

1 **Breeding phenology determines evolutionary transitions in migratory behaviour in finches and**
2 **allies**

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5 Jácint Tökölyi^{1,2} and Zoltán Barta¹

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8 ¹Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen,

9 Egyetem tér 1, 4032 Debrecen, Hungary

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12 ²E-mail: jtokolyi@vocs.unideb.hu

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24 **Abstract**

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26 The breeding season of long-distance migratory birds often starts later and is shorter than in resident or
27 short-distance species breeding at the same latitude, but the reason for this is unclear. Here we
28 investigate the association between migration distance and breeding phenology in a group of passerine
29 birds, the finches and their allies, using phylogenetic comparative methods. We **confirm** that migration
30 distance is related to aspects of the species' breeding phenology after controlling for the effect of
31 potentially confounding variables. Directional phylogenetic analyses suggest that evolutionary
32 transitions in migration distance are determined by the breeding phenology. A relatively long migration
33 distance is more likely to evolve in birds with a late, short breeding season, whereas transitions to short
34 distance migration are more likely to occur in lineages with an early, long breeding season. These
35 results suggest that migration distance is constrained by breeding phenology and not vice versa. Thus,
36 breeding phenology may be an important ultimate factor shaping the evolution of migratory strategies.

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38 *Keywords:* bird migration, annual cycle, life history, time allocation, spring predictability.

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44 Introduction

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46 The migratory behaviour of birds nesting in the temperate zone is often strikingly correlated with
47 aspects of their breeding phenology (Kipp 1943, Böhning-Gaese et al. 2000, Bruderer and Salewski
48 2009, García-Peña et al. 2009). Long distance migrants start to breed later and/or have a shorter
49 breeding season than short distant migrant or resident species breeding in several groups of birds,
50 including raptors (Newton 2008), shorebirds (García-Peña et al. 2009) and passerines (Bruderer and
51 Salewski 2009), among others. However, despite the widespread recognition of this phenomenon, the
52 reason why the breeding phenology of long distance migrants differs so markedly from less migratory
53 species **breeding on the same latitude** is not clear.

54 Possible explanations linking breeding phenology to migratory behaviour largely fall into four
55 classes. First, life history trade-offs between fecundity and mortality have been invoked in connection
56 with this phenomenon, based on the observation that the shorter breeding season of long distance
57 migrants is often associated with fewer number of broods per year, hence a lower annual fecundity
58 (Mönkkönen 1992, Martin 1995, Böhning-Gaese et al. 2000, Bruderer and Salewski 2009). **Life history**
59 **theory predicts that in a population of constant size, differences in reproductive effort should be**
60 **associated with different mortality rates. The reason for this is that under density dependence, any**
61 **increase in reproductive investment (and hence fecundity) will intensify competition, resulting in a**
62 **decrease in survivorship. High survival rates increase competition likewise, and this leads to less**
63 **resources available for reproduction, ultimately selecting for lower reproductive rates** (Ricklefs 1980,
64 Martin 1995, **McNamara et al. 2008**, Bruderer and Salewski 2009). Thus, if the non-breeding period
65 affects annual survival rate **and there is density dependence**, then the behaviour of birds during the
66 reproductive period and the non-breeding season should coevolve to reflect this trade-off (Bruderer
67 and Salewski 2009). Overwinter survival rates are thought to be higher in long distance migrants than

68 in species spending the winter at northern latitudes (Greenberg 1984, Sherry and Holmes 1995, Møller
69 2007). On the other hand, annual fecundity is directly related to the length of the breeding season
70 because the number of broods per year and the probability of raising replacement broods after failed
71 brood attempts is probably higher when the breeding season is longer. Therefore, the fecundity-
72 mortality trade-off could possibly result in a correlation between migration distance and the length of
73 breeding season because migration distance is related to overwinter survival, whereas the length of the
74 breeding season is related to annual fecundity (the “life history hypothesis”).

75 Second, the migratory behaviour adopted by a given population of birds may depend directly on
76 breeding phenology. The “time allocation hypothesis” (Greenberg 1980) proposes that with a relatively
77 short breeding season, the benefits of wintering at a more distant site with better survival prospects
78 may be higher, because the birds can spend more time at the favourable wintering site. The higher
79 costs of long distance movements, according to this scenario, are more likely to be outweighed by the
80 higher survival rate on the distant wintering ground for birds that spend more time there. Furthermore,
81 the cost of migration could be lower for individuals migrating relatively late in the spring because they
82 can exploit the higher food availability at that time and experience more favourable conditions during
83 migration than birds migrating early in spring, and this lowered cost of migration could ultimately lead
84 to longer migration distances (Bell 1996, 1997).

85 Third, predictability of environmental conditions on the breeding site could also affect
86 migratory behaviour (the “spring predictability hypothesis”, Alerstam and Högstedt 1980). If
87 conditions on the breeding grounds do not change from year to year, birds can rely on their internal
88 clock to arrive in spring at the earliest time when breeding becomes possible. Conversely, if the onset
89 of spring is unpredictable, individuals wintering closer may predict weather conditions on the breeding
90 grounds more accurately and respond more quickly than individuals migrating longer distances
91 (Alerstam and Högstedt 1980). Given that weather conditions early in spring tend to be more variable

92 than later (e.g. Newton 2008), one would predict that early breeders benefit more from staying close to
93 the breeding grounds and have shorter migration distances.

94 Fourth, migratory behaviour could also affect directly the breeding phenology. Moving between
95 the wintering and breeding grounds takes time, and some long distance migrants may need several
96 weeks to complete the journey (e.g. Alerstam 1990). **Moreover, there is a considerable mortality cost**
97 **associated with migration (e.g. Sillett and Holmes 2002), and this presumably exerts a strong selection**
98 **pressure on the birds to time their migration in a way that maximizes survival (e.g. by migrating late in**
99 **spring and early in autumn; Bell 1996, 1997).** This, in turn may affect the time available for other
100 activities during the annual cycle, including reproductive activities, such as the number of broods per
101 year (Bruderer and Salewski 2009), the length of the fledging period (Meiri and Yom Tov 2004), or
102 parental activities (García-Peña et al. 2009). **Thus, long distance migrants may reorganize their annual**
103 **cycle and/or their reproductive behaviour such that their reproductive cycle will fit into a short summer**
104 **period while simultaneously maximizing survival rate during migration (by migrating under more**
105 **favourable conditions). On the other hand, short-distance migrants and residents may be less**
106 **constrained by time, and could therefore freely extend their breeding season. Notice that this**
107 **hypothesis does not involve life history trade-offs because there is no change in reproductive effort *per***
108 ***se*, but it is the partition of the various reproductive activities that differs (e.g. it is possible to decrease**
109 **the time spent on parental activities but increase the effort during that time, resulting in no net**
110 **difference in reproductive investment).** We refer to this as the “migration time hypothesis”.

111 All these alternatives predict a correlation between migratory behaviour and aspects of the
112 breeding phenology. Therefore, we have designed this study to discriminate among the possible
113 alternatives. We collected data on the breeding phenology and migratory behaviour of a group of
114 passerine birds (the finches and allies of the Western Palearctic and the Nearctic), and employed
115 directional phylogenetic tests (Pagel 1994, Pagel and Meade 2006), which provide a framework to

116 analyze the temporal order and contingency of evolutionary transitions. Given a phylogenetic
117 hypothesis among a set of species and two traits with binary states, the method developed by Pagel
118 (1994) determines the rate of transition among the possible combination of states. Based on these rates
119 it is possible to determine which of the two traits is more likely to change spontaneously and whether
120 changes in one trait are contingent upon the background state of the other. Our predictions for these
121 directional tests were as follows: (1) if the relationship between migration and breeding phenology is
122 mediated by life history trade offs, then evolutionary transitions in migratory behaviour should be
123 contingent on breeding phenology, and vice versa, transitions in the length of the breeding season
124 should also be contingent on migratory behaviour. (2) If either the “time allocation” or the “spring
125 predictability hypothesis” is correct, the prediction is that transitions in migratory behaviour are
126 contingent upon breeding phenology (length of breeding season and start of breeding, respectively). (3)
127 Lastly, if the “migration time hypothesis” is true, then both the start and the length of the breeding are
128 predicted to be contingent upon migratory behaviour.

129

130 **Methods**

131

132 **Data collection**

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134 We investigated the relationship between migratory behaviour and breeding phenology in the finches
135 and their allies, a taxonomically diverse group of small to medium-sized passerines, including the
136 families *Parulidae* (New World warblers), *Thraupidae* (tanagers), *Emberizidae* (American sparrows,
137 Old World buntings, etc.), *Cardinalidae* (cardinals), *Icteridae* (orioles and blackbirds) and *Fringillidae*
138 (finches). Finches are an ideal group to investigate this problem, because they include species with a
139 wide range of migratory behaviour, including residents, short distance and long distance migrants, but

140 the group is relatively homogenous with respect to body size and the mode of migration (they all
141 migrate by flapping flight), thus extreme differences in the cost of migration are unlikely to bias the
142 analyses.

143 Crossbills (genus *Loxia*) and cowbirds (genus *Molothrus*) were not included in this study,
144 because the breeding season in these species cannot be determined in the same way as for the other
145 species. Crossbills are opportunistic breeders and can breed year-round, often moving large distances
146 between different breeding locations (Cramp and Perrins 1994, Poole 2005). Cowbirds on the other
147 hand are brood parasites that lay in the nest of other species and their offspring are raised by foster
148 parents (Poole 2005); as a consequence, reproductive investment per offspring is much lower in
149 cowbirds and this could affect both the outcome of life history trade-offs and the timing of breeding
150 differently than in other species (i.e. cowbirds can leave immediately after egg laying). The final
151 dataset contained 134 species (Appendix 1).

