is common among European breeding bird species and across life
49 stages. The dispersal estimates offer a first guide to selecting appropriate
50 dispersal kernels in range expansion studies and provide new avenues to
51 improve our understanding of the mechanisms and rules underlying dispersal
52 events.

53 **Keywords:** birds, Europe, ring-recovery, dispersal distance kernel, negative
54 exponential, weibull, half-Cauchy, gamma

55

56 Introduction

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

74 Quantifying how far and how often animals move across the landscape is extremely
75 challenging (Nathan, 2001). More recently, understanding of movement processes
76 has advanced through the implementation of new molecular tools (Hobson, 2005;
77 Woltmann et al., 2012) and the use of cutting-edge biotelemetry (Kays et al., 2020;
78 Kranstauber et al., 2011). Still, empirical dispersal measurements on vertebrates are
79 scarce, mostly constrained to few organisms, and geographically limited (Paradis et
80 al., 1998). As a consequence of these challenges, comparative dispersal analyses

81 across species have relied on standardised biometric indices as proxies to quantify
82 dispersal ability (Dawideit et al., 2009; Sheard et al., 2020), or imputation methods
83 that fill information gaps based on phylogenetic relatedness between species
84 (Barbet-Massin et al., 2012).

85 Syntheses of field movement and dispersal data provide a promising avenue for
86 overcoming empirical data limitations for many vertebrate species and large spatial
87 extents (Tucker et al., 2018). For example, two decades ago, Paradis et al. (1998)
88 estimated average natal and breeding dispersal distances for 75 British bird species
89 based on nearly 100 years of ringing data. This analysis explored how dispersal
90 distances vary according to certain life-history traits (e.g. migratory behaviour, range
91 size, habitat) and dispersal type (breeding or natal dispersal). These estimates have
92 subsequently been used to project bird dispersal and range dynamics under climate
93 change (Barbet-Massin et al., 2012). However, the original dispersal estimates by
94 Paradis et al. (1998) were constrained to Great Britain, to only a subset of European
95 breeding birds, and summarised only average dispersal distances rather than
96 explicitly estimating dispersal kernels and analysing their shapes. Dispersal kernels,
97 which represent the density of dispersing individuals at certain distances from the
98 source, provide a better understanding of the mechanisms and rules underlying
99 dispersal events and are a prerequisite for modelling spatial population dynamics for
100 scenarios of global change (Bullock et al., 2017; Nathan et al., 2012; Paradis et al.,
101 2002). Yet, building a large dataset of empirical dispersal kernels for a wide range of
102 species in large areas is challenging due to different biases and uncertainties in the
103 field observations (Nathan et al., 2012).

104 Different studies have implemented a variety of functions to represent the frequency
105 distribution of the dispersal distances (Exponential, Nathan et al., 2012; Gamma, van

106 Houtan et al., 2007; Half-Cauchy distribution, Paradis et al., 2002; Weibull, Nathan et
107 al., 2012). These functions differ in the shape of the dispersal kernel and thus in the
108 relative probability of different dispersal distances with consequent implications for
109 predicting range change. Functions like the exponential kernel are popular as they
110 have an underlying theoretical basis that represents movement in a random direction
111 with a time or distance-dependent settlement rate (Bullock et al., 2017; Nathan et al.,
112 2012). By contrast, heavy-tailed kernels such as the Half-Cauchy, Gamma and
113 Weibull distribution assume a combination of local and distant selective pressures
114 and they expect that a few individuals fly long distances (Viswanathan et al., 1996).
115 To date, only a few studies compared different dispersal kernel functions on birds
116 (Nathan et al., 2012; Paradis et al., 2002; Van Houtan et al., 2007, 2010). These
117 indicated that simple summary statistics of empirically measured dispersal distances
118 (rather than estimating dispersal kernels based on probability distributions)
119 underestimate the species' dispersal ability and that heavy-tailed kernels may best
120 explain empirical dispersal patterns (Paradis et al., 2002; Van Houtan et al., 2007).
121 Comparing the performance of alternative empirical dispersal kernels for large
122 numbers of species will improve our ecological understanding of relevant dispersal
123 processes and their proximate and ultimate causes (Stevens et al., 2014).

