

1 **Quantifying full phenological event distributions reveals simultaneous**  
2 **advances, temporal stability and delays in spring and autumn migration**  
3 **timing in long-distance migratory birds**

4

5 Running head: DIVERGENT CHANGES IN MIGRATION TIMING

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**26 Abstract**

27

28 Phenological changes in key seasonally-expressed life-history traits occurring across periods  
29 of climatic and environmental change can cause temporal mismatches between interacting  
30 species, and thereby impact population and community dynamics. However, studies  
31 quantifying long-term phenological changes have commonly only measured variation  
32 occurring in spring, measured as the first or mean dates on which focal traits or events were  
33 observed. Few studies have considered seasonally paired events spanning spring and autumn,  
34 or tested the key assumption that single convenient metrics accurately capture entire event  
35 distributions. We used 60 years (1955-2014) of daily bird migration census data from Fair  
36 Isle, Scotland, to comprehensively quantify the degree to which the full distributions of  
37 spring and autumn migration timing of 13 species of long-distance migratory bird changed  
38 across a period of substantial climatic and environmental change. In most species, mean  
39 spring and autumn migration dates changed little. However, the early migration phase ( $\leq 10^{\text{th}}$   
40 percentile date) commonly got earlier, while the late migration phase ( $\geq 90^{\text{th}}$  percentile date)  
41 commonly got later. Consequently, species' total migration durations typically lengthened  
42 across years. Spring and autumn migration phenologies were not consistently correlated  
43 within or between years within species, and hence were not tightly coupled. Furthermore,  
44 different metrics quantifying different aspects of migration phenology within seasons were  
45 not strongly cross-correlated, meaning that no single metric adequately described the full  
46 pattern of phenological change. These analyses therefore reveal complex patterns of  
47 simultaneous advancement, temporal stability and delay in spring and autumn migration  
48 phenologies, altering species' life-history structures. Additionally, they demonstrate that this  
49 complexity is only revealed if multiple metrics encompassing entire seasonal event  
50 distributions, rather than single metrics, are used to quantify phenological change. Existing

51 evidence of long-term phenological changes detected using only one or two metrics should  
52 consequently be interpreted cautiously because divergent changes occurring simultaneously  
53 could potentially have remained undetected.

54

## 55 **Introduction**

56

57 Phenological changes in key life-history traits can substantially impact population and  
58 community dynamics by causing temporal mismatches between species and their abiotic  
59 environment and between interacting species (Chuine, 2010; Forrest & Miller-Rushing, 2010;  
60 Miller-Rushing et al., 2010; Ibáñez et al., 2015). A major challenge facing ecologists is  
61 therefore to quantify long-term changes in year-round phenological dynamics, which can  
62 occur in response to both small-scale and large-scale environmental changes (Myneni et al.,  
63 1997; Hughes, 2000; Wuethrich, 2000; Walther et al., 2002; Parmesan & Yohe, 2003; Wilson  
64 et al., 2004; Parmesan, 2006; Both et al., 2006; Barbet-Massin et al., 2009; Chazal &  
65 Rounsevell, 2009; Butchart et al., 2010).

66 Many long-term phenological studies have been carried out in temperate regions and  
67 have focused on quantifying changes in the timing of spring events, for example plant  
68 shooting and leafing, insect emergence, amphibian spawning and bird singing and nesting  
69 (Beebee, 1995; Crick et al., 1997; Forchhammer et al., 1998; McCleery & Perrins, 1998;  
70 Visser et al., 1998; Menzel & Fabien, 1999; Roy & Sparks, 2000; Both & Visser, 2001;  
71 Sparks & Menzel, 2002; Walther et al., 2002; Parmesan & Yohe, 2003; Visser & Both, 2005;  
72 Cleland et al., 2007; Ibáñez et al., 2010; Thackeray et al., 2010; Gallinat et al., 2015).  
73 However, key biological activities that shape population and community dynamics also occur  
74 in summer, autumn and winter, but long-term changes in the timing of key traits expressed in  
75 these seasons have more rarely been quantified (Jenni & Kéry, 2003; Gallinat et al., 2015).

76 Furthermore, the life-histories of many temperate breeding species include seasonally paired  
77 events occurring in spring and autumn, such as bud burst and leaf fall, emergence from and  
78 entry into hibernation, and outward and return migration (Walther et al., 2002; Cleland et al.,  
79 2007; Gallinat et al., 2015). Phenologies of spring and autumn events occurring within the  
80 same year, or across consecutive years, could be strongly and mechanistically correlated, or  
81 could vary largely independently. However, very few studies have quantified long-term  
82 phenological changes in paired events across both seasons, or quantified cross-season  
83 linkages (Sokolov et al., 1998; Jenni & Kéry, 2003; Sparks & Mason, 2004; Gallinat et al.,  
84 2015). Since models predict relatively rapid and imminent season-specific climatic changes,  
85 determining to what degree phenological changes occurring in one season are correlated with  
86 or independent of changes occurring in other seasons is clearly necessary to fully understand  
87 species' responses to environmental change and resulting population dynamic consequences  
88 (Parmesan & Yohe, 2003; King, 2004; Parmesan, 2006; Ibáñez et al., 2010).

89         Quantifying changes in the timing of seasonal biological events requires appropriate  
90 phenological metrics to be enumerated for key traits. Previous studies have often measured  
91 phenological change using just one or two metrics, commonly the first date or mean date on  
92 which an event was observed each year (Tryjanowski & Sparks, 2001; Lehikoinen et al.,  
93 2004; Knudsen et al., 2007; Miller-Rushing et al., 2008). Such studies have demonstrated  
94 considerable changes across recent decades (e.g. Walther et al., 2002; Hüppop & Hüppop,  
95 2003; Sparks et al., 2005; Both et al., 2009; Ibáñez et al., 2010). However, it has been  
96 repeatedly highlighted that such restricted metrics might provide limited or misleading  
97 information regarding the dynamics of full phenological event distributions (Leopold &  
98 Jones, 1947; Sparks et al., 2001; Tryjanowski & Sparks, 2001; Mason, 1995; Sparks et al.,  
99 2005; Miller-Rushing et al., 2008; Newton, 2008; Knudsen et al., 2011). It remains unclear  
100 whether single metrics, such as first or mean date, are reliable proxies. If they are not, the

101 conclusions of some previous studies, and hence our current view of the overall phenological  
102 consequences of environmental change, might be partially invalidated. Full understanding of  
103 long-term phenological dynamics, and evaluation of existing evidence, therefore requires  
104 multi-faceted analyses of comprehensive data that quantify entire seasonal distributions of  
105 key biological events spanning many years.

106         Appropriate long-term datasets are rare, and often fall short of ideal completeness  
107 and standardisation (Knudsen et al., 2007; 2011). For example, many long-term datasets are  
108 affected by some degree of non-standardised or varying observer coverage, temporally-  
109 inconsistent sampling methods, low temporal and/or spatial sampling resolution, truncation  
110 caused by incomplete coverage of full seasonal event distributions, failure to record values of  
111 zero, and missing data due to uncontrollable factors such as weather or recording station  
112 closure (Sparks et al., 2001; Lehikoinen et al., 2004; Knudsen et al., 2007, 2011). Especially  
113 in combination, these factors can lead to biased or highly uncertain inferences (Knudsen et  
114 al., 2007). The ideal dataset for quantifying long-term phenological change across seasonally  
115 paired events would therefore comprise comprehensive high temporal resolution observations  
116 of key biological events spanning the entire spring and autumn periods across many decades  
117 for multiple species, with standardised and consistent sampling methods and effort and few  
118 missing data. Such datasets are extremely rare.

119         Migration constitutes one major biological response to natural seasonal environmental  
120 change (Newton, 2008; Alerstam, 2001; Milner-Gulland & Fryxell, 2011). Up to half of bird  
121 species migrate annually, and migration also occurs in reptiles, fish, mammals and insects  
122 (Alerstam et al., 2003; Robinson et al., 2009; Newton, 2008). Appropriate migration timing is  
123 crucial if populations are to maximise utilisation of geographically discrete seasonally  
124 abundant resources yet avoid seasonally inhospitable environments (Alerstam et al., 2003;  
125 Newton, 2008). However, migratory life-histories might be particularly susceptible to

126 disruption caused by spatially-structured climatic and environmental changes, because such  
127 changes can rapidly cause temporal asynchrony between migration and spatio-temporal  
128 variation in resource availability (Newton, 2004; Dingle, 2006). For example, the  
129 considerable climatic changes occurring across Western Europe are rapidly changing the  
130 phenologies of key seasonal resources for migrant species that breed in this region (Cotton,  
131 2003; Hüppop & Hüppop, 2003; Seneviratne et al., 2006; Araújo et al., 2011).