152 Data on breeding phenology was collected from several ornithological monographs and the
153 references therein (Appendix 1). For most species, phenology data were available from several
154 locations; in each case, the geographical coordinates where the study was performed, the start and end
155 of the laying period and the sample size (number of nests) was recorded. In a few cases (10 species),
156 the dates were only given as part of the month, i.e. “early”, “mid” or “late” period of a month and we
157 therefore substituted them with the 5th, 15th and the 25th day of the month, respectively. The length of
158 the breeding season was simply taken as the difference between the end and start dates.

159 Data on the start and length of the breeding season originated partly from field studies of
160 breeding biology and partly from museum collections and nest card programs encompassing larger
161 geographic regions (U.S. states, Canadian provinces or European countries). In this latter case, we took
162 the midpoint of the species' distribution in that specific region, assessed from distribution maps in
163 Cramp and Perrins (1994) and Poole (2005) to the nearest 0.5 decimal degree. Note however, that we

164 did not include regions with a latitudinal span larger than 10 degrees, thus the lowest precision for any
165 latitude data is about 5 degrees, and it is <<5 degrees in most of the cases.

166 Sampling intensity might introduce a bias in assessing breeding phenology, because more effort
167 typically increases the probability that very early or very late nests are discovered. Therefore, only data
168 based on a sample size of at least 20 nests were included in the analyses, and if more than one data
169 point was available for a given species, we selected the one with the largest sample size. **However, to**
170 **maximize variation in migration distance within the sample, we also checked our results on a different**
171 **dataset in which we selected the northernmost record for all species (i.e. the northernmost of all**
172 **records available for a species that are based on ≥ 20 nests).**

173 Another possible source of bias in recording breeding phenology is that different aspects of the
174 breeding cycle may be reported. Thus, some studies report laying dates (laying of first eggs in the nest)
175 whereas others report egg dates (dates on which viable eggs were found; McNair 1987, Peck and James
176 1987), and these may result in breeding periods with different start and length. To see whether this
177 affected our phenology variables, we used the original dataset with 496 records (with a median of 3
178 records per species) to compare data originating from laying dates and egg dates. The two type of data
179 indeed showed differences (Appendix 2), suggesting that the origin of phenology data needs to be
180 taken into account in the analyses (see the Results section).

181 **Migratory behavior was quantified by calculating the minimum geographical distance between**
182 **the point of origin of the phenological data and the wintering range, from digitized distribution maps.**
183 **We used the maps provided by Ridgely et al (2007) for North American species and digitized the**
184 **distribution of European species in our sample by hand, following range maps in Cramp and Perrins**
185 **(1994). The resulting variable is the minimal distance a bird has to migrate to reach the winter quarters**
186 **(where the breeding and wintering ranges overlap at the study location, the variable was set to 0).**
187 Although this measure may not represent the true migration distance of a species, (e.g. if some

188 populations migrate to the southern end of the wintering range), we do not expect any systematic bias
189 in this variable and assume that interspecific differences in the minimal migration distance reflect true
190 differences in the degree of migratoriness. **This assumption is supported by the very strong correlation**
191 **between the minimum migration distance and the distance between the latitudinal midpoint of the**
192 **breeding and wintering ranges (an approximation of the species-specific migratory behaviour;**
193 **Spearman's rank correlation, $r_s=0.865$, $p<0.001$, $n=134$).** In addition, this variable has the important
194 advantage of being specific to the population whose breeding phenology has been recorded.

195 Interspecific variation in migration distance may be affected by several other factors, such as
196 **the breeding latitude or** the ability of the birds to survive harsh winter conditions. **Species breeding at**
197 **more northern latitudes experience harsher winters and have to migrate longer distances to enjoy the**
198 **same winter conditions as birds breeding at more southern latitudes and these are more likely to be**
199 **migratory (Newton 2008).** In addition, birds of larger sizes can cope better with cold, because heat loss
200 is lower compared to small animals (Bergmann's rule) and an ability to forage on seeds may also
201 facilitate spending the winter at higher latitudes. To account for these confounding factors, we
202 compiled data on adult body mass (the mean of male and female mass, from Dunning (2008) and
203 winter diet, i.e. granivorous (composed primarily of seeds, 0) or insectivorous (mostly insects, 1) from
204 Cramp and Perrins (1994) and Poole (2005), and controlled for these variables in multivariate analyses.

205 Breeding habitat may also confound the relationship between migration and phenology, because
206 long distance migrants may differ in habitat use from short distance migrants and residents (Martin
207 1995, Böhning-Gaese and Oberrath 2003). Neotropical long distance migrants breeding in North
208 America are more likely to inhabit forested environments, whereas Trans-Saharan migrants in the
209 Western Palearctic are more likely to breed in open habitats, compared to short distance or resident
210 species in these areas. To account for any possible bias arising from these differences, we recorded the
211 continent where the breeding phenology was studied (North America or Europe) and following

212 Böhning-Gaese and Oberrath (2003), we assessed the type of breeding habitat based on a gradual scale
213 ranging from closed to open habitats. Typical breeding habitat types reported in Cramp and Perrins
214 (1994) and Poole (2005) were scored for each species on a scale from 1 to 7, as follows: 1 – closed
215 forest; 2 – open forest; 3 – forest edge; 4 – gardens, orchards, urban areas; 5 – shrubland; 6 – open area
216 with single trees or shrubs; and 7 – open area without trees or shrubs. If a species was reported to
217 typically breed in more than one type of habitat, the score of these habitat types was averaged.

218

219 **Comparative analyses**

220

221 To find out whether the relationship between migration distance and breeding phenology is not the
222 result of the confounding effects of breeding latitude, adult body size, winter diet, breeding habitat or
223 continent, we performed multivariate analyses where we controlled for these confounding variables.
224 Second, we ran directional phylogenetic tests between migratory behaviour and the explanatory
225 variables that were significantly related to migration distance in the multivariate analyses.

226 Before performing the multivariate analyses, we checked whether phylogenetic correction was
227 needed by calculating Pagel's lambda statistic for phylogenetic signal, using the *geiger* package in the R
228 statistical environment (Harmon et al. 2008, R Development Core Team 2008). Pagel's lambda is a
229 measure of the phylogenetic structure in the data; a value close to zero indicates phylogenetic
230 independence, while larger values indicate that closely related species are more similar to each other
231 than expected by chance (Pagel 1997, 1999). Significance was estimated by comparing the log-
232 likelihood of a model with the maximum likelihood estimate of lambda for a given trait to the log-
233 likelihood of a model where lambda was set to zero, using likelihood ratio tests. All traits showed
234 significant phylogenetic signal (Table 1).

235 The relationship between migration distance, breeding phenology and the potentially

236 confounding variables was tested using phylogenetic generalized least squares (PGLS) in R's *ape*
237 package (Paradis 2006). The PGLS method accounts for the nonindependence of the data points
238 arising from their phylogenetic relationship by incorporating a matrix of covariances among the
239 species into the model (Martins and Hansen 1997, Pagel 1997, 1999). This matrix can be adjusted to
240 reflect the degree of phylogenetic autocorrelation in the data by incorporating the maximum likelihood
241 estimate of Pagel's lambda (Freckleton et al. 2002). Migration distance, the dependent variable, was
242 square-root transformed prior to the analyses, as the distribution of this variable was highly skewed due
243 to the large number of non-migratory species in the sample. Although this transformation did not result
244 in a normally distributed variable, the residuals of the PGLS models were normally distributed
245 (Shapiro-Wilk tests of normality are reported along with the models). Breeding latitude, winter diet,
246 start of breeding, length of breeding season, adult body mass, breeding habitat and continent were
247 introduced as explanatory variables.

248 To find out the direction of evolutionary transitions and to corroborate the results of the PGLS
249 analyses, we applied Pagel's test (Pagel 1994, Pagel and Meade 2006), using the software BayesTraits
250 (available at <http://www.evolution.rdg.ac.uk/BayesTraits.html>). To test the correlated evolution of two
251 binary traits on a phylogenetic tree, this method uses reversible-jump Markov chain Monte Carlo to
252 estimate support for the hypothesis of correlated evolution between the two traits by searching among
253 possible models conforming either to independent or correlated evolution. The dependent and
254 independent models can be compared by means of the Bayes factor, i.e. by calculating $2[\log_e(\text{harmonic}$
255 $\text{mean of log likelihood of the dependent models}) - \log_e(\text{harmonic mean of the log likelihood of the}$
256 $\text{independent models})]$. A Bayes factor greater than 2 indicates positive evidence for the correlated
257 model, greater than 5 is strong and greater than 10 is very strong evidence (Pagel and Meade 2006).
258 Each model consists of up to eight different parameters describing the rate of transition among the four
259 possible combination of states. The posterior distribution of these transition rate parameters are

260 simultaneously estimated by the reversible-jump Markov chain Monte Carlo algorithm. Alternative
261 evolutionary hypotheses (such as the temporal order and contingency of evolutionary changes) can be
262 tested by comparing critical pairs of these parameters (e.g. by looking at the posterior probability that
263 a given parameter is zero). If transitions in one character depend on the background of the other
264 character, then evolutionary changes in the first are contingent upon the second character (the
265 contingent changes test). For example, if the the rate parameter for the $(0,0) \rightarrow (1,0)$ transition is higher
266 than zero, but the rate parameter for the $(0,1) \rightarrow (1,1)$ transition is assigned a value of zero with high
267 posterior probability, then this means that transitions in the first trait (from 0 to 1) are more likely
268 when the background state of the other character is 0. For the analyses we have used an exponential
269 hyperprior $(0 \ 100)$, which allows the estimation of the rate transition parameters from the data. The
270 Monte Carlo algorithm was run for 10^7 iterations, with a sampling frequency of 100 iterations. The first
271 10^6 iterations were discarded, because the harmonic means of the log-likelihood generally did not
272 stabilize before this. For further details on this method, see Pagel and Meade (2006) and the
273 BayesTraits manual (available at <http://www.ams.reading.ac.uk/zoology/pagel>).

