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

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Abstract

1. Dispersal is a key life-history trait for most species and 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 aim to estimate and compare empirical dispersal kernels for European breeding birds considering average dispersal, natal (before first breeding) and breeding dispersal (between subsequent breeding attempts), 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 average, the natal and the breeding 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 feature in almost all bird species. The overall phylogenetic signal in both median and long dispersal distances was low (Pagel's $\lambda < 0.40$), implying a high degree of 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

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, 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

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),

Methods
141

Ringing data
142

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 ringing and re-encounter

147   locations of birds ringed 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 ringing schemes in Europe (see supplemental material 1). Re-

150   encounters within the same breeding season as ringing 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 ±5km 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).

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.
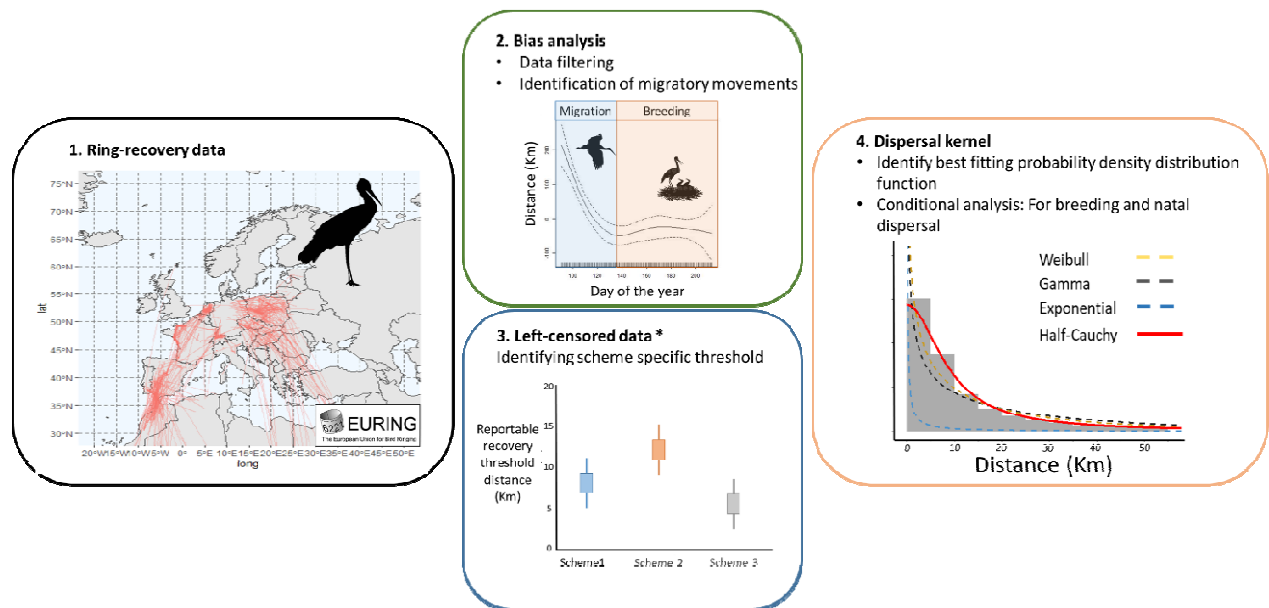
232

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
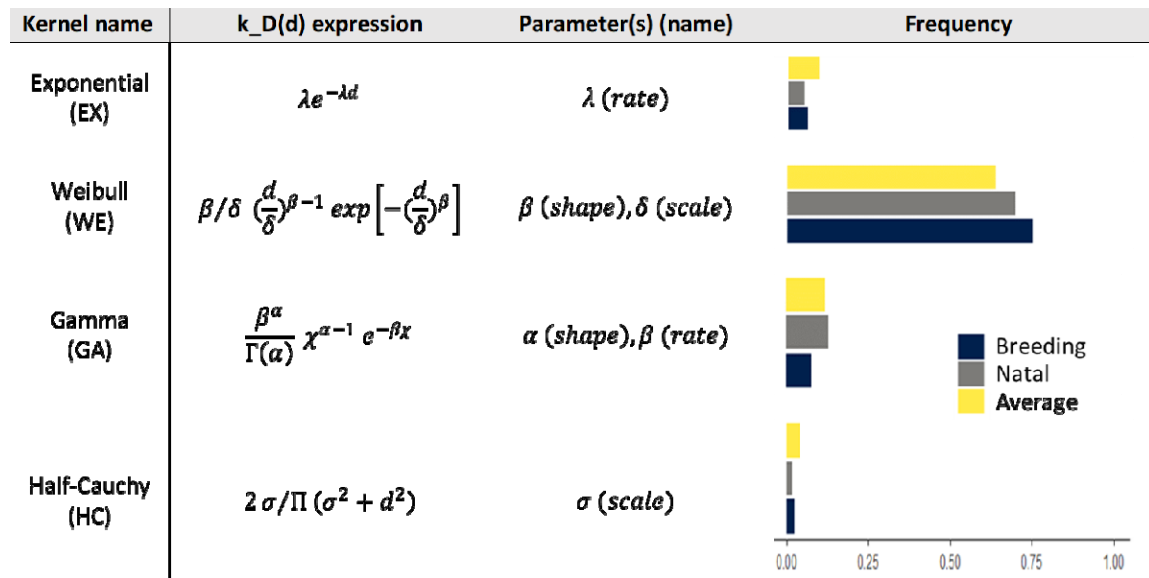
247   recovery varies between schemes. The resulting bias of omitting short dispersal