124 Here, we aim to quantify empirical dispersal kernels of breeding birds across Europe,
125 compare the dispersal characteristics of natal and breeding dispersal, and test for
126 phylogenetic signal in different dispersal metrics. We use data on marked birds from
127 EURING – The European Union for Bird Ringing database – that holds several
128 million records of European bird movements (Du Feu et al., 2016). Although a
129 uniquely rich data source on bird movements, analysis of dispersal distance based
130 on EURING data is challenging because dispersing and migrating birds are not

131 separated, and sampling effort is heterogeneous (Paradis et al., 1998; Korner-
132 Nievergelt et al 2010). Therefore, we develop a methodological framework that
133 addresses these potential biases. Based on this, we first estimate dispersal kernel
134 parameters for average dispersal (pooling all age stages when it was not possible to
135 separate them) as well as for breeding and natal dispersal using four different
136 probability density functions and assess the best-fitting one. Then, we calculate
137 multiple descriptors of dispersal (e.g. median and maximum dispersal distances) and
138 quantify the phylogenetic signal in these descriptors. The use of multiple dispersal
139 descriptors will allow us to disentangle different selective pressures on short- versus
140 long-distance dispersal patterns (Claramunt, 2021; Sheard et al., 2020),

141 **Methods**

142 **Ringling data**

143 Raw data on dispersal distances were obtained from the EURING database (Du Feu
144 et al., 2016). The data were requested following an approach that allowed us to keep
145 only the reliable observations and test for different sampling biases. Therefore, for
146 the present study, we included distances between the ringling and re-encounter
147 locations of birds ringling and subsequently re-encountered between April and July
148 (which represents the core breeding season for most species) from 1979 until 2018
149 from almost all ringling schemes in Europe (see supplemental material 1). Re-
150 encounters within the same breeding season as ringling were excluded. When
151 multiple subsequent encounters at the same coordinates as the previous encounter
152 were available, only the first one was considered. We re-classified the field codes for
153 the condition of the reencountered birds into two classes, dead (code: 1-3) and alive
154 (code: 4-8), and defined two age classes with respect to the age of the birds when

155 ringed: juvenile for birds ringed in their year of birth (age code 1 and 3), and adult for
156 birds ringed later than the first year of birth.

157 Because sampling effort varies across schemes and species, we selected a
158 balanced dataset in terms of sample size across Europe for all species, age groups
159 (nestling or adult), and types of recovery (dead or alive) that allowed us to estimate
160 dispersal and tackle the uneven spatial coverage and heterogeneous sampling
161 associated with different types of re-encounter. In particular, we used a stratified
162 random sampling by 5° grid cell to select ringing site locations across Europe, then
163 chose a minimum of 20 records and a maximum of 100 records per 5° grid cell with
164 c. 60% dead recoveries and 40% alive recoveries where possible. Only recoveries
165 where the location of the encounter was known to a precision of ± 5 km were
166 included. The data were further screened following the procedure described in
167 Paradis et al. (1998) to remove spurious effects and heterogeneity as far as possible
168 (birds in poor condition, ringing or recovered events in uncommon circumstances,
169 and lack of accuracy on the dates and places of ringing and/or recovery). Several
170 species are not separated in sex classes in the database; hence, we avoid to use
171 sex as a category in this study. In total, the ringing data obtained from EURING
172 consisted of 602,703 ringing and re-encounter events from 273 species.

173 **Potential bias analysis**

174 Ringing databases hold dispersal information that could not be acquired using
175 alternative techniques. Ring-recovery data are available for many species and are
176 not constrained by sampling being restricted to particular locations (Tellería et al.,
177 2012). However, drawing conclusions on dispersal from raw data can be misleading
178 because re-encounters, and hence dispersal distances, are the result of a
179 heterogeneous observation process and subject to strong sample biases (Fandos &

180 Tellería, 2018; Korner-Nievergelt et al., 2010; Naef-Daenzer et al., 2017; Thorup et
181 al., 2014). Here, we used different approaches to exclude data that can lead to
182 potential biases in the calculation of dispersal for the different species. In particular,
183 those biases related to (i) different recovery rates between types of recovery (live
184 recaptures, resightings and dead recoveries), (ii) migratory movements and (iii) the
185 minimum number of cases used to infer robust dispersal estimates:

186 (i) Although a large variation in ringing and recovery effort could potentially
187 bias the spatial and temporal distributions of ringing data, we expect that the large
188 spatial scale of our study can minimise the biases associated with the
189 heterogeneous recovery rates. Nevertheless, dead and alive recaptures may be
190 affected by different biases related to catching effort by ringers and reporting
191 probability (Paradis et al., 1998). For instance, the spatial distribution of birds
192 recaptured alive is likely to differ from dead recoveries as the former depends on the
193 spatial and temporal efforts in field ornithologist activities (more recoveries at places
194 with active research/ringing stations; Tellería et al., 2014), while the latter are mostly
195 reported by the general public and so are more evenly distributed. Therefore, in an
196 exploratory analysis, we compared the dispersal estimates obtained from using
197 different recovery types. Comparison of the results indicated that both dead and alive
198 recaptures (but excluding live resightings), showed similar dispersal patterns (see
199 supplemental material 2).