274 The drawback of the correlated changes test in our case is that it cannot account for the
275 confounding effects of other variables. Thus, while two traits can be shown to conform to correlated
276 evolution, it cannot be ruled out that transition in both traits happened because of transition in a third
277 variable. Here, both migration distance and breeding phenology depend on breeding latitude, and
278 transitions in the breeding range of a species may simultaneously affect both traits. To circumvent this
279 problem, we calculated residuals between migration distance and breeding latitude and subsequently
280 scored species with positive residuals (i.e. migration distance longer than expected for that latitude) as
281 long distance migrants (1) and short-distance migrants (0) otherwise. The problem with taking
282 residuals is that this categorization may depend on the species included in the analysis, or the latitude
283 from which their migration distance is calculated. To quantify this error, we repeated the calculation

284 the residuals using random points from within the breeding range of the species and the minimum
285 migration distances from these coordinates. That is, for every focal species, we selected random points
286 for all other species, but kept the original values for the focal species, calculated residuals and scored
287 the focal species as long-distance or short distance migrant based on the residuals. This procedure was
288 repeated 1000 times for each species. In this way, we were able to determine the rate of error of our
289 initial categorization for each species (i.e. the number of times a species will be scored differently if
290 the values of the other species changes). We found that our categorization is robust for most species,
291 but 15 species received a different score at least one time (a rate of error > 0). Therefore, we have
292 repeated the directional analyses by excluding these species.

293 The start of breeding, length of breeding season and body mass are all continuous variables, but
294 the correlated changes test can only be performed on binary variables. Therefore, we dichotomized
295 these variables using their median as the cutoff value. Thus, a species was scored as a late breeder (1)
296 if it starts breeding after 7th May and early breeder (0) otherwise; species with a breeding season longer
297 than 69.5 days were scored as having a long breeding season (1), all others were scored as having a
298 short breeding season (0). The median body mass in our sample was 19.55 g; species with a body size
299 larger than this value were scored as being large (1), those with a smaller value as small (0). As this
300 categorization may potentially introduce a bias, we repeated the analyses using two different cutoff
301 values, the 40 and 60 percentiles of body mass, start and length of the breeding season.

302 The phylogenetic relationship among the species was represented by a composite phylogeny
303 assembled from recent molecular studies (see Appendix 3 for the tree and the references). As the
304 phylogenetic information was obtained from different studies performed on different gene sequences,
305 we were not able to use branch length information. Therefore, we generated branch lengths in two
306 ways: first, we set all branch lengths to unity (conforming to a punctuational model of evolution);
307 second we repeated both the multivariate and the directional tests by transforming branch lengths using

308 Grafen's method, which is similar to a gradual model of evolution (Grafen 1989, Paradis 2006).

309

310 **Results**

311

312 Both the start of breeding and the length of the breeding season were significantly related to migration
313 distance and these relationships remained significant when we controlled for the potentially
314 confounding effects (Table 2a, b). Migration distance increased with breeding latitude and decreased
315 with adult body size, but it was not related to breeding habitat or continent (Table 2a, b). **Winter diet**
316 **had a significant effect in the full models, but in the minimal models it was only significant when the**
317 **start of the breeding season, but not its length, was introduced as the explanatory phenology variable**
318 **(Table 2a, b).** When the start and length of breeding season were introduced in the same model with
319 breeding latitude, body mass **and winter diet** as covariates, the start of breeding season was not
320 significantly associated with migration distance, whereas all other variables had a significant effect,
321 suggesting that the length of the breeding season may be more important than its starting date.
322 However, given the very strong correlation between the two phenology variables (Spearman's rank
323 correlation, $r_s = -0.78$, $P < 0.001$), multicollinearity may be a problem when these two variables are
324 introduced into the same model and therefore the possibility that the start of breeding may also have an
325 effect (in addition or instead of the length of the breeding season) cannot be excluded.

326 The PGLS analyses were repeated by including sample size (number of nests) and type of
327 phenology data (laying dates or egg dates) as covariates, in addition to the six explanatory variables.
328 However, neither sampling intensity nor the type of phenology data were significantly associated with
329 migration distance, thus interspecific differences in sampling should not affect our results. Backward
330 elimination of the nonsignificant predictors based on largest P -value resulted in the same minimum
331 adequate model (Crawley 2007) as in the first models where these two variables have not been

332 included, therefore they are not reported separately.

333 We found strong support for the correlated evolution of migratory behaviour and breeding
334 phenology (Bayes factor for migratory behaviour – start of breeding 27.01, migratory behaviour –
335 length of breeding season 26.12). Furthermore, the correlated evolution between migratory behaviour
336 and adult body size **and migratory behaviour and winter diet** were also supported (Bayes factor 8.32
337 **and 13.30, respectively**). The transition rate parameters strongly supported the hypothesis that breeding
338 phenology determines migratory behaviour (Table 3); transitions to long migration distance are more
339 likely from short breeding seasons ($q_{13} \gg q_{24}$) and transitions to short migration distance are more
340 likely from a long breeding season ($q_{42} \gg q_{31}$). Similarly, evolutionary transitions in migratory
341 behaviour are contingent upon the start of breeding: transitions to long migration distance are more
342 likely from a state of late breeding ($q_{24} \gg q_{13}$) and transitions to short migration distance are more
343 likely from a state of early breeding ($q_{31} \gg q_{42}$).

344 The transition rate parameters for the correlated evolution between migration and body mass
345 **and migration and winter diet both** showed a pattern opposite to that observed in the case of breeding
346 phenology. Both adult body size and winter diet were found to be contingent upon migratory
347 behaviour; thus, based on the transition rate parameters a large body size is more likely to evolve in
348 short distance migrants ($q_{12} \gg q_{34}$) **and transitions to a granivorous diet are more likely from a state of**
349 **short-distance migration ($q_{21} \gg q_{43}$).**

350 The PGLS analyses and the directional tests (both Bayes factors and the transition rate
351 parameters) were qualitatively similar if the branch lengths were transformed according to Grafen's
352 method. **Moreover, the results were virtually identical when using the northernmost data points**
353 **(Appendix 4), and were not affected by the exclusion of species with a rate of error greater than 0 in**
354 **the scoring of migratory behaviour.** Using the 40 or 60 percentiles as cutoff points to dichotomise the
355 variables resulted in qualitatively similar results, with **two exceptions (Appendix 5). In the analyses**

356 using the 60 percentiles to dichotomise the length of breeding season, three transition rate parameters
357 were assigned a value of zero with a relatively high posterior probability: q_{24} , q_{31} and q_{34} . That is,
358 transitions in migratory behaviour are still contingent upon the length of the breeding season, but it
359 also appears that a very long breeding season is more likely to evolve in short distance migrants ($q_{12} \gg$
360 q_{34}). Second, in the directional test using the 40 percentiles to dichotomize body size, two rate
361 parameters were assigned a value of zero with high posterior probability: q_{13} and q_{34} (Appendix 5),
362 indicating that not only is a large body size more likely to evolve from a state of short distance
363 migration, but also that a long distance migration is less likely to evolve from a very small body size.
364 However, support for this test was relatively weak (Bayes factor 3.31).

365

366 **Discussion**

367

368 Consistent with previous studies, we found that interspecific variability in the migratory behaviour of
369 the finches and their allies is associated with aspects of their breeding phenology. Results from the
370 directional analyses showed that transitions from a relatively short to a relatively long migration
371 distance are more likely when the breeding season is short and starts late, whereas the reverse
372 transition is more likely when the breeding season is long and starts early. Although we acknowledge
373 the difficulties associated with categorizing continuous variables into discrete traits, the results were
374 relatively robust to different categorizations. Furthermore, while the coevolution between migratory
375 behaviour and breeding phenology may involve complex interactions between the traits, with both
376 components affecting the other, we found a robust pattern in support of the hypothesis that the
377 evolution of migratory behaviour is affected by the breeding phenology of the species.

378 The results from the directional tests provided only weak support for the hypothesis that time
379 constraints arising from longer migration distances affect the breeding phenology, as transitions in the

380 start and length of the breeding season were not found to be contingent upon migratory behaviour
381 (except when we used the 60 percentiles as cutoff points for the length of breeding season). Thus,
382 while a long migration distance may lead to less parental investment in male shorebirds (García-Peña
383 et al. 2009) or select for shorter postembryonic developmental periods (Meiri and Yom Tov 2004), it
384 does not lead, in general, to shorter breeding seasons or a later onset of breeding in the finches and
385 their allies. These differences are not surprising, as the three traits are fundamentally different aspects
386 of reproductive behaviour and each may be affected differently by time constraints. In particular, as the
387 length of the breeding period in this study probably reflects the number of brood attempts per year
388 (either from multiple broods or replacement broods), it may have a greater effect on reproductive
389 success than either parental care or the length of the postembryonic developmental period. The
390 reproductive value of second broods or replacement broods in small passerines is probably large, given
391 their relatively short life span (Møller 2007), so it might not be advantageous to give up the
392 opportunity to raise these broods, if the environmental conditions enable it.