132 In birds, there is evidence that short-distance migrant species that both breed and  
133 winter within Western Europe can shift their migration timing in response to environmental  
134 changes that affect both the breeding and wintering habitats (Both & Visser, 2001; Hüppop &  
135 Hüppop, 2003; Newton, 2008). However in long-distance (trans-continental) migrants, such  
136 phenological plasticity may be hampered by the greater separation between breeding and  
137 wintering areas and relatively independent environmental conditions. Such species are  
138 potentially vulnerable to rapidly developing asynchrony between current migration and  
139 resource phenologies (Sokolov et al., 1998; Both & Visser, 2001; Tryjanowski et al., 2002;  
140 Alerstam et al., 2003; Hüppop & Hüppop, 2003; Newton, 2008). Long-distance migration  
141 timing in birds is also influenced by endogenous physiological changes triggered by day-  
142 length thresholds, meaning that phenotypic plasticity allowing rapid responses to changing  
143 environmental conditions may be limited (Visser et al., 1998; Both & Visser, 2001; Møller,  
144 2002). However, long-distance migrants that breed at northern latitudes but utilise stop-over  
145 sites further south could potentially adjust their migration timing on route. Consequently,  
146 even if departure timing was inflexible due to strong endogenous control, departure from  
147 stop-over locations and hence arrival at final destinations could potentially still be modulated  
148 to match environmental conditions encountered during initial migration phases. Furthermore,  
149 such species could potentially adjust autumn departure timing to match northern  
150 environmental conditions, even if spring migration phenology is set endogenously and/or

151 influenced by southern environments. Large-scale climate or environmental change could  
152 then cause major structural changes to species' life-histories, for example because earlier  
153 spring migrations and later autumn migrations mean that individuals spend more time in  
154 northern environments, impacting physiology and numerous dimensions of population and  
155 community ecology. Alternatively, a species' current life-history could be more simply  
156 shifted forward in time, if migration occurred earlier in both spring and autumn. Quantifying  
157 such divergent or parallel seasonal phenological dynamics requires the degrees to which  
158 spring and autumn long-distance migration timings have changed, and the degree to which  
159 phenological variation in one season is associated with variation in the other season within or  
160 across years, to be quantified.

161       Accordingly, we used 60 years of comprehensive daily spring and autumn migration  
162 census data for 13 species of long-distance migratory songbird, collected on Fair Isle,  
163 northern Scotland, to quantify long-term dynamics of seasonal migration phenology. First, we  
164 used a suite of ten metrics to quantify the full distributions of observed spring and autumn  
165 migration timing for each species in each year. We tested whether values of each metric, and  
166 hence the overall distribution of migration timing, changed over a 60 year period that spans  
167 substantial large-scale climate and environmental change. Second, we tested whether the ten  
168 metrics were cross-correlated within species-seasons, and hence whether phenological  
169 dynamics could have been adequately quantified using just one or two metrics (e.g. first date  
170 or mean date). Third, we quantified the degree to which spring and autumn phenologies were  
171 correlated within or across years, and hence examine whether key seasonally paired  
172 biological events show coupled or independent phenological dynamics. We consider  
173 mechanisms that might underlie the observed phenological dynamics, and highlight  
174 implications for interpreting dynamics estimated from less comprehensive datasets.

175

176 **Materials and methods**

177

178 *Study site and data collection*

179

180 Fair Isle (768ha) is located midway between the Shetland and Orkney archipelagos (59°54'N,  
181 01°62'W), and is used by birds migrating via north-westernmost routes within the Western  
182 Palaeartic-Afrotropical migration system (Newton, 2008). Each year during 1955 to 2014, in  
183 April to June and August to October inclusive (hereafter the 'core' census periods), three  
184 professional ornithologists from Fair Isle Bird Observatory (FIBO) carried out simultaneous  
185 daily observational censuses of migrant birds, across three standardised areas that collectively  
186 covered the whole of Fair Isle. Each observer walked routes within each census area that  
187 encompassed all key areas of foraging habitat and cover for migrant birds, taking a minimum  
188 of approximately three hours per area per day. All migrants encountered were identified to  
189 species and counted, and daily count totals across the three areas were compiled. Fair Isle's  
190 predominant vegetation is grass and heather, with cliffs, gardens and small areas of crop  
191 around croft houses providing the only areas of cover. Hence, while it is unlikely that all  
192 individual migrants that were present on Fair Isle each day would be observed, observation  
193 probability is high and observations are likely to provide a representative sample of the  
194 migrant species populations that were present and visible on passage on any day. The same  
195 census regime was also implemented in March, July and November each year. However,  
196 since the full staff of three ornithologists was not always present during these months, daily  
197 coverage was sometimes less comprehensive. This overall census regime spanning March to  
198 November each year was maintained unchanged throughout 1955-2014 (Figure S1). There  
199 was therefore no major systematic change in observer effort across years. Censuses were  
200 carried out in all weathers except particularly severe storms. During 1955 to 2014, the



201 number of core period days per year on which no counts were made averaged  $1.0 \pm 1.0$  SD in  
202 spring (April-June) and  $0.1 \pm 0.3$  SD in autumn (August-October) and did not change across  
203 the 60 years in either season (Spring: linear regression slope  $\beta_{58} = -0.03 \pm 0.03$  SE,  $p = 0.22$ ;  
204 Autumn:  $\beta_{58} = -0.02 \pm 0.03$  SE,  $p = 0.39$ ).

205 We extracted daily census count totals for 13 species of long-distance migrant  
206 songbird (Table 1). These species were selected because they are straightforward to identify,  
207 because the total cumulative distribution of records spanning 1955-2014 fell well within the  
208 annual census periods on Fair Isle (Figure S1), and because the mean annual migration  
209 periods (Table 1 and Figure S1) were shorter than the annual core census periods when daily  
210 observer effort was fully standardised. Any temporal truncation of observations within  
211 seasons is therefore negligible for these species (Figure S1). All 13 species breed in northern  
212 Europe and winter in Africa, south of the Sahara desert (Snow & Perrins 1998). All 13  
213 species occurred every year in spring. However, some species were not observed in a small  
214 number of years in autumn, namely 1955, 1957 and 1966 for Sedge Warbler, 1955, 1975,  
215 1983 and 2005 for Yellow Wagtail, 1959, 1983 and 2009 for House Martin and 1955 for  
216 Swallow. Only Sedge Warbler, Swallow and Yellow Wagtail have ever bred on Fair Isle, and  
217 did so infrequently (<30% of years) and always in very low numbers ( $\leq 3$  pairs). Counts of  
218 breeding individuals were excluded from daily migration census totals, thereby ensuring that  
219 the analysed counts of migrant individuals were not confounded by local breeders.

220 Ten metrics were computed to quantify the full distributions of spring and autumn  
221 migration phenologies for each species in each year. These comprised the first observation  
222 date and the 5<sup>th</sup>, 10<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup> (median), 75<sup>th</sup>, 90<sup>th</sup> and 95<sup>th</sup> percentile dates and the last  
223 observation date, and the arithmetic mean (Figure S2).

224 Annual values of these metrics were calculated by compiling the full distribution of  
225 observation dates across all individuals of each species in spring and autumn in each year,

226 and extracting the ordinal date (days from 1<sup>st</sup> January) corresponding to each percentile (1<sup>st</sup>  
227 March = day 61 in leap-years and day 60 otherwise). The first date and 5<sup>th</sup> and 10<sup>th</sup> percentile  
228 dates describe the phenology of the early phase of migration distributions, the 25<sup>th</sup> percentile,  
229 median, mean and 75<sup>th</sup> percentile dates describe the phenology of the core phase and the 90<sup>th</sup>  
230 and 95<sup>th</sup> percentile dates and the last date describe the phenology of the late phase. Two  
231 further metrics were computed to quantify change in the duration of the spring and autumn  
232 migration of each species across years: the numbers of days between the 5<sup>th</sup> and 95<sup>th</sup>  
233 percentile dates and between the 10<sup>th</sup> and 90<sup>th</sup> percentile dates in each year. Percentiles were  
234 used because the full distributions of observation dates were commonly non-Gaussian and  
235 often multi-modal and asymmetrically leptokurtic, meaning that hierarchies of moments  
236 (mean, variance, skewness, kurtosis) did not always provide easily interpretable comparisons  
237 of phenology across years. By contrast, the percentiles provide directly comparable  
238 summaries of distributions of different shapes and the first and last dates explicitly quantify  
239 the distribution extremities, allowing direct comparison to previous phenological studies that  
240 focussed on these extremities.

241

242 *Within-season, between-metric and between-season analyses*

243

244 Least squares linear regression models were fitted to quantify overall changes in metrics of  
245 spring and autumn migration phenologies across the 60 year study period. Separate models  
246 were fitted for each of the ten phenology metrics for each species in spring and autumn.  
247 Negative and positive slopes show that migration timing advanced and delayed respectively.  
248 Separate models were also fitted for each of the two migration duration metrics for each  
249 species in spring and autumn. Here, negative and positive slopes show that the migration  
250 duration shortened and lengthened respectively. The model-estimated total numbers of days

251 by which migration timing advanced or delayed and by which migration duration shortened  
252 or lengthened during 1955-2014 were calculated as 60x the regression slopes. To test whether  
253 the overall change in spring migration timing across the study period differed from the  
254 overall change in autumn timing, we additionally tested for season by year interactions for  
255 each of the ten metrics for each species. This analysis tests for divergent changes in spring  
256 and autumn phenologies in the same metric, but does not test for direct linkage in metrics  
257 across consecutive seasons. Further models showed no evidence of substantial non-linear (i.e.  
258 quadratic) changes in any species-season-metrics (zero significant quadratic terms). Results  
259 remained quantitatively similar when models were refitted after excluding the very small  
260 number of seasons with <5 observations of a particular species.