200 (ii) The dispersal analysis of migratory or partial migratory species is
201 particularly challenging because of variation in migration phenology between
202 individuals and populations across Europe (Lehikoinen et al., 2019). Because
203 migratory movements may lead to overestimation of dispersal distances, we aimed
204 to exclude individuals captured or recovered during migration in the late or early

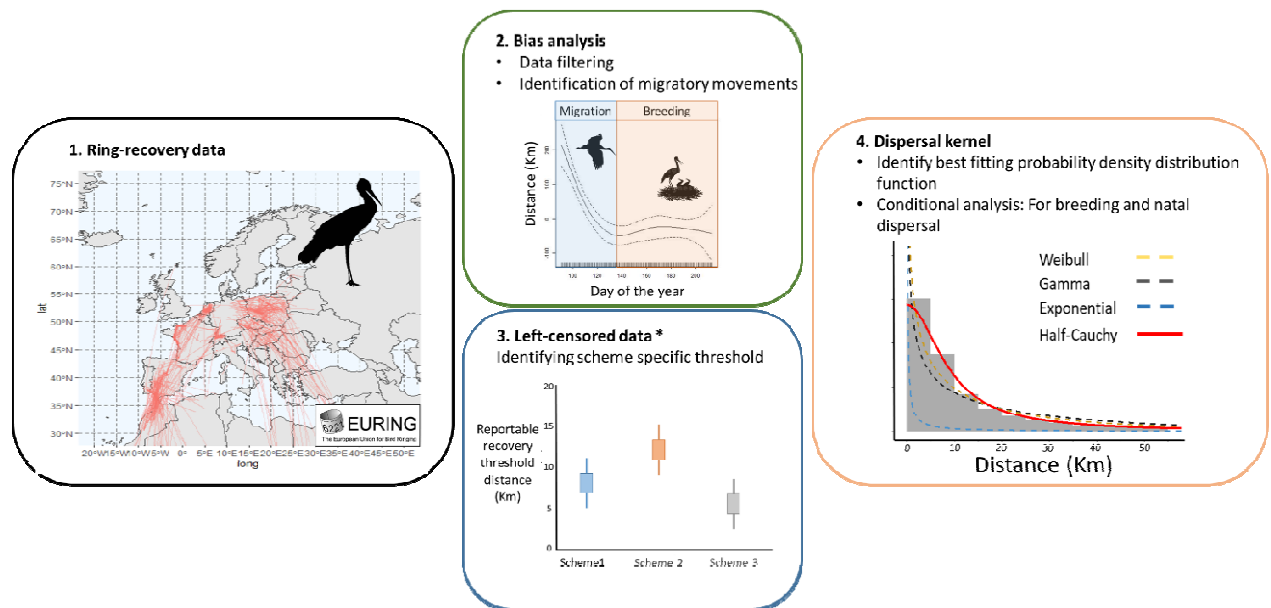
205 breeding season, using a two-step approach. First, we estimated the potential core
206 breeding period for each species and each spatial (5°) grid cell in Europe to account
207 for the breeding time variation across space. For this, we used generalised additive
208 models (GAMs) to regress dispersal distance against a smoothed function of the
209 time of the year and used the second derivative to distinguish peak migratory periods
210 with sudden increases in dispersal distances from the core breeding season with
211 comparably stable dispersal distances. Second, we used the 95% quantile of the
212 distances observed in the core breeding period as a conservative cut-off distance to
213 distinguish between dispersal events and migratory movements (Supplemental
214 material 3).

215 (iii) Finally, we ran an exploratory analysis, where we used different subsets of
216 ring-recoveries to assess how the number of events would affect the dispersal
217 estimation. We concluded that a minimum of 20 individuals per analysis was
218 sufficient to ensure robust dispersal estimates (ensuring a minimum sample size of
219 $n=10$ per parameter in two-parameter dispersal kernels).

220 **Statistical modelling of dispersal distance kernels**

221 For each species, we fitted an average dispersal kernel (not distinguishing natal and
222 breeding dispersal), and if enough data were available, we additionally fitted a natal
223 dispersal kernel and a breeding dispersal kernel. We used a Bayesian approach to fit
224 four commonly used dispersal kernel functions in their one-dimensional form (i.e.
225 probability density functions) directly to the distribution of dispersal distances (Table
226 1). These four 1- or 2-parameter probability density functions have been commonly
227 used in analysing bird dispersal data (Nathan et al., 2012). Overall, we fitted average
228 dispersal kernels for 234 species. Because of sample size issues, natal dispersal
229 kernels and breeding dispersal kernels were fitted only for 113 and 122 species,

230 respectively; thus we estimated 1,876 dispersal kernels for the combinations of
231 species x four dispersal functions x average /natal/breeding dispersal events.