393 Our results do not support the hypothesis that the association between migratory behaviour and
394 breeding phenology is the result of life history trade-offs affecting these traits simultaneously. First,
395 while arguments based on life history theory may explain the lower number of annual broods and the
396 corresponding shorter breeding season in long distance migrants, they cannot account for the later start
397 of the breeding season in these species. Second, if the fecundity-mortality trade-off would be
398 responsible for the observed correlation between migration and breeding phenology, we would expect
399 that evolutionary transitions in the length of the breeding season depend on the background state of
400 migratory behaviour (i.e. transition rates to a short breeding season higher in relatively long distance
401 migrants *and* transition rates to long breeding season higher in short distance migrants), a prediction
402 not supported by our results. This is not to say that differences in annual survival due to contrasting
403 migration strategies cannot not lead to differences in reproductive investment, because selection can

404 affect other reproductive traits as well, e.g. clutch size (Martin 1995, Böhning-Gaese et al. 2000).
405 However, our results make it unlikely that the shorter breeding season is the consequence of the high
406 annual survival rate of long distance migrants, which selects for fewer broods per year (and hence a
407 shorter breeding season). Furthermore, the fact that not all species migrate long distances (although
408 this would supposedly increase their annual survival rate; Greenberg 1980, Bruderer and Salewski
409 2009), suggests that additional factors may operate which select for shorter migration distances in
410 some species.

411 The most likely scenario based on our results is that reproductive phenology is determined by
412 ecological factors, such as the species-specific type of food exploited during breeding. Reproduction in
413 birds is an energy-demanding process and selection should act to maximally match the timing of
414 reproduction with the peak of food availability (Lack 1968, Perrins 1970). The length and timing of
415 this peak in food availability is likely to differ among different types of habitat, but differences may
416 exist within habitats as well, if birds breeding at the same location rely on different types of food to
417 feed their nestlings. The reproductive phenology in turn may determine the costs and benefits of
418 migration, constraining migration distance such that only species with a short, late-starting breeding
419 season can afford to migrate long distances while species with an extended breeding season can travel
420 only short distances. The evolutionary explanation for this phenomenon could be that species with a
421 relatively long breeding season 1) have to migrate under less favourable weather conditions early in
422 spring and late in autumn, and 2) can spend less time on the wintering grounds, both factors decreasing
423 the benefit of migrating long distances (Greenberg 1980, Bell 1996, 1997). In addition, a long breeding
424 season is likely to start early in spring, when environmental conditions tend to show a higher year-to-
425 year variability. This, in turn, could increase the benefit of staying close to the breeding grounds, as
426 individuals can respond more quickly to improving or deteriorating conditions and have a higher
427 fecundity as a result (Alerstam and Högstedt 1980). Unfortunately, we could not clearly discriminate

428 among these possible mechanisms; the length of the breeding season appeared to be more important in
429 multivariate analyses, but the start and length of breeding season were very strongly correlated.
430 Furthermore, as most of our data points are based on data collected from multiple years, a longer
431 breeding season may result from high year-to-year variability. Lastly, our measure of spring
432 predictability (the start of breeding) is only indirect; unfortunately, very few long term breeding data
433 for our species were available to enable a more thorough analysis. It is not unlikely, however, that all
434 these mechanisms act in concert to shape the migratory behavior of a species.

435 The origin and evolution of avian migration has attracted much interest and several hypotheses
436 have been proposed to explain it (for recent reviews and discussions see for example Rappole and Jones
437 2002, Alerstam et al. 2003, Helbig 2003, Salewski and Bruderer 2007). For example, the phylogenetic
438 study of Outlaw and Voelker (2006) suggests that the increasing seasonality of the breeding
439 environments (through the expansion of breeding ranges from southern latitudes to temperate and
440 boreal areas) played a key role in the evolution of migratory behaviour in the pipits and wagtails
441 (*Motacillidae*). Similarly, other studies have emphasized the importance of expanding breeding ranges
442 for the origin of migratory behaviour (e.g. Joseph et al. 1999, Böhning-Gaese 2005, Milá et al. 2006).
443 It is likely however, that other factors may also affect the outcome of this colonization, because closely
444 related species, supposedly with similar biogeographical history, often show contrasting migratory
445 behaviour. For example, in a molecular phylogenetic study, Outlaw et al. (2003) have shown that the 5
446 species of *Catharus* thrushes breeding in North America most likely originate from Central or South
447 America, and migration most likely evolved in this clade by the expansion of the breeding range, while
448 the wintering range changed relatively little. Yet the wintering range of one of the species (*C. guttatus*),
449 **extends far more to the north than the supposed center** of origin of this taxon, suggesting that the
450 migration distance was subsequently shortened in this species (Outlaw et al. 2003). On the other hand,
451 some species do not evolve migratory behaviour after a northward range shift, the European Collared

452 Dove (*Streptopelia decaocto*) being a well-known example. Thus, the expansion from the tropics does
453 not always result in long distance migration. Our results imply that the breeding phenology may
454 explain at least partly the outcome of these range shifts, with long distance migration evolving only
455 when breeding phenology does not constrain it. This is in accordance with current views that regard
456 the evolution of migration as a consequence of birds exploiting the seasonal flush of food at higher
457 latitudes for breeding yet returning to more benign environments to increase survival, but refines this
458 scenario by highlighting ecological conditions that could determine whether the birds keep returning to
459 these ancestral areas or adapt to the year-round occupation of the new breeding areas.

460 Migratory behaviour was negatively associated with adult body size and migration distance was
461 shorter in species with a granivorous winter diet. The directional analyses revealed that transitions in
462 adult body size and winter diet are contingent upon migratory behaviour, with a large adult body size
463 and a granivorous diet being more likely to evolve from a state of a relatively short migration distance.
464 Thus, in the finches and their allies, body mass and winter diet do not appear to constrain migratory
465 behaviour, but rather, these trait adapt to increase the survival chances of birds spending the winter at
466 high latitudes (see Pravosudov et al. 2007 for a similar conclusion on brain size).

467 Although the present study was restricted to the finches and allies, the relationship between
468 phenology and migration could apply to other taxonomic groups as well. However, other factors, the
469 cost of migration in particular, will certainly affect the outcome of the coevolution between migration
470 and breeding phenology (Greenberg 1980). For example, swallows and martins (family *Hirundinidae*)
471 breeding at temperate latitudes have an extended breeding season yet migrate long distances (Bruderer
472 and Salewski 2009). As these birds are highly adapted for aerial life and can forage while in flight
473 during migration, moving between the summer and winter quarters may be less costly for these species
474 (both in terms of mortality and time) and a longer migration distance may be possible even with an
475 extended breeding season. In addition, the relationship between breeding phenology and migration

476 may apply not only to interspecific comparisons, but also to differences in the migratory behaviour of
477 populations of the same species. Both the “time allocation” and the “spring predictability” hypotheses
478 have been applied to explain leap-frog migration (the pattern in which northern populations of a
479 species migrate longer distances than the southern ones; Alerstam and Högstedt 1980, Greenberg 1980,
480 Bell 1996, 1997). Although alternative explanations for leap-frog migration do exist (and indeed are
481 more commonly accepted; Greenberg 1986, Drent and Piersma 1990), our results provide phylogenetic
482 comparative evidence that breeding phenology may also play an important role in shaping migration
483 strategies.

484

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486

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593 Table 1. Lambda statistics for phylogenetic signal for the variables investigated. Branch lengths were
594 set to unity.

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Variable	Lambda	Likelihood ratio	<i>P</i>
Migration distance	0.21	48.40	< 0.001
Length of breeding season	0.08	44.07	< 0.001
Start of breeding season	0.05	8.86	0.003
Breeding latitude	0.82	44.42	< 0.001
Adult body size	0.56	107.16	< 0.001
Winter diet	0.93	90.50	< 0.001
Breeding habitat	0.92	82.72	< 0.001

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612 Table 2. Full and minimal phylogenetic generalized least squares models for explaining migration
 613 distance (km, square-root transformed) by (a) start of breeding season (julian day) or (b) length of
 614 breeding season (days), together with additional explanatory variables: breeding latitude (degrees
 615 North), adult body size (g), winter diet (granivorous/insectivorous), breeding habitat (for
 616 categorisation, see text) and continent (Europe/North America). Minimal models were obtained by
 617 eliminating nonsignificant predictors from the full model in a backward stepwise manner based on the
 618 largest P-value. Branch lengths were set to unity.

619 (a)

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Start of breeding season	0.126 (0.053)	2.390 (0.018)	0.142 (0.050)	2.850 (0.005)
Breeding latitude	1.182 (0.188)	6.288 (<0.001)	1.077 (0.170)	6.321 (<0.001)
Adult body size	-0.239 (0.086)	-2.776 (0.006)	-0.244 (0.088)	-2.782 (0.006)
Winter diet	11.617 (4.661)	2.492 (0.014)	10.853 (4.662)	2.328 (0.022)
Breeding habitat	0.456 (0.793)	0.575 (0.566)	-	-
Continent	-8.963 (6.018)	-1.489 (0.139)	-	-

620 Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.993$, $P = 0.725$; for the
 621 minimal model: $W = 0.988$, $P = 0.318$.

622 (b)

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Length of breeding season	-0.154 (0.038)	-4.043 (<0.001)	-0.172 (0.036)	-4.732 (<0.001)
Breeding latitude	1.124 (0.166)	6.786 (<0.001)	1.010 (0.152)	6.639 (<0.001)
Adult body size	-0.262 (0.085)	-3.118 (0.002)	-0.296 (0.088)	-3.372 (0.001)
Winter diet	9.042 (4.568)	1.980 (0.050)	-	-
Breeding habitat	0.333 (0.765)	0.437 (0.663)	-	-
Continent	-9.279 (5.757)	-1.612 (0.110)	-	-

623 Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.993$, $P = 0.791$; for the
 624 minimal model: $W = 0.989$, $P = 0.362$.