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

290

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 ($V = 1$, $v = 0.002$). 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 λ = 0.373 [0.115-0.636], whereas the phylogenetic signal for

346   the long-distance dispersal was λ = 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).

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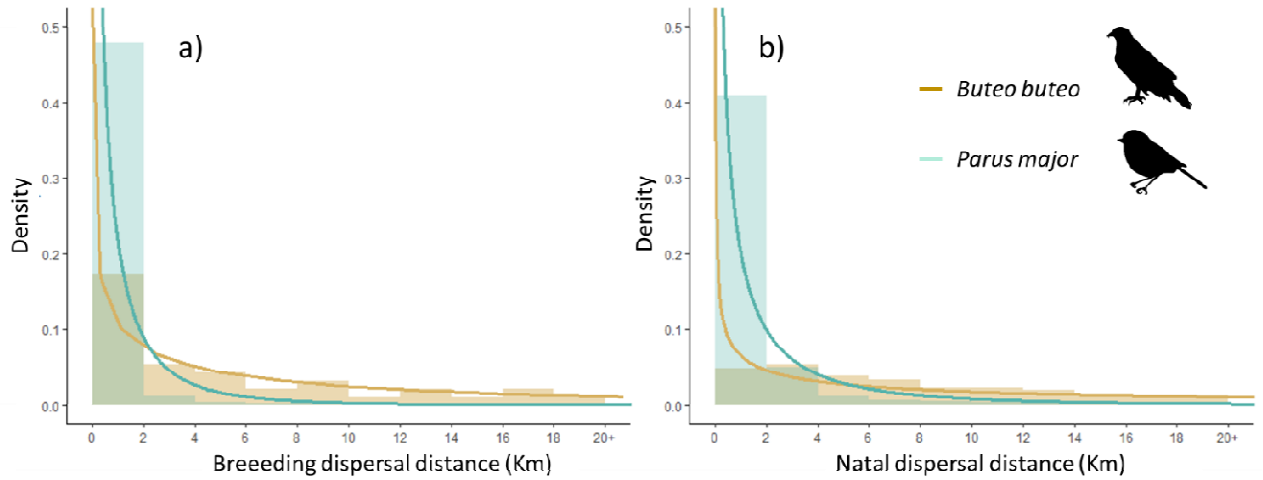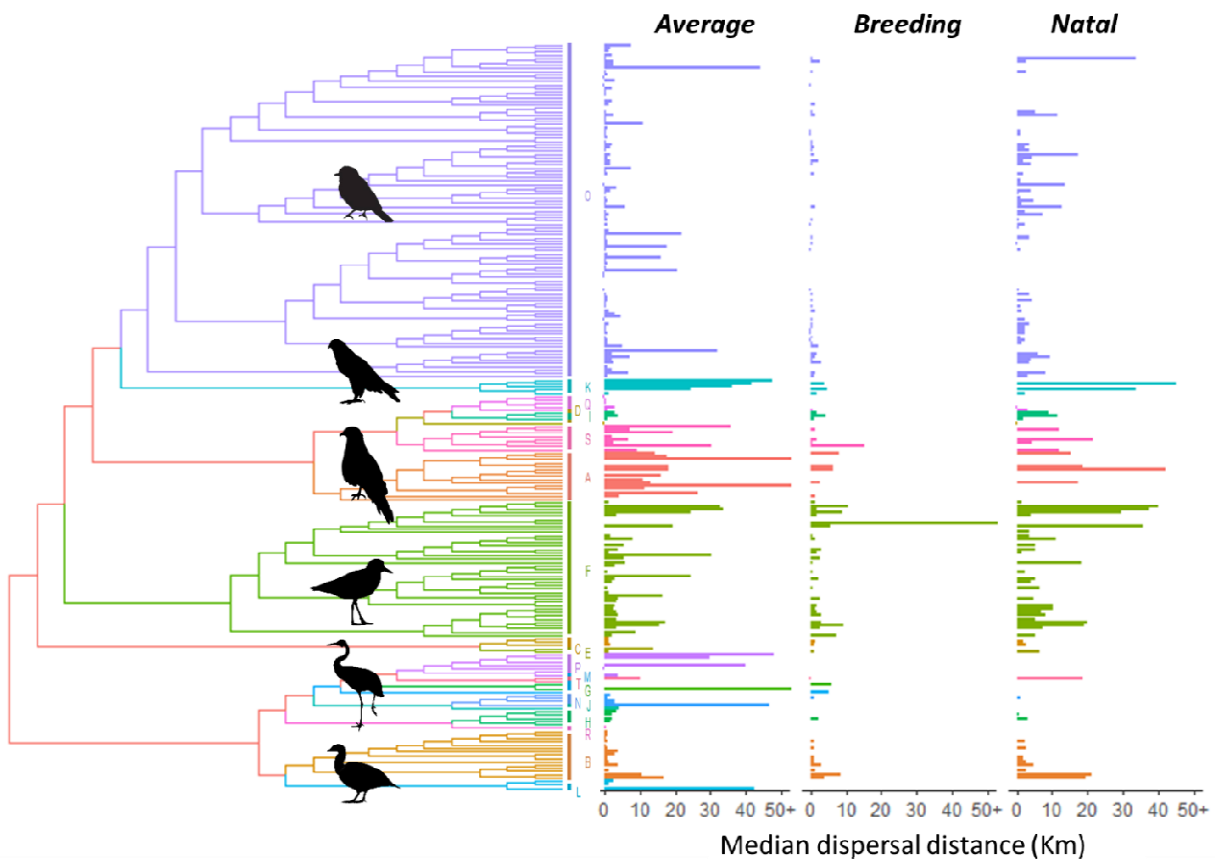
Figure 2: Breeding (a) and natal (b) dispersal kernels for two species: *Parus major* and *Buteo buteo*. Bars represent observed frequency distributions and lines the Weibull probability density curves, which was the best-fitting one for both species.