261 To explicitly examine whether the overall distribution of migration timing, and hence  
262 overall phenological dynamics, could be adequately quantified using any single metric we  
263 tested whether the annual values of each of the ten phenology metrics were correlated with  
264 the annual values of the other nine metrics for each species in spring or autumn.

265 To quantify associations in migration phenology between consecutive springs and  
266 autumns, we implemented three further sets of analyses for each species. These analyses were  
267 designed to provide a multi-faceted assessment of phenological links between seasonally  
268 paired life-history events that does not rely entirely on any single phenological metric for  
269 either season. First, to quantify whether spring migration phenology was associated with  
270 analogous phases of autumn phenology within the same year, we quantified the correlations  
271 between the spring and autumn values of each of the ten phenology metrics within each  
272 calendar year (e.g. spring and autumn first dates, spring and autumn 5<sup>th</sup> percentile dates, etc.).  
273 Second, to quantify whether migration phenology in late spring was associated with  
274 migration phenology in early autumn within the same year, we quantified the correlations  
275 between each species' last date in spring and first date in autumn, 95<sup>th</sup> percentile date in

276 spring and 5<sup>th</sup> percentile date in autumn, 90<sup>th</sup> percentile date in spring and 10<sup>th</sup> percentile date  
277 in autumn, and 75<sup>th</sup> percentile date in spring and 25<sup>th</sup> percentile date in autumn. Third, to  
278 quantify whether migration phenology in late autumn was associated with migration  
279 phenology in early spring in the following year, we quantified the correlations between each  
280 species' last date in autumn and first date in the following spring, 95<sup>th</sup> percentile date in  
281 autumn and 5<sup>th</sup> percentile date in the following spring, 90<sup>th</sup> percentile date in autumn and 10<sup>th</sup>  
282 percentile date in the following spring, and the 75<sup>th</sup> percentile date in autumn and 25<sup>th</sup>  
283 percentile date in the following spring. The first two sets of analyses used 60 years of within-  
284 year comparisons, while the third set of analyses used 59 available pairs of between-year  
285 comparisons. Positive correlations would show that phenology in consecutive seasons varied  
286 synchronously, for example that delayed spring migration was followed by delayed autumn  
287 migration. Such correlations could arise even if there were no overall changes in spring or  
288 autumn migration phenology across the 60-year study period for any species, simply  
289 reflecting among-year variation that was correlated across seasonally paired events.

290         Standard checks showed no inadequacies in model fit; residuals were approximately  
291 normally distributed with minimal temporal autocorrelation. In principle, hypothesis tests  
292 could be further validated by bootstrapping, thereby allowing uncertainty in focal percentile  
293 values to be estimated and incorporated into regression analyses. However, appropriate  
294 bootstrapping is not readily feasible because the most appropriate resampling unit would be  
295 individual birds, but individuals are not generally recognisable across days in migration  
296 census data. Rather, the common synchronized arrival of multiple individuals of any focal  
297 species means that core period percentiles are directly estimated with little uncertainty. All  
298 analyses were implemented in R version 2.15.0 (R Core Team, 2015). Due to the large  
299 number of non-independent analyses we view results holistically and do not focus primarily  
300 on the statistical 'significance' of estimated effects in any one species. Rather than apply

301 explicit corrections for multiple testing, we summarise general patterns emerging across the  
302 13 focal species. Throughout, we use the term ‘significant’ to mean ‘nominally significant’ at  
303  $p < 0.05$ .

304

### 305 *Abundance*

306

307 Our primary objective was to quantify changes in migration phenology, not changes in  
308 species abundance on Fair Isle during 1955-2014. However, changes in abundance could  
309 potentially influence the shape of observed migration phenology distributions and hence  
310 influence phenology metrics, or could indicate changing observer efficiency across years  
311 which might also affect estimates of phenology (Miller-Rushing et al. 2008). For example,  
312 increasing abundance could conceivably cause the tails of observed distributions of migration  
313 timing to lengthen, simply due to increased sampling from a static underlying distribution.  
314 This might cause early and late phase phenology metrics such as first date and last date to  
315 respectively advance and delay across years even if there was no change in underlying  
316 biological phenology. To evaluate this possibility, each species’ total abundance on Fair Isle  
317 in spring and autumn in each year during 1955-2014 was estimated as ‘total bird days’,  
318 calculated for each species as the sum of all census counts in each season in each year. Linear  
319 regression models were fitted to test whether total bird days changed across years in each  
320 species and season. Positive and negative slopes respectively show that species increased and  
321 decreased in observed abundance across years. Preliminary data exploration and model  
322 diagnostics identified a small number of outliers in total bird days (i.e. datapoints with  
323 Cook’s distance  $> 0.5$  when standardised residuals were plotted against leverage). These  
324 outliers, which stemmed from occasional remarkable migration ‘falls’, totalled 22 species-  
325 seasons involving nine species (1.4% of the total of 1560 species-season-years). However,

326 results and conclusions remained quantitatively similar when models were refitted after  
327 excluding the outlying species-seasons. Finally, to directly test whether changes in spring and  
328 autumn phenology metrics across years could be explained by changes in total bird days, all  
329 linear regression models for the phenology metrics were refitted with total bird days as a  
330 covariate.

331

## 332 **Results**

333

### 334 *Spring migration phenology*

335

336 There was evidence of advancements in migration timing across the early phase of the spring  
337 migration distributions in most of the 13 focal species (Fig. 1). Specifically, in 11 species,  
338 regression slopes on year were negative for at least two of the three early phase metrics (i.e.  
339 first date, 5<sup>th</sup> and 10<sup>th</sup> percentile dates). These advancements were nominally significant for  
340 19 (49%) of the 39 species-metrics, involving seven species (Fig. 1, Table S1). The estimated  
341 magnitudes of the advancements across the 60 year study period exceeded five days for 20  
342 species-metrics, and exceeded ten days for 13 species-metrics (Fig. 1, Table S1). Most  
343 substantially, first date advanced by approximately 18 days in Willow Warbler, 15 days in  
344 Swallow, 14 days in Lesser Whitethroat and House Martin, and 11 days in Tree Pipit (Fig. 1,  
345 Table S1).

346 However, despite the widespread advancements in early phase migration, the core  
347 phase of species' spring migration distributions (i.e. 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> percentile dates and  
348 mean date) changed relatively little across years (Fig. 1). Specifically, regression slopes on  
349 year were non-significant for 43 (83%) of 52 species-metrics, comprising 33 (77%) negative  
350 slopes and ten (23%) positive slopes. Indeed, in five species the estimated change in 50<sup>th</sup>

351 percentile (median) date was less than one day across 60 years (Fig. 1, Table S1). Regression  
352 slopes were significant for nine (17%) species-metrics involving three species, all  
353 demonstrating advancements in core phase migration timing (Fig. 1, Table S1).

354         Meanwhile, across the late phase of species' spring migration distributions there was  
355 widespread evidence of temporal stability and delays in migration timing (Fig. 1, Table S1).  
356 In seven species, regression slopes on year were positive for two or all three late phase  
357 metrics (90<sup>th</sup> and 95<sup>th</sup> percentile dates and last date). Such delays in late phase migration  
358 timing were significant for four (10%) of the 39 species-metrics, involving three species (Fig.  
359 1, Table S1). Across the 60 year study period, last date was delayed by approximately 14  
360 days in Willow Warbler, 13 days in Pied Flycatcher and 11 days in Lesser Whitethroat (Fig.  
361 1, Table S1). In five species regression slopes on year were negative for two or all three late  
362 phase metrics. However, such advancements in late phase migration timing were significant  
363 for only two (5%) of the 39 species-metrics; the 90<sup>th</sup> and 95<sup>th</sup> percentile dates for Swallow  
364 advanced by seven and 11 days respectively (Fig. 1, Table S1).

365         Overall, therefore, several species showed a 'fan-shaped' pattern of spring migration  
366 timing over 60 years, comprising advancements in the early phase, temporal stability in the  
367 core phase, and delays in the late phase (Fig. 1). The migration duration consequently  
368 lengthened in most species (Fig. 1). Indeed, regression slopes of the number of days between  
369 the 5<sup>th</sup> and 95<sup>th</sup> percentile dates, and between the 10<sup>th</sup> and 90<sup>th</sup> percentile dates, on year were  
370 positive in all species except Redstart (Table S2). Such lengthening was significant in five  
371 species, for example the time between the 5<sup>th</sup> and 95<sup>th</sup> percentile dates increased by  
372 approximately ten days in Common Whitethroat, 16 days in Lesser Whitethroat and 24 days  
373 in Willow Warbler (Fig. 1, Table S2). Swallow and House Martin migration durations did not  
374 increase significantly due to their relatively consistent advancements in migration timing  
375 across the early, core and late phases (Fig. 1).

376

377 *Autumn migration phenology*

378

379 As in spring, there was evidence of advancements in migration timing across the early phase  
380 of species' autumn migration distributions (Fig. 2). In 11 species, regression slopes on year  
381 were negative for two or all three early phase metrics. These advancements were significant  
382 for nine (23%) of 39 species-metrics, involving five species (Fig. 2, Table S3). The estimated  
383 magnitude of the advancements across the 60 year study period exceeded five days for 15  
384 species-metrics and exceeded ten days for seven species-metrics (Fig. 2, Table S3). In Yellow  
385 Wagtail and House Martin regression slopes were positive for all three early phase metrics,  
386 indicating that the start of autumn migration became later across years. However, these slopes  
387 were all non-significant, although the estimated magnitude of delay was up to ten days (Table  
388 S3).