232

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

241 One of the main challenges of fitting dispersal kernels to the EURING database for
242 dispersal analysis is that different schemes have different procedures for reporting
243 birds ringed and subsequently encountered again (Du Feu et al., 2016). For
244 example, some schemes have minimum distances before a bird's re-encounter will
245 be deemed reportable. This means that recaptures below a specific distance from
246 the ringing location are not always reported, and this lower threshold of reporting a




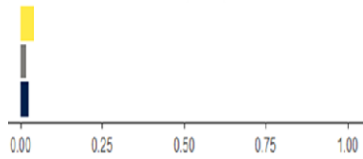
247 recovery varies between schemes. The resulting bias of omitting short dispersal
248 events is problematic because it affects the dispersal kernel's shape. For
249 overcoming this problem, we defined two kinds of observation. When the dispersal
250 distance is 0 m, we specified the observation as potentially *censored*. When the
251 observation is precisely known and greater than 0 m, we defined it as *accurate*.
252 Preliminary analyses showed that France had a particularly high threshold for
253 reporting recoveries, but the thresholds for the other schemes also seemed variable.
254 To avoid any arbitrary choices for the censoring thresholds, we decided to infer
255 these from the model.

256 In the following, we describe the steps to estimate the scheme-specific censoring
257 thresholds and fit the four probability density functions (distributions) to our empirical
258 data (Figure 1; see [code availability](#)). The procedure was carried out separately for
259 average , breeding and natal dispersal.

- 260 1. To make use of maximum information for identifying the scheme-specific
261 censoring thresholds, we first fitted a separate dispersal kernel for each
262 specie, with a shared parameter describing the threshold for each scheme.
263 We repeat this process for each dispersal function (Exponential, Gamma,
264 Weibull, Half-Cauchy). We selected the best-fitting distribution by computing
265 the marginal log-likelihood via bridge sampling for each model and computing
266 the posterior probability with the `bridgersampler` R package (Gronau et al.,
267 2020). Finally, using this best model, we estimated the posterior distribution of
268 the scheme-specific censoring threshold parameter.
- 269 2. We used the posterior distribution of the scheme-specific threshold parameter
270 from the previous step as an informative prior in single-species models and
271 for each dispersal function. The objective of these models was to estimate the

272 dispersal kernels for each species, given the degree of left-censoring,
273 compute the posterior model probabilities from marginal likelihoods, and
274 assess which distribution is the “best” for each species using the marginal log-
275 likelihood via bridge sampling. For all species and dispersal functions, a) we
276 extracted the dispersal kernel parameters (the mean and the credible interval
277 of each parameter), b) we derived the empirical median dispersal distance
278 (and the 95% credible interval for the median) analytically from the dispersal
279 kernels, and c) derived long-distance dispersal measures, which we defined
280 as the 95% percentile from a posterior predictive dispersal simulation with the
281 estimated parameters.

282 *Table 1. Alternative probability density functions to estimate dispersal kernels k for European*
283 *birds. We provide the expressions of the one-dimensional dispersal distance kernels k_D as*
284 *function of the distance d , as well as the parameters to estimate for each function. The*
285 *frequency corresponds to the posterior model probabilities from the computed marginal log-*
286 *likelihoods via bridge sampling divided by the number of species (frequency = 1 indicates*
287 *the most likely distribution). The three bars represent the frequency with which each*
288 *dispersal kernel best fitted the different dispersal types (average : yellow, breeding: blue and*
289 *natal: grey)*

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)	$\frac{\beta^\alpha}{\Gamma(\alpha)} x^{\alpha-1} e^{-\beta x}$	α (shape), β (rate)	
Half-Cauchy (HC)	$2\sigma/\pi(\sigma^2 + d^2)$	σ (scale)	

290

291 Phylogenetic signal in dispersal estimates

292 We used multivariate generalised linear mixed models to estimate the phylogenetic
 293 dependency in both descriptors of the dispersal ability, the median, and the long-
 294 distance dispersal (95% upper percentile of dispersal distances) estimates from the
 295 best-fitted distribution for each species. Dispersal estimates were log-transformed to
 296 satisfy assumptions of normality and linearity and scaled to have a mean of 0 and a
 297 variance of 1. We fitted two separated multivariate Gaussian models for the median
 298 and the long-distance dispersal and included phylogenetic relatedness as a random
 299 effect. We fitted both models, including no fixed effects and estimated the amount of
 300 variation in the dispersal estimates explained by shared ancestry between species
 301 (i.e. phylogenetic signal) by calculating the parameter λ (Pagel's λ ; Pagel, 1999).