355

356

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).

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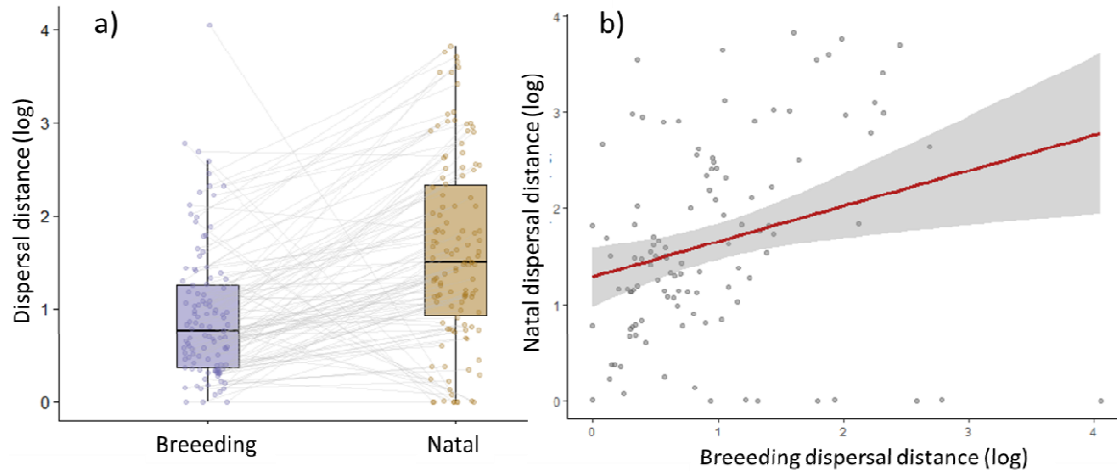
Figure 4: a) Boxplot diagram for the log median dispersal distance (km) from the best-fitting distribution for natal and breeding dispersal. Lines connect the same species in both types of dispersal. c) Linear relationship between breeding and natal dispersal (log).

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, a 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 and natal and breeding dispersal kernels for a subset of 122 and 113 species, respectively. 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 and across age (natal and breeding dispersal) follows a heavy-tailed distribution, indicating a general tendency towards long-distance dispersal in birds. This result supports previous findings that although most individuals from the different species do not move far, a small proportion of 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 & Dahirel, 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 & Dahirel,

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-

484   macroecology/European_bird_dispersal)

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489

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