389 Meanwhile, the four metrics quantifying the core phase of species' autumn migration  
390 distributions changed relatively little across years in most of the 13 species. Regression  
391 slopes were non-significant for 44 (85%) of 52 species-metrics, comprising 22 (50%) positive  
392 slopes and 22 negative slopes. Slopes were significant for only eight species-metrics,  
393 showing advancements in two species (Garden Warbler and Swallow) and delays in two  
394 species (House Martin and Whinchat, Fig. 2, Table S3).

395 Across the late phase of species' autumn migration distributions, there was evidence  
396 of temporal stability and delays in migration timing (Fig. 2). In 11 species, regression slopes  
397 on year were positive in two or all three late phase metrics. Such delays in late phase  
398 migration timing were significant for nine (23%) of 39 species-metrics, involving six species  
399 (Fig. 2, Table S3). Estimated delays in last date were substantial; approximately 24 days in  
400 Lesser Whitethroat, 16 days in Swallow, 15 days in House Martin and 14 days in Sedge



401 Warbler (Fig. 2 and Table S3). For Garden Warbler and Redstart regression slopes on year  
402 were negative for all three late phase metrics indicating advanced late phase migration  
403 timing, but these slopes were not significant.

404         Consequently, as in spring, several species showed a ‘fan-shaped’ pattern of change in  
405 autumn migration timing over 60 years, comprising advancements in the early phase,  
406 temporal stability in the core phase and delays in the late phase, meaning that the autumn  
407 migration duration lengthened (Fig. 2). Regression slopes of the number of days between the  
408 5<sup>th</sup> and 95<sup>th</sup> percentile dates, and between the 10<sup>th</sup> and 90<sup>th</sup> percentile dates, on year were  
409 positive in all species (Table S4). Such lengthening was significant in 5 species, for example  
410 the time between the 5<sup>th</sup> and 95<sup>th</sup> percentile dates increased by approximately nine days in  
411 Willow Warbler, 17 days in Lesser Whitethroat and 30 days in Sedge Warbler (Fig. 2, Table  
412 S4).

413

#### 414 *Season by year interactions*

415

416 Linear models fitted to test whether changes in spring migration timing across the study  
417 period differed from changes in autumn timing, as measured by each of the ten metrics,  
418 revealed relatively few season by year interactions. Specifically, 16 (12%) of 130 interactions  
419 were nominally significant, involving six species (Figs. 1 & 2, Table S5). Most strikingly,  
420 these interactions showed that the first date and the 5<sup>th</sup> and 10<sup>th</sup> percentile dates in Willow  
421 Warbler all advanced more in spring than in autumn, while the 95<sup>th</sup> percentile and last date in  
422 Swallow and all metrics except last date in House Martin advanced in spring but delayed in  
423 autumn (Figs. 1 & 2, Table S5). Overall, significant season by year interactions occurred  
424 more in the early and late migration phases than in the core phase (Figs. 1 & 2, Table S5).

425

426 *Cross-correlations between phenological metrics*

427

428 For all species in both seasons, the values of adjacent phenological metrics (e.g. first date  
429 versus 5<sup>th</sup> percentile date, 5<sup>th</sup> versus 10<sup>th</sup> percentile dates) were relatively strongly correlated;  
430 mean pairwise correlation coefficients were  $0.76 \pm 0.16$  SD in spring and  $0.79 \pm 0.16$  SD in  
431 autumn (Figs. 3 and 4). Similarly, mean dates were correlated with median date, 25<sup>th</sup>  
432 percentile date and 75<sup>th</sup> percentile date (mean pairwise correlation coefficients of  $0.88 \pm 0.04$   
433 SD in spring and  $0.87 \pm 0.05$  SD in autumn). However, correlations between non-adjacent  
434 metrics were relatively weak, and decreased with increasing separation between metrics  
435 across the migration distribution (Figs. 3 & 4). For example, the mean pairwise correlation  
436 coefficients between first date and median date pairings were  $0.29 \pm 0.10$  SD in spring and  
437  $0.29 \pm 0.17$  SD in autumn, and first date was uncorrelated with last date (mean correlation  
438 coefficients of  $-0.09 \pm 0.09$  SD in spring and  $0.01 \pm 0.14$  SD in autumn, Figs. 3 and 4).

439

440 *Between-season associations*

441

442 The analogous spring and autumn values of each individual percentile metric and the mean  
443 were generally weakly correlated within each year. Specifically, the distribution of  
444 correlation coefficients was approximately centred on zero (mean  $0.09 \pm 0.12$  SD, Fig. 5a,  
445 Table S6). The absolute correlation coefficients never exceeded 0.5, and only ten (8%) of 130  
446 values were nominally significant. Similarly, there were no strong or consistently positive or  
447 negative correlations between metrics describing the late phase of spring migration and those  
448 describing the early phase of autumn migration within the same year (Figure 5b, Table S6).  
449 Five (10%) of 52 correlations were significant, and the distribution of correlation coefficients  
450 was again centred on zero (Fig. 5b, Table S6). Furthermore, there were no strong or

451 consistently positive or negative correlations between metrics describing the late phase of  
452 autumn migration and those describing the early phase of spring migration in the following  
453 calendar year (Fig. 5c, Table S6). One of 52 correlations was significant, and the distribution  
454 of correlation coefficients was again centred on zero (Fig. 5c, Table S6). Overall, therefore,  
455 the timing of any one migration season was not strongly or consistently correlated with the  
456 timing of the preceding season.

457

#### 458 *Abundance*

459

460 Across all years where a species was recorded at least once, mean total bird days varied  
461 among species in both seasons, ranging from 37.7 (Yellow Wagtail) to 804.1 (Swallow) in  
462 spring, and from 16.4 (Sedge Warbler) to 678.7 (Willow Warbler) in autumn (Table 1).  
463 Across all 60 study years there was no consistent pattern of increase or decrease in total bird  
464 days in either spring or autumn across the 13 species (Table 1). Specifically, regression  
465 slopes on year were positive for nine species and negative for four species in spring, and  
466 ranged between 12.3 (Swallow) and -0.3 (Tree Pipit; Table 1). Similarly, slopes were positive  
467 for eight species and negative for five species in autumn and ranged between 4.5 (Swallow)  
468 and -0.4 (Redstart; Table 1).

469 Linear regression slopes quantifying overall changes in spring and autumn phenology  
470 metrics across the 60 year study period remained quantitatively similar with and without bird  
471 days included as a covariate, indicating that estimated phenological changes were not directly  
472 caused by changes in observed abundance.

473

474

475

476 **Discussion**

477

478 *Dynamics of spring and autumn migration phenologies*

479

480 Understanding the phenological dynamics of key life-history traits in the context of large-  
481 scale environmental change requires entire event distributions to be quantified across  
482 multiple seasons spanning numerous years. However, sufficiently comprehensive data have  
483 rarely been collected, particularly across paired seasonal events. We measured a suite of ten  
484 metrics, which together describe the full distributions of spring and autumn migration  
485 phenology, across daily census data for 13 species of long-distance migrant bird spanning 60  
486 years, revealing complex patterns of simultaneous advancement, temporal stability and delay  
487 in spring and autumn migration timing.

488 The phenology of the core phase (i.e. 25<sup>th</sup>-75<sup>th</sup> percentiles) of most species' spring and  
489 autumn migration distributions did not change greatly during 1955-2014. The exceptions  
490 were Swallow and House Martin: the core phase advanced by eight days in both species in  
491 spring and by eight days in Swallow in autumn. Our 60-year dataset spans a period of  
492 substantial and relatively rapid global climatic and environmental change, including changes  
493 in vegetation growth and reproductive phenology in north-western Europe (Myneni et al.,  
494 1997; Visser et al., 1998; Walther et al., 2002; Chazal & Rounsevell, 2009). Given this  
495 context, the temporal stability of most species' core migration timing is consistent with  
496 existing evidence that long-distance migration phenology is under strong endogenous control,  
497 and hence that phenotypic responses to changing conditions are constrained (Both & Visser,  
498 2001; Seneviratne et al., 2006; Araújo et al., 2011).

499 However, despite the predominant temporal stability of the core migration phase, the  
500 timing of the early and late phases of species' migration distributions commonly changed

501 across years. In 12 species in spring and/or autumn, the early phase got earlier across years,  
502 or the late phase got later, or both changes occurred. Consequently, there was a widespread  
503 pattern of lengthening of spring and autumn migration periods during 1955-2014, as shown  
504 by the ‘fan-shaped’ patterns of changes across the ten phenological metrics across years. In  
505 many cases the magnitude of change in phenology measured by individual metrics was  
506 considerable. For example advancements and delays in autumn migration timing exceeding  
507 20 days occurred in Swallow and Lesser Whitethroat respectively. Overall, these patterns  
508 suggest that migration timing in long-distance migrants is not completely constrained, but is  
509 somewhat flexible.