302 We also explored the relationship between median versus long-distance dispersal by
 303 fitting multivariate generalised linear mixed models, with the median dispersal
 304 distance as a response variable, the long-distance as a fixed effect and the
 305 phylogenetic relatedness as a random effect. All models were implemented in a
 306 Bayesian framework using Markov chain Monte Carlo (MCMC) sampling in the

307 package MCMCglmm (Hadfield, 2010) in R version 4.0.5. We ran all models with
308 three chains and 100 000 iterations, with a burn-in period of 1000 and a sampling
309 interval of 50. The convergence of the models was confirmed by examining the
310 effective sample size (greater than 1000) and autocorrelation between samples (less
311 than 0.10) for each chain, as well as the Gelman–Rubin statistics (less than 1.1)
312 among chains. Priors were initially set using inverse-Wishart priors for the
313 phylogenetic and residual variance ($V_{\phi} = \phi^{-1}$, $v = 0.002$). Parameter estimates from
314 models are reported as the posterior modes with 95% lower and upper credible
315 intervals (CIs). All phylogenetic analyses were conducted on a sample of 100 trees
316 obtained from the Hackett backbone of the global bird phylogeny (www.birdtree.org;
317 Jetz et al., 2012).

318 **Association between natal and breeding dispersal**

319 We explored the association between natal and breeding dispersal estimates from
320 the best-fitting distributions for each species while accounting for the non-
321 independence of species related to their joint evolutionary history by using a
322 multivariate generalised linear mixed model. We fitted the model using the median
323 natal dispersal distance as a response variable, the median breeding dispersal
324 distance as a fixed effect and phylogeny as a random effect (see above for details
325 about priors and model fitting). We fitted the model for the subset of 108 species
326 where all measures were available. Dispersal estimates were log-transformed to
327 satisfy assumptions of normality and linearity and scaled to have a mean of 0 and a
328 variance of 1.

329 We ran the same models to estimate the association between the mean dispersal
330 distances reported in Paradis et al. (1998) and our median dispersal estimates from

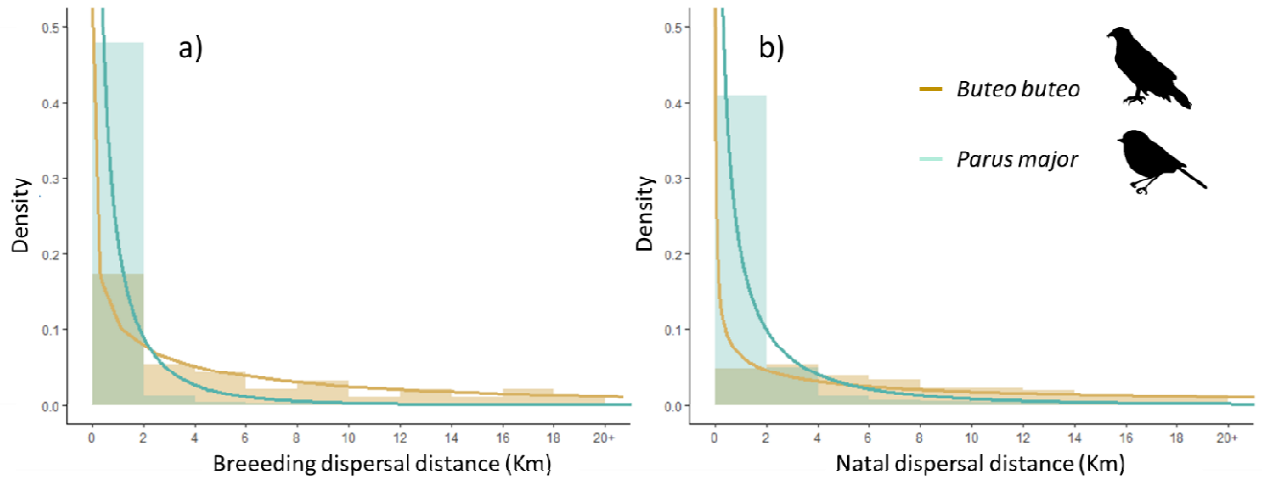
331 the best-fitting distribution for the subset of 75 species where both measures were
332 available.

333 Results

334 We analysed a total of 563,276 capture-recapture events from 234 species (median
335 capture-recapture event per species $n = 419$, $\max = 27'837$, $\min = 21$), covering 55
336 bird families. The four probability density functions converged for all species. The
337 Weibull distribution was the best-fitting function for 156 out of 234 species (Fig. 2;
338 Table 1). The Gamma distribution was the best one for 34 species, the exponential
339 for 32 and the Half-Cauchy for 12 species. We analysed a total of 122 species for
340 natal dispersal, and the Weibull was the best-fitting function for the majority of the
341 species (92 out of 122 species). In the case of the breeding dispersal, the Weibull
342 was the best-fitting function for 88 out of 113 species analysed.