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626 Table 3. Mean \pm SD and Z-scores of the transition rate parameters, estimated from the directional tests.
 627 Migratory behaviour is the first variable in all cases, and length of breeding season, start of breeding
 628 season, **adult body size and winter diet were the second character, respectively**. All variables are
 629 dichotomous (see the Methods section for scoring species). Parameters which were assigned a value of
 630 0 with high posterior probability (high Z-scores), suggesting that the given transition occurs with very
 631 **low probability, are shown** in bold. The meaning of the parameters is clarified in Figure 1.

Parameter	Length of breeding season		Start of breeding season		Adult body size		Winter diet	
	Mean \pm SD	Z-score	Mean \pm SD	Z-score	Mean \pm SD	Z-score	Mean \pm SD	Z-score
q_{12}	0.56 \pm 0.43	0.00	0.41 \pm 0.09	0.00	0.19 \pm 0.08	0.00	0.05 \pm 0.02	0.04
q_{13}	0.47 \pm 0.20	0.02	0.00\pm0.02	0.99	0.09 \pm 0.06	0.20	0.14 \pm 0.13	0.00
q_{21}	0.39 \pm 0.12	0.00	0.42 \pm 0.13	0.00	0.16 \pm 0.07	0.00	0.22 \pm 0.13	0.00
q_{24}	0.02\pm0.06	0.92	0.41 \pm 0.10	0.00	0.20 \pm 0.14	0.00	0.12 \pm 0.12	0.16
q_{31}	0.01\pm0.06	0.93	0.42 \pm 0.10	0.00	0.10 \pm 0.04	0.00	0.26 \pm 0.13	0.00
q_{34}	0.39 \pm 0.12	0.00	0.42 \pm 0.12	0.00	0.00\pm0.02	0.93	0.07 \pm 0.04	0.05
q_{42}	0.46 \pm 0.20	0.03	0.00\pm0.02	1.00	0.21 \pm 0.14	0.00	0.06 \pm 0.03	0.00
q_{43}	0.55 \pm 0.43	0.00	0.41 \pm 0.09	0.00	0.14 \pm 0.06	0.00	0.00\pm0.01	0.92

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639 Figures

640 Fig. 1. Schematic representation of the transition rate parameters (q_{ij}) estimated by the directional tests.
641 The numbers in the boxes represent the four possible combinations of two binary traits. The first
642 number represents the state of migratory behaviour whereas the second stands for the state of either of
643 the three explanatory variables: start of breeding season, length of breeding, adult body size or winter
644 diet. The parameters q_{ij} denote the rate of transition among these combination of states.

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646 Fig. 2. Relationship between migration distance (km, square root transformed) and five explanatory
647 variables: start (a) and length of breeding season (b), breeding latitude (c), adult body size (log-
648 transformed for better visualization) (d) and winter diet (e). The outlier with the longest migration
649 distance is the Bobolink (*Dolichonyx oryzivorus*); excluding this species does not affect the results.

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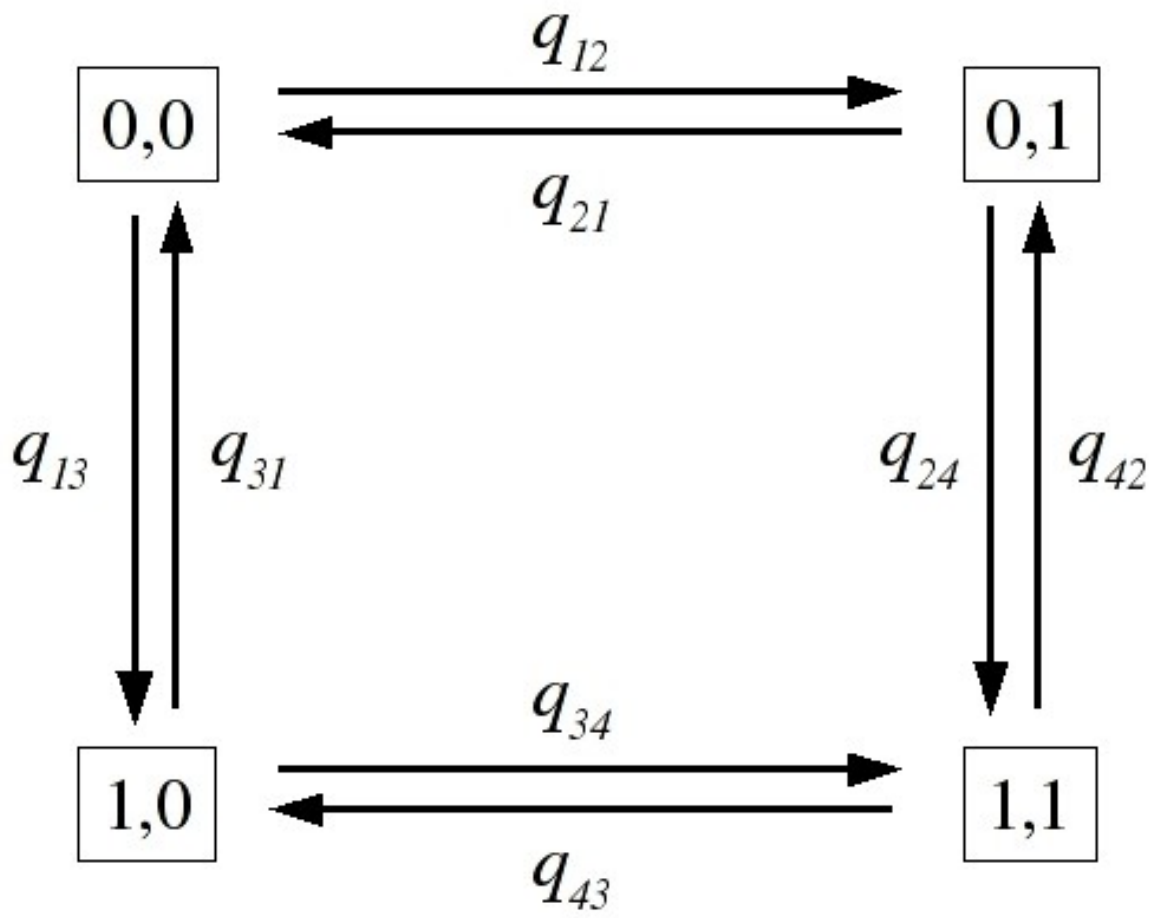
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663 Fig. 1.