510 Our results concur with previous studies that demonstrated advances in early phase  
511 migration dates, specifically the first arrival and 10<sup>th</sup> percentile dates, of trans-Saharan  
512 migrants across the last 50 years (e.g. Tryjanowski et al., 2002; Sparks et al., 2005; Jonzén et  
513 al., 2006; Zalakevicius et al., 2006). Some studies also demonstrated advances in other  
514 metrics, including median, mean and 90<sup>th</sup> percentile dates, predominantly in spring (e.g.  
515 Tryjanowski et al., 2002; Hüppop & Hüppop, 2003; Jenni and Kéry, 2003, Sparks et al.,  
516 2005; Jonzén et al., 2006; Newton, 2008). Our results do not conform to such uniform  
517 advancements but revealed greater complexity in migration phenology dynamics, involving  
518 simultaneous advancements, temporal stability and delays within individual species in both  
519 seasons. Our results therefore contrast somewhat with the conclusions of previous studies of  
520 phenological change in long-distance migrant birds and other spring life-history events in  
521 diverse taxa, which frequently advance in association with climate change (e.g. Myneni et al.,  
522 1997; Visser et al., 1998; Hughes, 2000; Roy & Sparks, 2000; Walther et al., 2002; Crick,  
523 2004; Zalakevicius et al., 2006; Cleland et al., 2007; Both et al., 2009; Chazal & Rounsevell,  
524 2009; Robinson et al., 2009; Ibáñez et al., 2010). In our study, only Swallow and House  
525 Martin broadly conformed to this established pattern.

526 Models that tested for season by year interactions for each phenology metric showed  
527 consistent divergence in spring and autumn migration timing only in House Martin. In this  
528 species, as spring migration got earlier across years, autumn migration got significantly later.  
529 This implies that the total time that House Martins spend in Europe has increased, while the  
530 time spent in Africa has decreased. Recent climatic and environmental changes in Europe  
531 include warmer summers and lengthened growing seasons that might benefit insectivores and  
532 facilitate multiple breeding attempts in species such as House Martins (Myneni et al., 1997;  
533 Menzel & Fabian, 1999; Hughes, 2000; Cleland et al., 2007). The lengthened inter-migration  
534 period might therefore result directly from increased duration of food abundance, or  
535 indirectly from consequent increased breeding attempts.

536

### 537 *Quantifying phenological change*

538

539 Our analyses showed that the form of phenological change across years can be complex, and  
540 this complexity is only revealed if multiple metrics encompassing full seasonal event  
541 distributions are quantified. Specifically, there were no consistently strong positive  
542 correlations between the annual values of different metrics of migration timing, except  
543 among immediately adjacent metrics (e.g. adjacent percentiles). Consequently, no one metric  
544 could have been used as an accurate proxy for all the others. For example, simply quantifying  
545 changes in first date would have indicated advancing migration timing in multiple species,  
546 but would not have revealed the temporal stability and delays in the core and late phases of  
547 species' migration. Similarly, quantifying mean date would have indicated temporal stability  
548 in migration timing in most species, but would not have revealed the advancements and  
549 delays in the early and late phases. Many studies have used just one or a few metrics to  
550 quantify phenological change, commonly first arrival date and mean date, often because data

551 are sparse or otherwise limiting (Sparks et al., 2001, 2005; Miller-Rushing et al., 2008;  
552 Goodenough et al., 2014). Our analyses imply that reported phenological changes measured  
553 using only one or two metrics should be interpreted with caution, because such metrics do not  
554 necessarily comprehensively describe phenological dynamics and can fail to detect complex  
555 phenological changes occurring simultaneously. Indeed, small or negative correlations  
556 between percentiles located on opposite sides of the mean or median of an event distribution  
557 could generally arise if the mean changes little across years but the variance increases.  
558 However, more complex correlation structures might arise given more complex changes in  
559 distribution shapes, involving altered skewness or kurtosis, or multimodality or other  
560 irregularities. Overall, future studies must therefore strive to measure phenology using  
561 multiple metrics that collectively quantify the full biological event distribution of interest.

562

#### 563 *Between-season phenological associations*

564

565 Spring and autumn migration are seasonally paired events. Cross-season linking of such  
566 events could potentially drive or constrain year-round phenological dynamics in many  
567 species, but has rarely been quantified (Gallinat et al., 2015). However, we found little  
568 evidence that migration timing was correlated across analogous metrics for spring and  
569 autumn in the same year, between late spring and early autumn in the same year, or between  
570 late autumn and early spring in the following year. Such decoupling might be expected if  
571 individual migrants recorded in spring and autumn on Fair Isle are from different breeding  
572 populations. However, our focal species breed across much of western Scandinavia and  
573 ringing recoveries suggest that at least some individuals recorded on Fair Isle in spring and  
574 autumn are from the same breeding populations (Wernham et al., 2002). Furthermore, ringing  
575 recoveries have shown that the same individuals have migrated via Fair Isle in consecutive

576 spring and autumn periods (Fair Isle Bird Observatory annual reports, 1955-2014). Overall,  
577 therefore, our results suggest that spring and autumn migration timings occur largely  
578 independently across consecutive seasons. In contrast, Van Buskirk et al. (2008) found that  
579 changes in spring migration timing were correlated with changes in autumn migration timing  
580 in long- and short-distance migrant North American passerine birds.

581

582 *Mechanisms of observed phenological change*

583

584 Advancements and delays in early and late phase migration, such as those observed in  
585 multiple species on Fair Isle, might conceivably arise in the absence of any change in  
586 underlying migration strategy if species abundance increased across years. This is because  
587 the corresponding increased sampling from a static true distribution of migration timing  
588 might increase the probability of observing rare extremely early or late dates, while the  
589 timing of the core migration phase would remain unchanged. However, any such sampling  
590 effects are likely to be small and affect only the very tails of observed distributions (i.e. first  
591 and last dates). Furthermore, ‘total bird days’ recorded for each species in each year on Fair  
592 Isle did not change consistently across the study duration; there was no general pattern of  
593 increase or decrease across species, and statistically significant changes were few. Moreover,  
594 in some species-seasons total bird days decreased but the observed migration duration  
595 lengthened (e.g. House Martin in spring) while in others total bird days increased slightly but  
596 the observed migration duration remained constant (e.g. Spotted Flycatcher in spring, Table  
597 1, Figs. 1 & 2). Overall, all estimated changes in spring and autumn migration phenology  
598 metrics remained quantitatively similar when total bird days was modelled as a covariate.  
599 These analyses strongly suggest that variation in species’ observed spring and autumn  
600 migration phenology were caused by changes in the underlying distributions of migration



601 timing, and did not simply result from changing abundance. Furthermore, the absence of  
602 consistent changes in total bird days across species and seasons supports the view that there  
603 was no overarching substantial change in observer effort or efficiency across years, as  
604 expected since the census methodology remained consistent throughout the study period.

605       Observed delays in late phase migration phenology could potentially result from  
606 increased stop-over durations of individual migrants on Fair Isle rather than from delayed  
607 arrival. Since censused individuals were typically not marked, their stop-over durations  
608 cannot be quantified directly. We therefore used two indirect methods to investigate whether  
609 stop-over durations might have changed during 1955-2014, causing observed changes in  
610 overall distributions of spring or autumn migration phenologies (Appendix S1). First, we  
611 quantified whether the proportional decrease from the number of individuals of each species  
612 recorded on its peak census day in each season to the next day decreased during 1955-2014.  
613 Second, we directly quantified stop-over durations of nine additional trans-Saharan species  
614 that occurred infrequently on Fair Isle, meaning that individual birds could be tracked across  
615 consecutive days. These analyses provided no indication that stop-over durations had  
616 consistently increased or decreased across the study period (Appendix S1). Consequently, the  
617 observed delays in late phase migration timing are most likely attributable to delayed arrivals  
618 rather than increasing stop-over duration and hence solely delayed departure.

619       Advances and delays in migration timing at a single location such as Fair Isle can  
620 result from changes in departure timing from the wintering or breeding quarters, changes in  
621 migratory speed and/or changes in route, reflecting evolution or phenotypic plasticity  
622 (Berthold, 1996; Møller et al., 2008; Newton, 2008). Although there is evidence that initial  
623 departure timing among trans-Saharan migrant birds is influenced by endogenous processes,  
624 weak connectivity between climatic conditions in Africa and Europe has been recently  
625 demonstrated (Gordo et al., 2005; Saino & Ambrosini, 2008). Migrants may consequently be

626 able to judge conditions at long range and adjust departure in both spring and autumn in  
627 response to inter-continental climatic flux. Additionally, since Fair Isle lies approximately  
628 60° north and 2° west, migrants moving to northerly breeding locations must traverse  
629 relatively long distances across Western Europe. The observed changes in migration  
630 phenology might therefore stem from changes in migration speeds and/or routes in response  
631 to climate change or other factors such as food availability within Europe, as demonstrated in  
632 other systems (e.g. Visbeck et al., 2001; Hüppop & Hüppop, 2003; Bearhop et al., 2005).