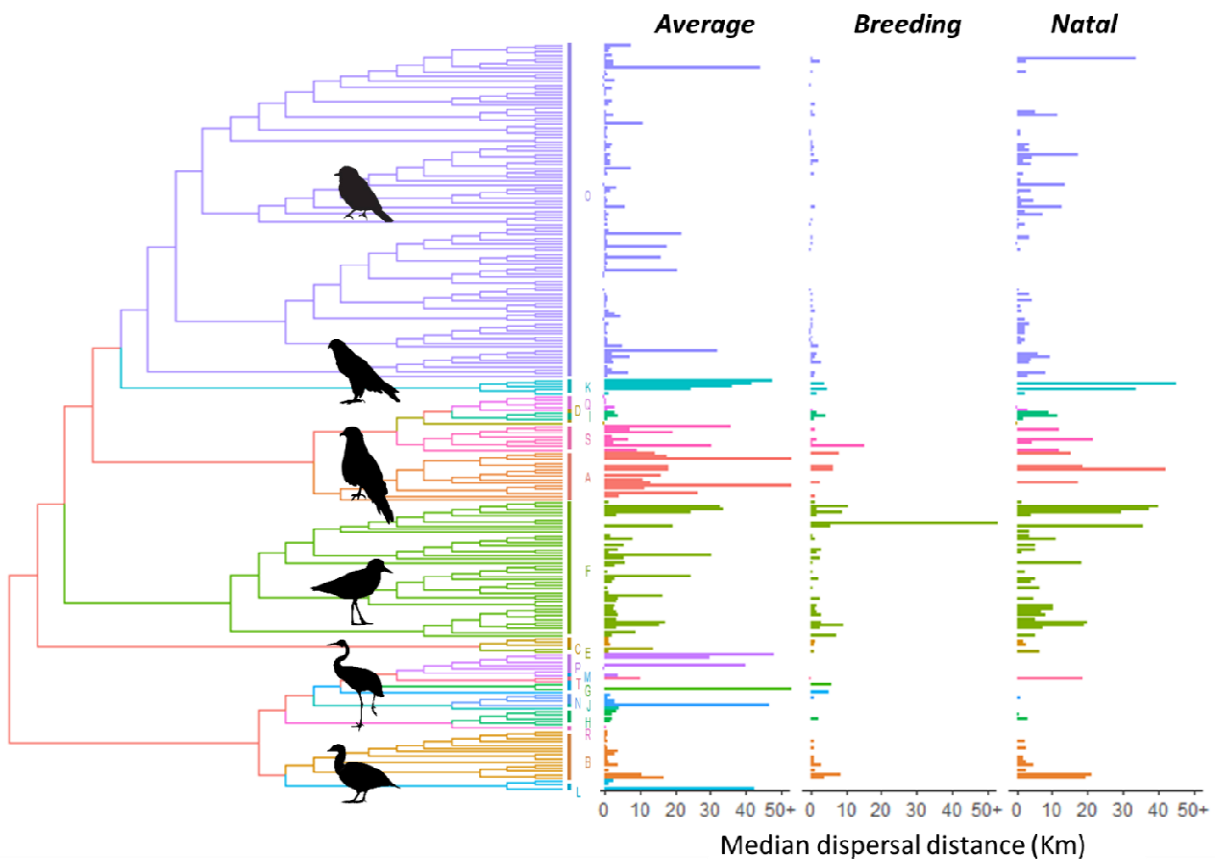
343 The dispersal estimates (median and long-distance dispersal) varied between
344 species and species orders (Fig 3; Fig S7.1). The phylogenetic signal for the median
345 dispersal distances was $\lambda = 0.373$ [0.115-0.636], whereas the phylogenetic signal for
346 the long-distance dispersal was $\lambda = 0.236$ [0.056-0.462]. Reassuringly, the subset of
347 species with large enough sample sizes to estimate breeding ($n=122$) and natal
348 dispersal ($n=113$) reflected well the range of dispersal distances found over all
349 species ($n=234$; Fig. S8.1).

350



352 *Figure 2: Breeding (a) and natal (b) dispersal kernels for two species: Parus major and*
353 *Buteo buteo. Bars represent observed frequency distributions and lines the Weibull*
354 *probability density curves, which was the best-fitting one for both species.*