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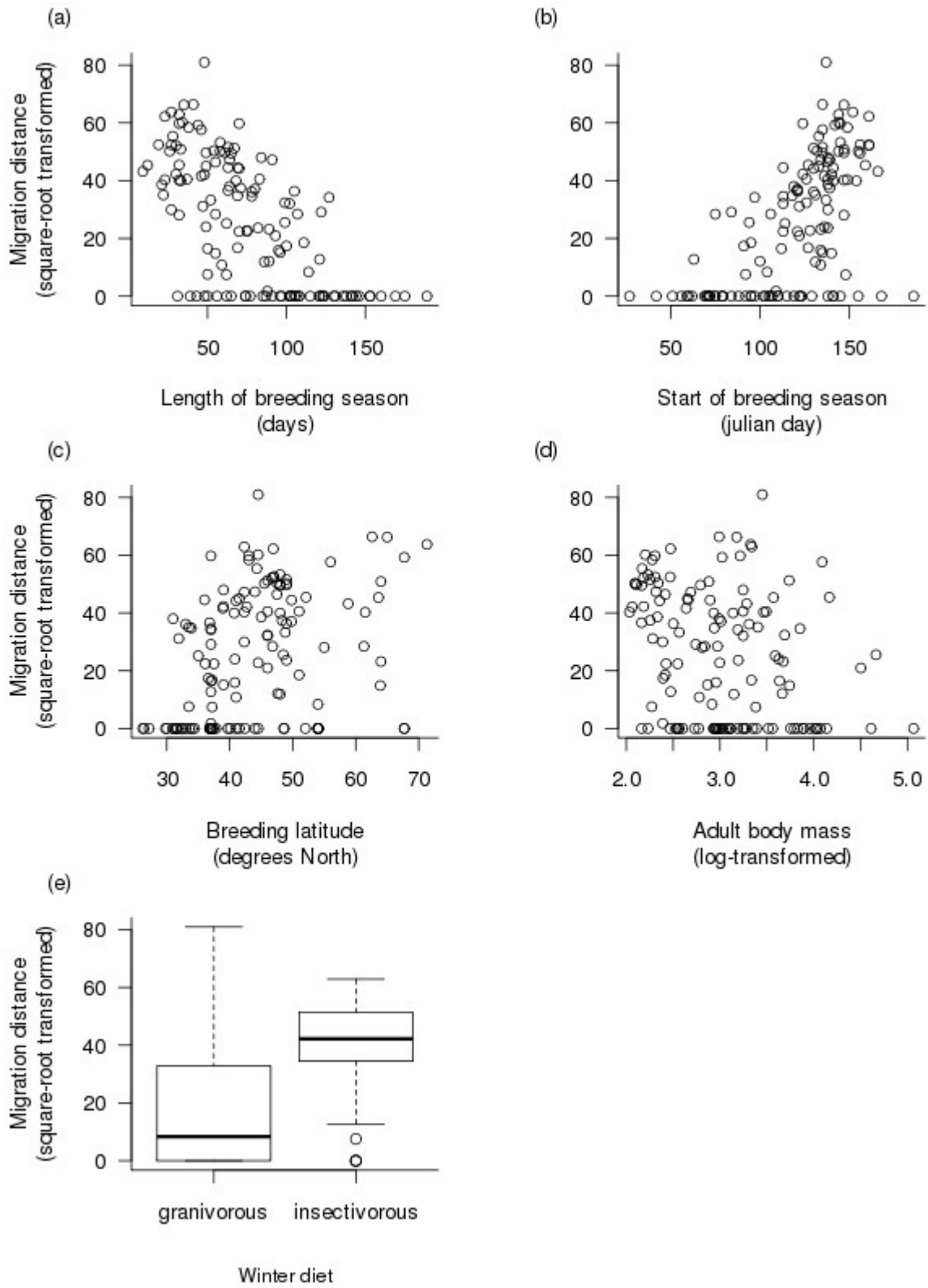
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Species	Migration distance (km)	Migratory behaviour ¹	Breeding latitude (degrees)	Start of breeding (Julian day)	Length of breeding season (days)	Winter diet ²	Adult body mass (g)	Breeding habitat type ³	Breeding phenology references
<i>Agelaius phoeniceus</i>	0	0	41.5	123	62	0	52.4	7	Robertson 1973
<i>A. tricolor</i>	0	0	36.75	71	108	0	58.7	6.5	Hamilton 1998
<i>Aimophila aestivalis</i>	0	0	34.36	107	131	0	19.16	3	Haggerty 1988
<i>A. botterii</i>	0	0	31.5	168	56	1	19.9	7	Poole 2005
<i>A. carpalis</i>	0	0	31.7	110	144	0	15.3	6	Bent 1968
<i>A. cassinii</i>	0	0	31	60	153	0	18.9	6	Poole 2005
<i>A. quinquestriata</i>	0	0	31.5	155	77	0	19.55	3	Poole 2005
<i>A. ruficeps</i>	0	0	36.85	70	121	0	18.7	6	Poole 2005
<i>Ammodramus bairdii</i>	1974	1	49.75	141	69	0	18.07	6	Davis 2003
<i>A. caudacutus</i>	253	0	40.75	134	95	1	19.25	7	Poole 2005
<i>A. henslowii</i>	501	1	37.5	121	70	0	12.8	7	Winter 1999
<i>A. leconteii</i>	1107	1	48.8	137	52	0	13	7	Poole 2005
<i>A. maritimus</i>	1596	1	40.7	154	33	0	23.08	7	Bent 1968
<i>A. savannarum</i>	228	0	39	135	96	0	17.57	6.5	Bent 1968
<i>Amphispiza belli</i>	806	1	46.8	75	55	0	17.07	6	Washington Birds Breeding Phenology Program
<i>A. bilineata</i>	0	0	29.8	79	146	0	13.5	6	Bent 1968
<i>Arremonops rufivirgatus</i>	0	0	27.25	75	169	0	22.45	5	Bent 1968
<i>Bucanetes githagineus</i>	0	0	37	51	115	0	19.4	7	Barrientos et al. 2007
<i>Calamospiza melanocorys</i>	576	1	40.83	136	49	0	37.6	6.5	Creighton and Baldwin 1974
<i>Calcarius lapponicus</i>	4059	1	71.3	152	27	0	27.85	7	Custer and Pitelka 1977
<i>C. mccownii</i>	1645	1	51	126	83	0	25.7	7	Poole 2005
<i>C. ornatus</i>	1374	1	49.75	121	80	0	20.3	7	Davis 2003
<i>C. pictus</i>	1865	1	58.82	166	9	0	26.7	6	Jehl 1968
<i>Cardellina rubrifrons</i>	968	1	31.91	122	47	1	9.8	1	Kirkpatrick and Conway 2005
<i>Cardinalis cardinalis</i>	0	0	44.5	103	124	0	42.65	3.8	Peck and James 1987
<i>C. sinuatus</i>	0	0	30	72	138	0	35.2	4.67	Bent 1968
<i>Carduelis cannabina</i>	808	0	61.3	106	107	0	19.55	5	Tast 1970

<i>C. carduelis</i>	0	0	48.6	115	102	0	16	4.33	Glück 1983
<i>C. chloris</i>	0	0	54	102	121	0	26	4.33	Monk 1954
<i>C. flammea</i>	0	0	67.7	141	65	0	13	4	Pulliainen and Peiponen 1981
<i>C. lawrencei</i>	302	0	36.58	91	100	0	10.95	6	Bent 1968
<i>C. pinus</i>	0	0	37.01	97	103	0	12.7	2	Poole 2005
<i>C. psaltria</i>	0	0	36.77	92	123	0	9.32	3.5	Bent 1968
<i>C. tristis</i>	0	0	44	186	74	0	12.8	4.33	Bent 1968
<i>Carpodacus cassinii</i>	0	0	42.35	138	50	0	26.5	2	Mewaldt and King 1985
<i>C. erythrinus</i>	4387	1	65	147	35	0	24	4	Reinikainen 1939
<i>C. mexicanus</i>	0	0	37	59	160	0	21.4	4.8	Bent 1968
<i>C. purpureus</i>	141	0	48	131	86	0	23.3	3.5	Peck and James 1998
<i>Chondestes grammacus</i>	0	0	31	119	39	0	49	6	Poole 2005
<i>Coccothraustes coccothraustes</i>	0	0	54.12	105	91	0	56.65	1	Mountfort 1957
<i>Dendroica caerulescens</i>	2238	1	44	139	64	1	10.15	1	Holmes et al. 1995
<i>D. castanea</i>	2749	1	47	156	27	1	11.8	1	Bent 1963
<i>D. cerulea</i>	3619	1	44.5	144	34	1	9.05	1	Peck and James 1987
<i>D. coronata</i>	162	0	37	63	121	1	11.87	1	Poole 2005
<i>D. discolor</i>	1624	1	42.3	149	23	1	7.65	3.33	Bent 1963
<i>D. dominica</i>	57	0	33.5	92	50	1	9.7	1	Bent 1963
<i>D. fusca</i>	3408	1	43	149	38	1	9.75	1	Bent 1963
<i>D. magnolia</i>	2520	1	45.5	155	26	1	8.15	1	Bent 1963
<i>D. nigrescens</i>	1340	1	36.83	121	63	1	8.7	2.67	Bent 1963
<i>D. palmarum</i>	1490	1	45	138	21	1	10.3	6	Bent 1963
<i>D. pensylvanica</i>	2834	1	48	145	58	1	9.3	3	Peck and James 1987
<i>D. petechia</i>	2659	1	49	135	63	1	9.52	4.5	Peck and James 1987
<i>D. pinus</i>	0	0	40.07	98	48	0	11.78	1	Bent 1963
<i>D. striata</i>	3872	1	46.87	161	23	1	11.85	1	Bent 1963
<i>D. tigrina</i>	2749	1	47	161	19	1	10.05	1	Bent 1963
<i>D. virens</i>	2447	1	48	156	65	1	8.7	1	Peck and James 1987
<i>Dolichonyx oryzivorus</i>	6554	1	44.5	137	48	0	31.55	7	Perlut 2007
<i>Emberiza cirrus</i>	0	0	39.7	84	102	0	25.6	4.33	Ponz et al. 1996
<i>E. citrinella</i>	0	0	54	95	153	0	29.7	4.5	Cramp and Perrins 1994b
<i>E. hortulana</i>	4404	1	62.56	135	41	0	19.9	5	Cramp and Perrins 1994b
<i>E. rustica</i>	3509	1	67.7	142	44	0	20.55	2.5	Pulliainen and Saari 1989
<i>E. schoeniclus</i>	70	0	54	104	114	0	18.45	6.5	Glutz von Blotzheim and Bauer (1966-1997)
<i>Euphagus carolinus</i>	3322	1	56	135	46	0	59.75	1	Bent 1965
<i>E. cyanocephalus</i>	0	0	37	88	103	0	62.65	4	Bent 1965