633         The observed delays in late phase spring migration were atypical in a European  
634 context, given that most previous studies have described phenological advancements in  
635 spring, and early arrival at breeding grounds is commonly reproductively advantageous  
636 (Perrins, 1970; Møller, 2001; Lehikoinen et al., 2004; Sparks et al., 2007; Sparks &  
637 Tryjanowski, 2007; Miller-Rushing et al., 2008; Saino & Ambrosini, 2008). However, our  
638 results concur with evidence from Pennsylvania that the migration periods of long- and short-  
639 distance migrant birds have lengthened in both spring and autumn because early phases got  
640 earlier and late phases remained unchanged or got later (Van Buskirk et al., 2009). This  
641 scenario might arise if selection on optimal migration timing has weakened across years, such  
642 that migrating and breeding within a broader temporal window is less disadvantageous now  
643 than in the past. However, if the optimal migration timing has in fact shifted forward or back,  
644 the extended migration periods in the same direction (wherein individuals would experience  
645 increased fitness) or opposite direction (wherein individuals would experience reduced  
646 fitness) could, respectively, facilitate or impede evolution towards optimal migration timing.  
647 Alternatively, lengthening migration periods might reflect cryptic sub-structuring of  
648 migratory populations, whereby observed migrations comprise individuals from multiple sub-  
649 populations with different phenologies and responses to climate change (Nolan & Ketterson,  
650 1990; Bearhop et al., 2005; MacMynowski & Root, 2005; Van Buskirk et al., 2009).

651 Plumage, ringing and DNA analyses of migrants on Fair Isle in limited instances have shown  
652 migrant species comprise individuals from different sub-populations (Fair Isle Bird  
653 Observatory annual reports, 1955-2014). However, more comprehensive data on population  
654 composition and individual reproductive success and survival in relation to migration timing  
655 would be needed to test these hypotheses. Individual tracking studies may, in future, facilitate  
656 the required integration of large-scale spatio-temporal data on individual migration and life-  
657 history.

658

659

660

661

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663

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924 **Supporting Information**

925

926 Figure S1. Species cumulative count distributions.

927 Figure S2. Suite of ten metrics defined to quantify the full distribution of migration  
928 phenology for any species in spring or autumn in one year.

929 Table S1. Summary statistics for spring migration phenology.

930 Table S2. Summary statistics for spring migration duration.

931 Table S3. Summary statistics for autumn migration phenology.

932 Table S4. Summary statistics for autumn migration duration.

933 Table S5. Summary statistics for season by year interactions.

934 Table S6. Summary statistics for between-season associations.

935 Appendix S1. Stop-over duration analyses.

936 Table S7. Summary statistics for spring stop-over duration analyses for focal species.

937 Table S8. Summary statistics for autumn stop-over duration analyses for focal species.

938 Table S9. Summary statistics for spring stop-over duration analyses for additional species.

939 Table S10. Summary statistics for autumn stop-over duration analyses for additional species.

940 Figure S3. Modelled proportional difference between the maximum species count and the  
941 count on the following day for focal species in spring and autumn.

942 Figure S4. Modelled stop-over duration for additional species in spring and autumn.

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949 **Table 1** Study species and summary of mean total migration period<sup>a</sup>, mean total bird days<sup>b</sup>  
 950 and regression coefficients ( $\beta$ ) of total bird days on year across 60 years (1955-2014) for 13  
 951 species of trans-Saharan migrant birds in spring and autumn. SE = standard error. \* denotes p  
 952 < 0.05.

Species	Season	Total migration period (mean $\pm$ SD days)	Total bird days (mean $\pm$ SD)	$\beta$ total bird days ( $\pm$ SE)
Garden Warbler	Spring	43.2 $\pm$ 12.3	66.9 $\pm$ 49.9	0.5 $\pm$ 0.6
<i>Sylvia borin</i>	Autumn	76.0 $\pm$ 11.1	297.9 $\pm$ 181.1	0.5 $\pm$ 1.4
Common Whitethroat	Spring	50.8 $\pm$ 14.1	121.1 $\pm$ 80.9	-0.6 $\pm$ 0.6
<i>Sylvia communis</i>	Autumn	48.0 $\pm$ 14.9	47.0 $\pm$ 38.5	0.5 $\pm$ 0.3
Lesser Whitethroat	Spring	43.6 $\pm$ 13.1	77.4 $\pm$ 48.7	1.4 $\pm$ 0.4 *
<i>Sylvia curruca</i>	Autumn	56.9 $\pm$ 15.6	65.2 $\pm$ 46.1	1.5 $\pm$ 0.3 *
Sedge Warbler	Spring	41.9 $\pm$ 12.4	69.6 $\pm$ 43.9	0.5 $\pm$ 0.3
<i>Acrocephalus schoenobaenus</i>	Autumn	38.9 $\pm$ 23.6	16.4 $\pm$ 13.8	0.5 $\pm$ 0.1 *
Willow Warbler	Spring	51.9 $\pm$ 16.0	262.2 $\pm$ 171.3	2.3 $\pm$ 1.3
<i>Phylloscopus trochilus</i>	Autumn	66.6 $\pm$ 10.7	678.7 $\pm$ 452.7	5.8 $\pm$ 3.4
Tree Pipit	Spring	41.7 $\pm$ 8.9	275.6 $\pm$ 316.2	2.2 $\pm$ 2.5
<i>Anthus trivialis</i>	Autumn	50.5 $\pm$ 12.1	178.9 $\pm$ 178.8	1.3 $\pm$ 1.4
Yellow Wagtail	Spring	39.9 $\pm$ 16.5	37.7 $\pm$ 29.0	0.1 $\pm$ 0.2
<i>Motacilla flava</i>	Autumn	33.7 $\pm$ 17.6	21.9 $\pm$ 20.3	0.2 $\pm$ 0.2
House Martin	Spring	73.9 $\pm$ 14.4	431.8 $\pm$ 254.5	-4.3 $\pm$ 1.8 *
<i>Delichon urbicum</i>	Autumn	41.0 $\pm$ 23.5	21.4 $\pm$ 28.3	-0.2 $\pm$ 0.2
Swallow	Spring	87.8 $\pm$ 9.9	804.1 $\pm$ 341.8	12.3 $\pm$ 2.0 *
<i>Hirundo rustica</i>	Autumn	70.5 $\pm$ 19.9	145.2 $\pm$ 140.2	4.5 $\pm$ 0.9 *
Spotted Flycatcher	Spring	41.3 $\pm$ 10.1	126.4 $\pm$ 80.5	0.3 $\pm$ 0.6
<i>Muscicapa striata</i>	Autumn	37.4 $\pm$ 14.5	42.2 $\pm$ 49.8	0.4 $\pm$ 0.4
Pied Flycatcher	Spring	30.9 $\pm$ 13.4	47.1 $\pm$ 48.8	-0.1 $\pm$ 0.4
<i>Ficedula hypoleuca</i>	Autumn	55.1 $\pm$ 11.7	122.4 $\pm$ 72.0	-0.3 $\pm$ 0.6
Redstart	Spring	43.3 $\pm$ 12.0	126.1 $\pm$ 132.8	-1.7 $\pm$ 1.0
<i>Phoenicurus phoenicurus</i>	Autumn	57.7 $\pm$ 13.5	176.5 $\pm$ 174.3	-0.4 $\pm$ 1.4
Whinchat	Spring	40.3 $\pm$ 11.7	125.5 $\pm$ 152.9	-1.1 $\pm$ 1.2
<i>Saxicola rubetra</i>	Autumn	67.6 $\pm$ 11.5	400.7 $\pm$ 277.9	-0.1 $\pm$ 2.1

953 <sup>a</sup> For each species in each season the total migration period was calculated as the number of  
 954 days from the first record to the last record. The mean length of this period was computed  
 955 across the 60 study years.

956 <sup>b</sup> For each species in each season total bird days was calculated as the sum of all counts on all  
 957 days. The mean total bird days was computed across the 60 study years.

958 **Figure captions**

959

960 **Fig. 1** Summary of modelled spring migration phenology across 60 years (1955-2014) for 13  
961 species of trans-Saharan migrant bird, measured using ten metrics for each species. Lines  
962 represent linear regressions of each metric on year. Metrics are first date (bold dotted line),  
963 5<sup>th</sup> percentile date (bold short dashes), 10<sup>th</sup> percentile date (bold dash-dot), 25<sup>th</sup> percentile  
964 date (bold long dashes), median date (bold solid black), mean date (bold solid grey), 75<sup>th</sup>  
965 percentile date (long dashes), 90<sup>th</sup> percentile date (dash-dot), 95<sup>th</sup> percentile date (short  
966 dashes), last date (dotted). \*  $p < 0.05$  for the linear regression. <sup>o</sup>  $p < 0.05$  for the season by  
967 year interaction.

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970 **Fig. 2** Summary of modelled autumn migration phenology across 60 years (1955-2014) for  
971 13 species of trans-Saharan migrant bird, measured using ten metrics for each species. Lines  
972 represent linear regressions of each metric on year. Metrics are first date (bold dotted line),  
973 5<sup>th</sup> percentile date (bold short dashes), 10<sup>th</sup> percentile date (bold dash-dot), 25<sup>th</sup> percentile  
974 date (bold long dashes), median date (bold solid black), mean date (bold solid grey), 75<sup>th</sup>  
975 percentile date (long dashes), 90<sup>th</sup> percentile date (dash-dot), 95<sup>th</sup> percentile date (short  
976 dashes), last date (dotted). \*  $p < 0.05$  for the linear regression. <sup>o</sup>  $p < 0.05$  for the season by  
977 year interaction.