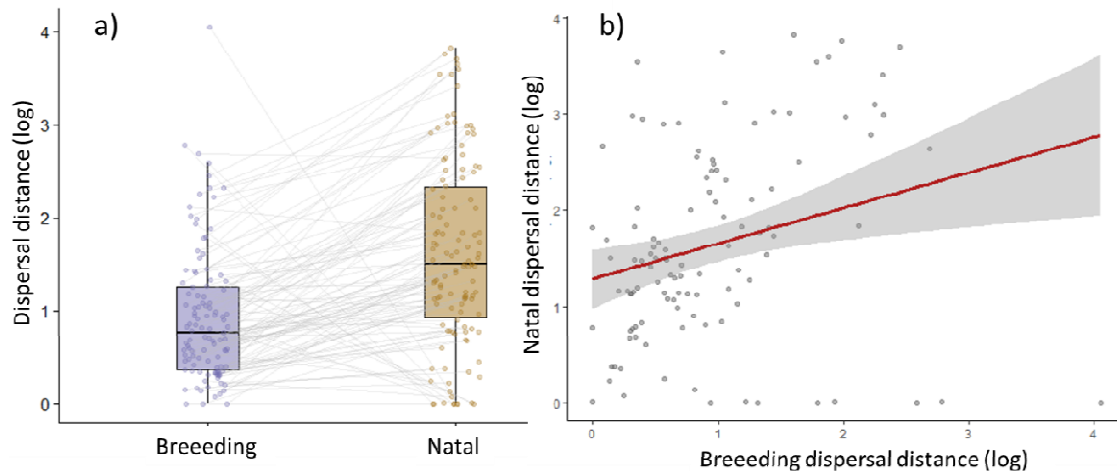
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357 *Figure 3.* Median dispersal distance (km) from the best-fitting distribution along the bird
358 phylogeny for the average (234 species), breeding (113 species) and natal dispersal (121
359 species). The dispersal distance is truncated at 50 Km for visualisation purposes. Each
360 colour and letter represent the same Order in the phylogeny and the bar plots. *A:*
361 *Accipitiformes*, *B: Anseriformes*, *C: Apodiformes*, *D: Bucerotiformes*, *E: Caprimulgiformes*, *F:*
362 *Charadriiformes*, *G: Ciconiiformes*, *H: Columbiformes*, *I: Coraciiformes*, *J: Cuculiformes*, *K:*
363 *Falconiformes*, *L: Galliformes*, *M: Gaviformes*, *N: Gruiformes*; *O: Passeriformes*, *P:*
364 *Pelecaniformes*, *Q: Piciformes*, *R: Podicipediformes*, *S: Strigiformes*, *T: Suliformes*.

365

366 On average, median natal dispersal distances were larger than median breeding
367 dispersal distances (Fig. 4a). Natal and breeding dispersal estimates from the best-
368 fitting kernels had a positive correlation 0.237 (95% CI: 0.036-0.473; pMCMC=
369 0.039; Fig. 4b). Better correlations resulted when we compared natal and breeding
370 dispersal estimates for the same distribution functions (see figure S5.1 for Weibull
371 distribution). Median dispersal estimates (from the best-fitting kernels) were also
372 significantly correlated with mean dispersal distances reported for n=75 species in
373 Paradis et al. (1998), although the dispersal distances from Paradis et al. (1998)
374 based on summary statistics were larger than our kernel-based estimates (Fig S6.1).



375

376 *Figure 4:* a) Boxplot diagram for the log median dispersal distance (km) from the best-fitting
377 distribution for natal and breeding dispersal. Lines connect the same species in both types of
378 dispersal. c) Linear relationship between breeding and natal dispersal (log).

379 Discussion

380 While much theory has been developed around bird dispersal and their impacts on
381 populations, few empirical studies have estimated and synthesised dispersal kernels
382 for multiple species, a prerequisite for modelling species spatial dynamics (but see
383 Paradis et al., 2002; Van Houtan et al., 2007). In this paper, we estimated average
384 dispersal kernels for 234 bird species across Europe and natal and breeding
385 dispersal kernels for a subset of 122 and 113 species, respectively. This extensive
386 analysis allows an improved understanding of interspecific variations in dispersal
387 patterns and strategies in European birds. Specifically, we found that the dispersal of
388 almost all bird species and across age (natal and breeding dispersal) follows a
389 heavy-tailed distribution, indicating a general tendency towards long-distance
390 dispersal in birds. This result supports previous findings that although most
391 individuals from the different species do not move far, a small proportion of
392 individuals disperse very long distances (Paradis et al., 2002; Van Houtan et al.,

393 2007). More importantly, the phylogenetic signal in dispersal characteristics was
394 weak, indicating that phylogenetic relatedness is a poor predictor of dispersal across
395 bird species but that other internal and external factors may play important roles in
396 determining this phenotypic trait.