<i>Fringilla coelebs</i>	0	0	54	69	96	0	21.97	1	Newton 1964
<i>Geothlypis trichas</i>	1400	1	48.3	139	71	1	9.53	3	Peck and James 1987
<i>Helmitheros vermivorus</i>	2022	1	41.5	133	49	1	14.2	1	Poole 2005
<i>Icteria virens</i>	3571	1	37	124	70	1	24.9	4	Bent 1963
<i>Icterus bullockii</i>	271	0	37	112	50	1	37.9	6	Bent 1965
<i>I. cucullatus</i>	1169	1	37	97	127	1	24.3	6	Bent 1965
<i>I. galbula</i>	1640	1	46	138	37	1	32.85	4.5	Peck and James 1987
<i>I. gularis</i>	0	0	26.18	110	87	1	55.3	6	Werner 2004
<i>I. parisorum</i>	634	1	35	114	62	1	36.19	6	Bent 1965
<i>I. spurius</i>	1444	1	31	119	64	1	19.89	5	Bent 1965
<i>Junco hyemalis</i>	0	0	37.25	79	136	0	19.04	2	Bent 1968
<i>J. phaeonotus</i>	0	0	32.18	106	74	0	20.7	5	Kirkpatrick and Conway 2005
<i>Leucosticte tephrocotis</i>	537	0	64	134	89	0	39.47	7	Bent 1968
<i>Limnothlypis swainsonii</i>	1209	1	33.87	118	69	1	18.9	1	Thompson 2005
<i>Melospiza georgiana</i>	117	0	41	134	59	0	16.1	4.5	Poole 2005
<i>M. lincolnii</i>	787	0	55	147	32	0	16.6	4.67	Bent 1968
<i>M. melodia</i>	0	0	48.6	56	130	0	20.1	3	Smith and Arcese 1994
<i>Miliaria calandra</i>	0	0	54	122	97	0	48.75	6.5	Glutz von Blotzheim and Bauer (1966-1997)
<i>Mniotilta varia</i>	897	1	42.3	138	27	1	10.9	1	Bent 1963
<i>Oporornis formosus</i>	1730	1	38.9	136	46	1	14	1	Poole 2005
<i>O. tolmiei</i>	2535	1	47.5	132	54	1	10.4	2.5	Washington Birds Breeding Phenology Program
<i>Parula americana</i>	1770	1	42.67	140	48	1	7.87	1	Bent 1963
<i>Passerculus sandwichensis</i>	517	0	44.5	128	75	0	20.02	7	Perlut 2007
<i>Passerella iliaca</i>	0	0	37.37	141	48	0	33.64	3	Bent 1968
<i>Passerina amoena</i>	848	1	37	84	122	0	15.5	4	Bent 1968
<i>P. caerulea</i>	1304	1	33	130	78	0	27.4	4.4	Bent 1968
<i>P. cyanea</i>	2228	1	42.27	134	91	0	14.7	3.5	Payne and Payne 1998
<i>Pheucticus ludovicianus</i>	2625	1	46	130	67	1	42	3	Peck and James 1987
<i>P. melanocephalus</i>	1194	1	37	113	78	0	47.15	4.5	Bent 1968
<i>Pinicola enucleator</i>	0	0	67.7	145	31	0	56.4	2	Pulliainen 1979
<i>Pipilo aberti</i>	0	0	33.61	72	108	1	45.95	2	Finch 1984
<i>P. chlorurus</i>	55	0	37.24	148	62	0	29.4	4	Bent 1968
<i>P. erythrophthalmus</i>	1046	1	46	126	99	0	40.05	3.33	Peck and James 1987
<i>P. fuscus</i>	0	0	34	62	189	0	44.4	5	Bent 1968
<i>P. maculatus</i>	146	0	47.55	100	89	0	39	5	Washington Birds Breeding Phenology Program
<i>Piranga ludoviciana</i>	280	0	37.24	127	69	1	28.1	2	Bent 1965

<i>P. olivacea</i>	3955	1	42.3	144	32	1	28.2	1	Bent 1965
<i>P. rubra</i>	1228	1	33.5	131	22	1	30.1	2.5	Bent 1965
<i>Plectrophenax nivalis</i>	220	0	63.87	140	55	0	42.2	7	Bent 1968
<i>Poocetes gramineus</i>	1029	1	46	113	102	0	25.7	6.5	Peck and James 1987
<i>Protonotaria citrea</i>	1982	1	36	113	63	1	14.3	1	Petit 1989
<i>Pyrrhula pyrrhula</i>	0	0	52.03	95	142	0	22.47	1	Bijlsma 1982
<i>Quiscalus major</i>	0	0	33	79	105	0	158.5	6.5	Post 1995
<i>Q. quiscula</i>	651	0	48.5	94	99	0	106.1	3.75	Peck and James 1987
<i>Seiurus aurocapillus</i>	1594	1	48	141	68	1	18.8	1	Peck and James 1987
<i>S. novaboracensis</i>	2465	1	49	135	49	1	16.3	2	Peck and James 1987
<i>Serinus canaria</i>	0	0	32.6	27	123	0	24.3	5	Voigt and Leitner 1998
<i>S. serinus</i>	343	0	51	95	111	0	11.2	3.5	Cramp and Perrins 1994a
<i>Setophaga ruticilla</i>	2469	1	48	147	61	1	8.25	1	Peck and James 1987
<i>Spiza americana</i>	2301	1	39	138	84	0	25.71	7	Zimmerman 1983
<i>Spizella arborea</i>	2588	1	64	147	33	0	17.85	6	Bent 1968
<i>S. atrogularis</i>	503	1	36.11	113	75	0	11.3	5	Bent 1968
<i>S. breweri</i>	3	0	37	109	88	0	10.9	5	Bent 1968
<i>S. pallida</i>	2154	1	47.5	138	55	0	11.2	4.67	Grant et al. 2005
<i>S. passerina</i>	1319	1	49	121	105	0	12.2	2.5	Peck and James 1987
<i>S. pusilla</i>	0	0	41	123	85	0	12.5	4.5	Poole 2005
<i>Sporophila torqueola</i>	0	0	26.4	71	175	0	8.7	7	Bent 1968
<i>Sturnella magna</i>	438	0	46	122	93	0	90.23	7	Peck and James 1987
<i>S. neglecta</i>	0	0	37	42	141	0	100.7	7	Bent 1965
<i>Vermivora chrysoptera</i>	3064	1	44.3	133	28	1	8.75	3	Bent 1963
<i>V. peregrina</i>	2718	1	46.7	161	30	1	8.9	1	Bent 1963
<i>V. pinus</i>	1783	1	39	124	30	1	8.9	3.33	Poole 2005
<i>V. ruficapilla</i>	2517	1	49	144	58	1	8.1	2	Peck and James 1987
<i>Wilsonia canadensis</i>	3571	1	43	145	32	1	10.05	1	Bent 1963
<i>W. citrina</i>	1954	1	41	130	70	1	10.55	1	Poole 2005
<i>Xanthocephalus</i> <i>xanthocephalus</i>	2063	1	52.13	127	32	0	64.5	5.5	Poole 2005
<i>Zonotrichia albicollis</i>	558	0	49	138	82	0	24.4	2	Peck and James 1987
<i>Z. atricapilla</i>	1617	0	61.5	147	32	0	32	5.5	Bent 1968
<i>Z. leucophrys</i>	0	0	37.8	75	106	0	28.52	4	Petrinovich Patterson 1983
<i>Z. querula</i>	2055	1	63.6	159	12	0	35.55	6	Norment 1992

677 Notes:

678 ¹0 – short-distance migrant (migration distance shorter than expected for breeding latitude), 1 – long-

679 distance migrant (migration distance longer than expected for breeding latitude)

680 ²0 – granivorous; 1 – insectivorous.

681 ³ 1-closed forest; 2-open forest; 3-forest edge; 4 – gardens, orchards, urban areas; 5 – shrubland; 6 –
682 open area with single trees or shrubs; and 7 – open area without trees or shrubs. If more than one
683 habitat type was reported for a species, they were averaged.

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790 Appendix 2. Sampling bias.

791 Differences in sampling may affect the the start and and **length** of the breeding season and thereby
792 confound the relationship between breeding phenology and migration. First, sampling intensity might
793 introduce a bias because more effort typically increases the probability of very early or very late nests
794 to be discovered. Second, some studies report laying dates, whereas others report the dates on which
795 viable eggs were found. Assuming identical sampling effort, earliest egg dates should not differ
796 considerably from earliest laying dates, but the latest egg dates should be later than the latest laying
797 dates, because the former incorporate the incubation period as well. However, egg collectors may have
798 concentrated their efforts to specific part(s) of the breeding cycle (McNair 1987), thus the difference
799 between the two types of data are not straightforward. To check that the two type of phenology data
800 are indeed different and whether any kind of correction is needed, we used the original dataset with all
801 phenology data (n=496 records for 134 species, with a median of 3 records per species) to build
802 generalized estimating equation (GEE) models. GEEs are extensions of generalized linear models
803 (Liang and Zeger 1986, Hardin and Hilbe 2003) that can be used for correlated data (ie. multiple data
804 points from a single species in our case). GEE models were constructed using the *geepack* package in
805 the R statistical environment (Yan and Fine 2004, R Development Core Team 2008), with an
806 exchangeable correlation structure that assumes multiple observations within clusters (species) to be
807 equally correlated. Start and end date of the breeding season were separately used as independent
808 variables, location (the latitude where the phenology was recorded), sample size (number of nests) and
809 type of the data (laying date or egg date) were introduced as explanatory variables, and species as a
810 grouping factor. These analyses showed that the end date of the breeding season does not differ
811 significantly at the 5% level between egg dates and laying dates (after controlling for sample size and
812 location), but that the starting date in the case of egg dates is significantly later compared to laying
813 dates. Furthermore, sample size is negatively correlated with the start and end dates such that earlier
814 dates were recorded for larger sample sizes). Although this is what we would expect for the start date,

815 the direction of the relationship in the case of end dates is strange. It turns out however, that this
816 relationship is not significant when one data point with extremely large sample size, ~500 000 nests of
817 *Tricolored Blackbirds (Agelaius tricolor)*, is excluded.

818 To summarize, the start of breeding season is affected by both sampling intensity and the type
819 of phenology data, whereas the end of the breeding season is not affected by these factors.

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840 Appendix 3. The phylogenetic tree used in the analyses and the references used to compile the tree.