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980 **Fig. 3** Pairwise correlation matrix for 10 metrics of spring migration phenology measured  
981 across 60 years (1955-2014), for 13 species of trans-Saharan migrant bird. Grey bar heights  
982 represent within-species pairwise Pearson correlation coefficient values among first,



983 percentile and last dates. Black bar heights represent within-species pairwise correlation  
 984 coefficient values between first, percentile and last dates and mean date. Y-axes span -0.5 to  
 985 1.0. Each bar represents one species, denoted (G) Garden Warbler; (W) Common  
 986 Whitethroat; (L) Lesser Whitethroat; (S) Sedge Warbler; (Wi) Willow Warbler; (T) Tree  
 987 Pipit and (Y) Yellow Wagtail above the leading diagonal, and (H) House Martin; (Sw)  
 988 Swallow; (Sp) Spotted Flycatcher; (P) Pied Flycatcher; (R) Redstart and (Wh) Whinchat  
 989 below the leading diagonal.

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992 **Fig. 4** Pairwise correlation matrix for 10 metrics of autumn migration phenology measured  
 993 across 60 years (1955-2014), for 13 species of trans-Saharan migrant bird. Grey bar heights  
 994 represent within-species pairwise Pearson correlation coefficient values among first,  
 995 percentile and last dates. Black bar heights represent within-species pairwise correlation  
 996 coefficient values between first, percentile and last dates and mean date. Y-axes span -0.5 to  
 997 1.0. Each bar represents one species denoted (G) Garden Warbler; (W) Common Whitethroat;  
 998 (L) Lesser Whitethroat; (S) Sedge Warbler; (Wi) Willow Warbler; (T) Tree Pipit and (Y)  
 999 Yellow Wagtail above the leading diagonal, and (H) House Martin; (Sw) Swallow; (Sp)  
 1000 Spotted Flycatcher; (P) Pied Flycatcher; (R) Redstart and (Wh) Whinchat below the leading  
 1001 diagonal.

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1004 **Fig. 5** Histograms summarising the between-season Pearson correlation coefficients among  
 1005 phenology metrics measured across 1955-2014, for 13 species of trans-Saharan migrant bird.  
 1006 a) Correlations between analogous early phase metrics (black), core phase metrics (dark grey)  
 1007 and late phase metrics (light grey) and mean date (white) in spring and autumn of the same

1008 year (130 tests). b) Correlations between last date in spring and first date in autumn (black),  
1009 95<sup>th</sup> percentile date in spring and 5<sup>th</sup> percentile date in autumn (dark grey), 90<sup>th</sup> percentile date  
1010 in spring and 10<sup>th</sup> percentile date in autumn (light grey), and 75<sup>th</sup> percentile date in spring and  
1011 25<sup>th</sup> percentile date in autumn (white), of the same year (52 tests). c) Correlations between the  
1012 last date in autumn and first date in the following spring (black), 95<sup>th</sup> percentile date in  
1013 autumn and 5<sup>th</sup> percentile date in the following spring (dark grey), 90<sup>th</sup> percentile date in  
1014 autumn and 10<sup>th</sup> percentile date in the following spring (light grey), and 75<sup>th</sup> percentile date in  
1015 autumn and 25<sup>th</sup> percentile date in the following spring (white) (52 tests).