397 Long-distance dispersal events are extremely relevant for population dynamics and
398 range colonisation across changing landscapes, but their low frequency and
399 detectability make them hard to measure and quantify (Clobert et al., 2012; Travis et
400 al., 2013). Empirical dispersal kernels are a fundamental tool to address many of the
401 limitations for characterising dispersal patterns (Bullock et al., 2017; Nathan et al.,
402 2012), in particular when direct measures of dispersal fail to capture the frequency of
403 potential long-distance dispersal events (Koenig et al., 1996; Whitmee & Orme,
404 2013). The standardisation of dispersal kernels across a wide range of species
405 should allow more realistic and representative forecasts of potential species
406 distributions and better integration of dispersal in comparative life-history analysis
407 (Nathan et al., 2012; Stevens et al., 2012, Bullock et al., 2017). The heavy-tailed
408 distributions probably result from the interplay or overlap of multiple movement
409 modes that widen dispersal kernels when considered simultaneously (Nathan, 2008).
410 Dispersers may switch between movement modes based on the complex trade-offs
411 between internal state, environmental context, motion capacity, and navigational
412 ability (Nathan, 2008). Future analyses will benefit from integrating detailed
413 movement behaviour with improved analytical methods to understand how
414 environmental context affects dispersal, and consequently, eco-evolutionary
415 dynamics in space (Bonte & Doherty, 2017).

416 Phylogenetic information has been extensively used to infer dispersal distances for
417 species without data (Barbet-Massin et al., 2012; Thomas, 2008). However, this

418 approach neglects that dispersal can evolve rapidly by adaptive processes (Stevens
419 et al., 2010), and that contrasting environmental conditions can generate variability in
420 phenotypic dispersal patterns among individuals or populations (Bonte & Doherty,
421 2017; Clobert et al., 2009). Our results show that both long and median dispersal
422 distances have weak phylogenetic conservatism, indicating that population-level
423 drivers such as landscape structure, or more labile behavioural traits, could play an
424 essential role in determining dispersal (Blomberg et al., 2003; Nathan, 2001). Our
425 results revealed lower phylogenetic signals in long-distance (compared to median)
426 dispersal events, which could indicate that particularly long-distance movement are
427 strongly context-dependent (Lowe, 2009). The overall phylogenetic lability on bird
428 dispersal suggests that evolutionary history should only be used as predictor of
429 dispersal ability when data are scarce and should otherwise be used with caution.

430 Accurately measuring age dispersal differences for many species has typically been
431 hampered by the low juvenile survival rates compared to adults and because
432 dispersal distances often exceed study area boundaries (Greenwood & Harvey,
433 1982; Newton, 1998). Here, we take advantage of continent-wide ringing and
434 recovery efforts to show that natal dispersal of immature individuals that depart their
435 natal range in search of new sites is generally more extensive and covers a wider
436 geographical area than breeding dispersal (Greenwood & Harvey, 1982; Hollenbeck
437 et al., 2018; Paradis et al., 1998). This considerable dispersal asymmetry between
438 ages could arise from a range of selective pressures, such as inbreeding avoidance,
439 competition among offspring, or simply finding suitable habitat (Clobert et al., 2012;
440 Hendry et al., 2004). In contrast, mature breeders have evolved comparably lower
441 breeding dispersal rates favouring territories they already know from previous
442 breeding attempts (Kokko & Lundberg, 2001). Disentangling whether dispersal

443 strategies are conditional on age is essential to understanding how demography and
444 fitness influence the overall dispersal process (Bonte et al., 2012).

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

465 The robust empirical characterisation of the avian dispersal kernels as presented in
466 this study is crucial for conservation and management since and for predicting
467 potential future range changes. The estimated dispersal distances as well as the

468 analytical tools designed here provide many avenues for future research.
469 Outstanding questions include, among others, the assessment of dispersal
470 syndromes to understand how dispersal kernels vary across species traits and
471 explore covariation patterns between dispersal and other traits (Clobert et al., 2009;
472 Ronce & Clobert, 2012) and the exploration of how dispersal processes respond to
473 habitat fragmentation and climate change (Bowler & Benton, 2005; Travis et al.,
474 2013). The presented study paves the road towards a new generation of more
475 realistic modelling and comparative studies to evaluate the role of dispersal in
476 several issues of population biology and their eco-evolutionary dynamics under
477 global change.

478 **Data and Code availability**

479 Ring-recovery data is available upon request through the EURING Data Bank.
480 Dispersal estimates and code will be available after publication from ZENODO
481 repository: Guillermo Fandos (2021). guifandos/European_bird_dispersal: v0.1.0-
482 Edispersal (v0.1.0_Edispersal). Zenodo. <https://doi.org/10.5281/zenodo.5565077>.
483 Code available until publication [https://github.com/UP-](https://github.com/UP-macroecology/European_bird_dispersal)
484 [macroecology/European_bird_dispersal](https://github.com/UP-macroecology/European_bird_dispersal))

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495 **Author contributions**

496 **Guillermo Fandos:** Conceptualization (lead); Investigation (equal); Data request (lead);
497 Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing-review &
498 editing (equal). **Matthew Talluto:** Conceptualization (supporting); Formal analysis (equal);
499 Methodology (equal); Writing – original draft (supporting). Writing-review & editing (equal).
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