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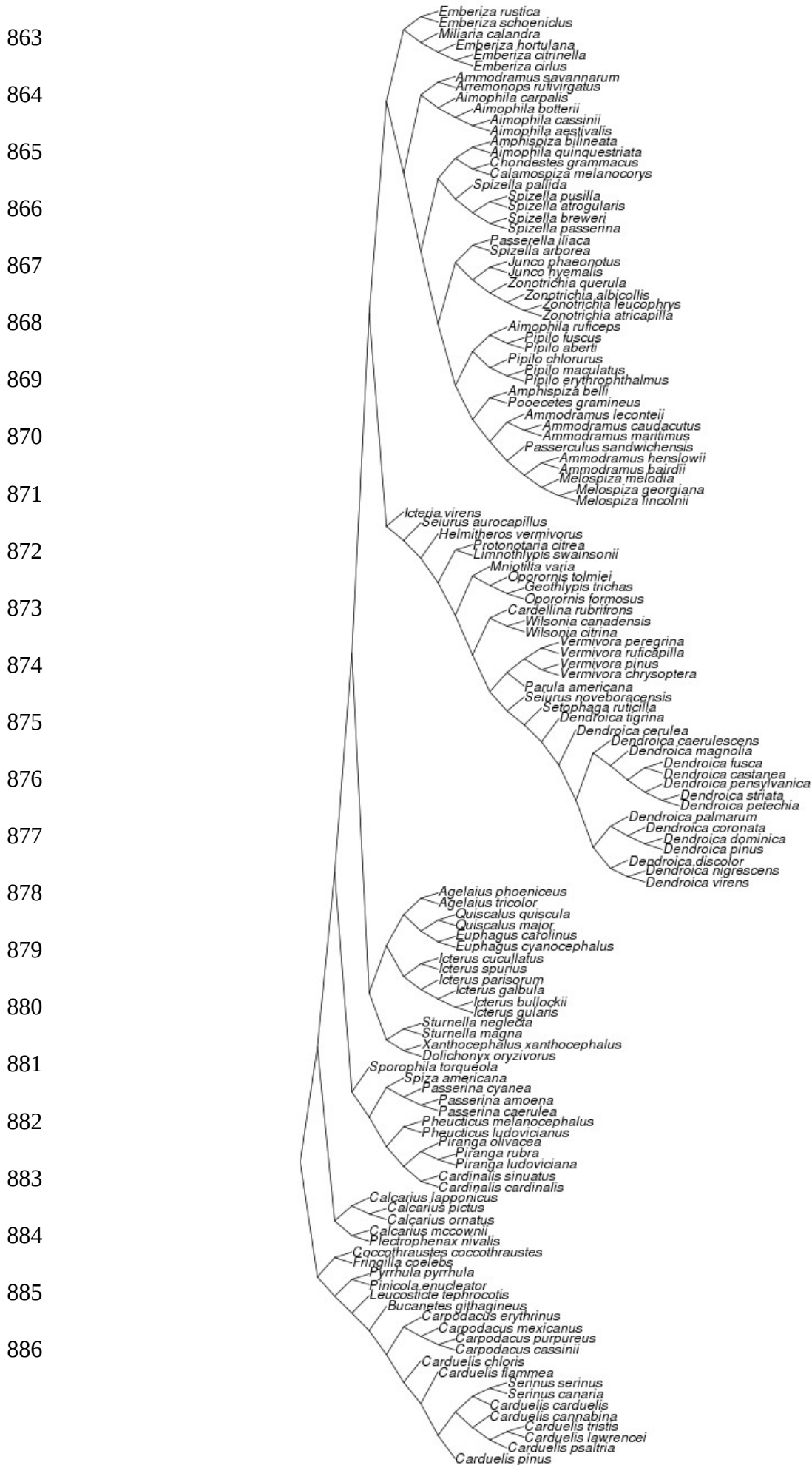
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932

933 Appendix 4. Results from the dataset with the northernmost phenology records. For all species where
 934 phenology data with a sample size of at least 20 nests was available from several locations, we
 935 selected the northernmost record and computed the minimum migration distance from these
 936 coordinates. Records matching these criteria were available for 54 out of 134 species. The median
 937 breeding latitude in this sample was 47.3 degrees North and the median migration distance 1137.5 km,
 938 compared to 42.55 degrees North and 642.5 km in the original sample in which data was selected
 939 based on the largest sample size. In this appendix we present the results of the multivariate analyses
 940 using this dataset with either the start (a) or the length of the breeding season (b) included as the
 941 explanatory phenology variable and the results of the directional tests (c).

942

943 (a)

944

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Start of breeding season	0.187 (0.065)	2.887 (0.005)	0.210 (0.062)	3.323 (0.001)
Breeding latitude	0.935 (0.179)	5.226 (<0.001)	0.838 (0.168)	4.984 (<0.001)
Adult body size	-0.200 (0.083)	-2.399 (0.018)	-0.212 (0.087)	-2.440 (0.016)
Winter diet	11.601 (4.717)	2.459 (0.015)	10.113 (4.776)	2.118 (0.036)
Breeding habitat	0.681 (0.813)	0.838 (0.404)	-	
Continent	-9.034 (5.592)	-1.616 (0.109)	-	

945 Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.990$, $P = 0.422$; for the
 946 minimal model: $W = 0.980$, $P = 0.043$.

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948

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953 (b)

954

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Length of breeding season	-0.173 (0.046)	-3.774 (<0.001)	-0.193 (0.044)	-4.420 (<0.001)
Breeding latitude	0.941 (0.162)	5.811 (<0.001)	0.829 (0.153)	5.435 (<0.001)
Adult body size	-0.234 (0.082)	-2.839 (0.005)	-0.283 (0.089)	-3.166 (0.002)
Winter diet	10.699 (4.618)	2.317 (0.022)	-	
Breeding habitat	0.792 (0.796)	0.995 (0.322)	-	
Continent	-10.101 (5.358)	-1.885 (0.062)	-	

955 Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.988$, $P = 0.277$; for the

956 minimal model: $W = 0.979$, $P = 0.036$.

957

958 (c)

959

Parameter	Length of breeding season		Start of breeding season		Adult body size		Winter diet	
	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score
q_{12}	0.46±0.17	0.00	0.63±1.10	0.00	0.20±0.10	0.00	0.05±0.02	0.00
q_{13}	0.43±0.13	0.02	0.07±0.21	0.79	0.10±0.07	0.17	0.40±1.10	0.00
q_{21}	0.42±0.11	0.00	1.10±2.85	0.00	0.20±0.09	0.00	0.30±0.22	0.00
q_{24}	0.02±0.07	0.92	0.49±0.30	0.12	0.41±1.86	0.00	0.13±0.20	0.18
q_{31}	0.00±0.03	0.98	0.55±0.44	0.06	0.10±0.04	0.00	0.45±1.12	0.00
q_{34}	0.42±0.13	0.00	1.09±2.83	0.00	0.00±0.02	0.93	0.05±0.03	0.04
q_{42}	0.44±0.12	0.01	0.02±0.07	0.91	0.42±1.86	0.00	0.05±0.02	0.00
q_{43}	0.45±0.20	0.00	0.63±1.10	0.00	0.11±0.05	0.01	0.00±0.01	0.90

960 Bayes factors: migratory behaviour – length of breeding season: 18.07; migratory behaviour – start of

961 breeding season: 24.41; migratory behaviour – adult body size: 8.46; migratory behaviour – winter

962 diet: 19.49.

963

964

965 Appendix 5. Mean \pm SD and Z-scores of the transition rate parameters, estimated from the directional
 966 tests. In these tests, migratory behaviour was the first variable in all cases. The length of breeding
 967 season, start of breeding season and body size were the second character, respectively, and these
 968 variables were dichotomized with either the 40 (a) or the 60 percentiles (b) as cutoff points. The 40
 969 and 60 percentiles were as follows: 62 and 82.8 days for the length of the breeding season, 30th April
 970 and 15th May for the start of the breeding season, 17.2 and 23 grams for adult body size respectively.
 971 Migratory behaviour was dichotomized by regressing breeding latitude over migration distance and
 972 setting it to 1 for species with positive residuals and to 0 for species with negative residuals.

973

974 (a)

975

Parameter	Length of breeding season		Start of breeding season		Adult body size	
	Mean \pm SD	Z-score	Mean \pm SD	Z-score	Mean \pm SD	Z-score
q_{12}	0.46 \pm 0.27	0.00	0.50 \pm 0.56	0.00	0.15 \pm 0.08	0.00
q_{13}	0.45 \pm 0.21	0.00	0.01 \pm 0.03	0.96	0.06 \pm 0.06	0.37
q_{21}	0.37 \pm 0.09	0.00	0.51 \pm 0.57	0.00	0.06 \pm 0.03	0.00
q_{24}	0.00 \pm 0.02	0.99	0.40 \pm 0.11	0.00	0.22 \pm 0.37	0.00
q_{31}	0.01 \pm 0.07	0.96	0.42 \pm 0.17	0.02	0.06 \pm 0.03	0.01
q_{34}	0.45 \pm 0.40	0.00	0.41 \pm 0.23	0.01	0.04 \pm 0.03	0.38
q_{42}	0.37 \pm 0.10	0.02	0.01 \pm 0.05	0.92	0.23 \pm 0.37	0.00
q_{43}	0.44 \pm 0.40	0.00	0.34 \pm 0.12	0.00	0.14 \pm 0.07	0.00

976 Bayes factors: migratory behaviour – length of breeding season: 18.79; migratory behaviour – start of
 977 breeding season: 23.18; migratory behaviour – adult body size: 3.31.

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983 (b)

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Parameter	Length of breeding season		Start of breeding season		Adult body size	
	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score
q_{12}	2.44±10.95	0.00	0.38±0.09	0.00	0.17±0.06	0.00
q_{13}	0.34±0.20	0.07	0.00±0.03	0.98	0.11±0.06	0.07
q_{21}	2.19±10.86	0.00	0.61±0.40	0.00	0.17±0.06	0.01
q_{24}	0.10±0.12	0.43	0.57±0.33	0.00	0.20±0.20	0.00
q_{31}	0.07±0.09	0.56	0.38±0.11	0.02	0.11±0.05	0.01
q_{34}	0.20±0.19	0.32	0.57±0.52	0.00	0.01±0.03	0.90
q_{42}	0.75±0.77	0.06	0.01±0.07	0.96	0.20±0.20	0.00
q_{43}	1.09±1.10	0.01	0.58±0.51	0.00	0.18±0.06	0.00

985 Bayes factors: migratory behaviour – length of breeding season: 30.89; migratory behaviour – start of
986 breeding season: 19.06; migratory behaviour – adult body size: 6.53.