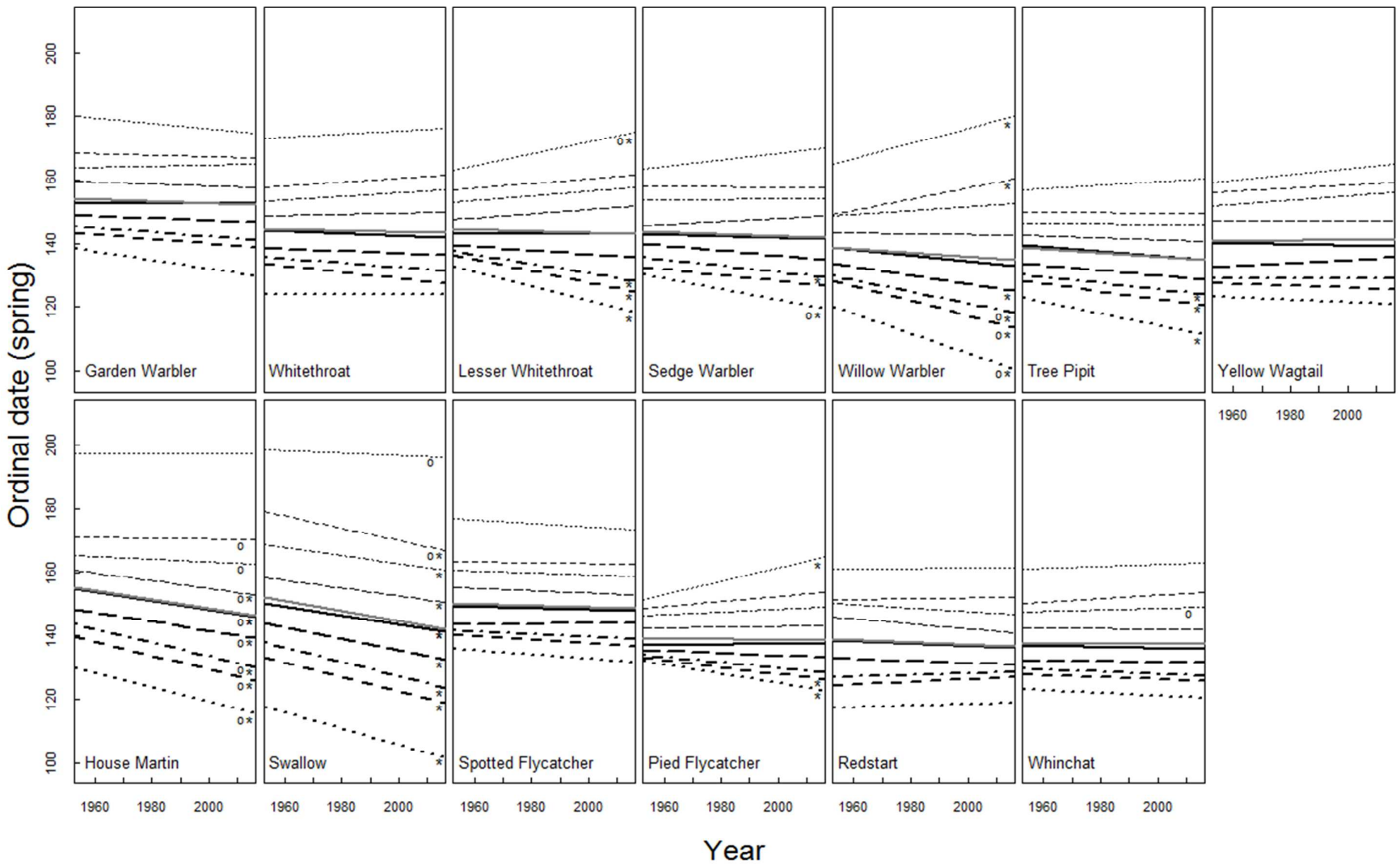


Fig. 1

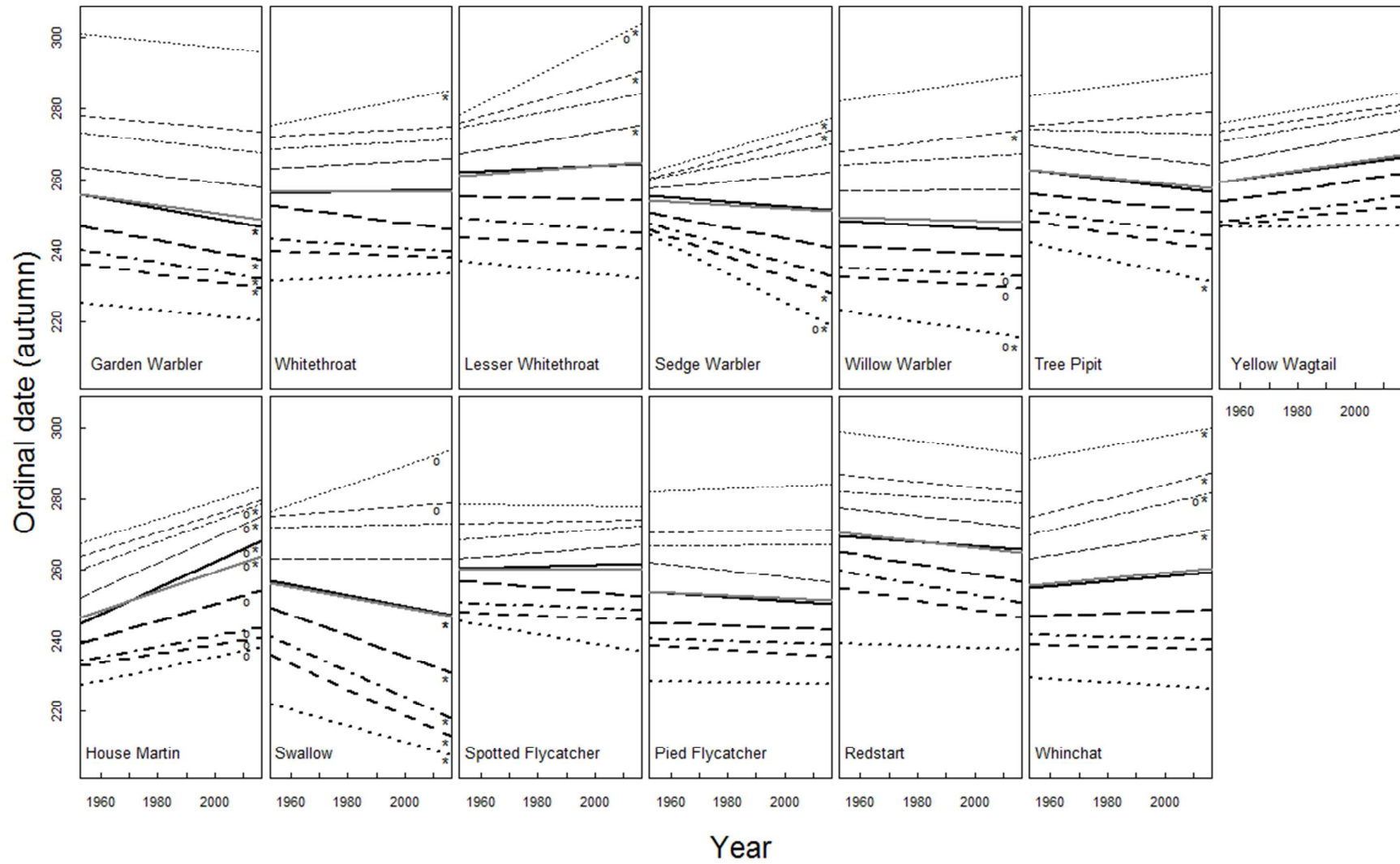


Fig. 2

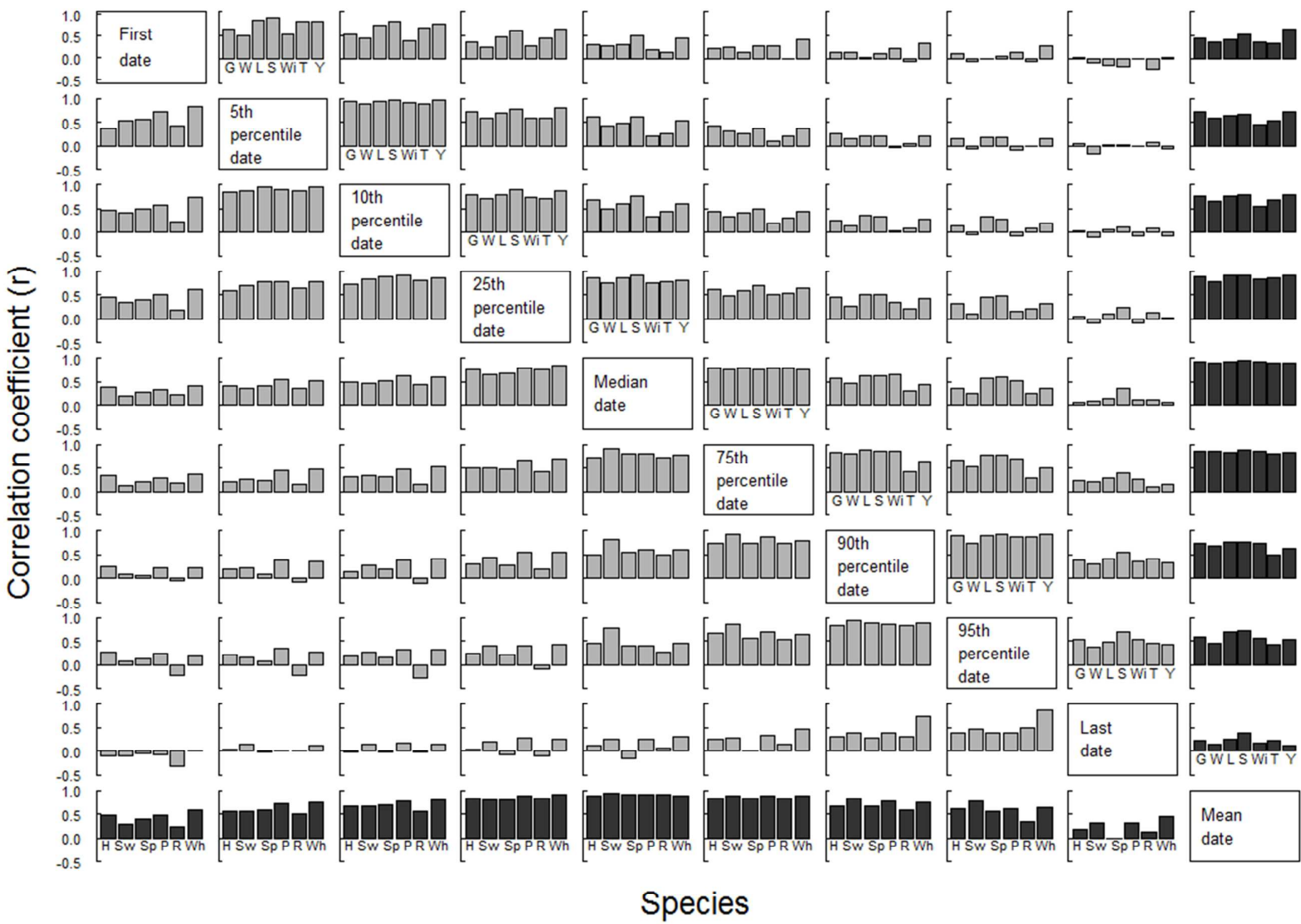


Fig. 3

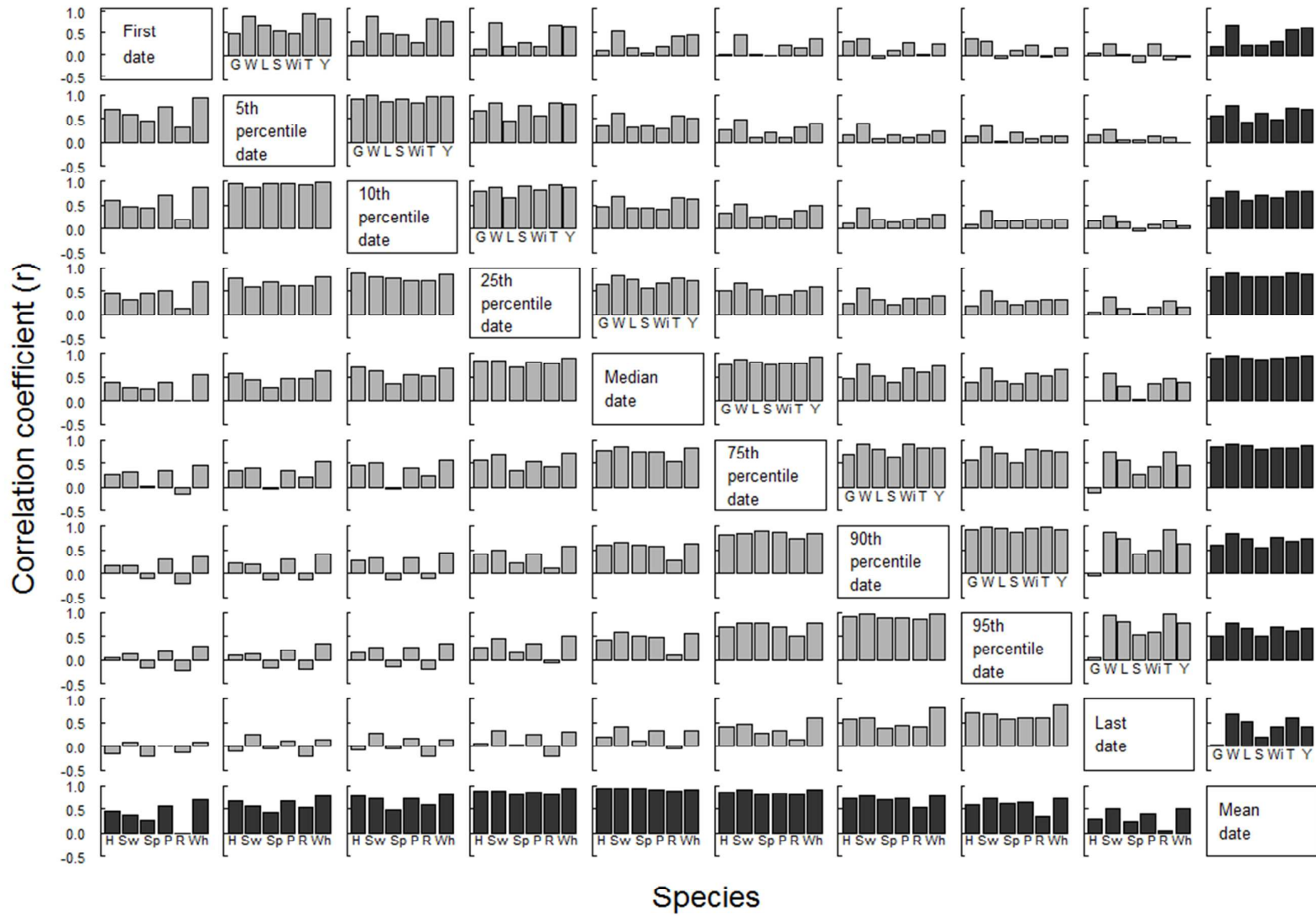


Fig. 4

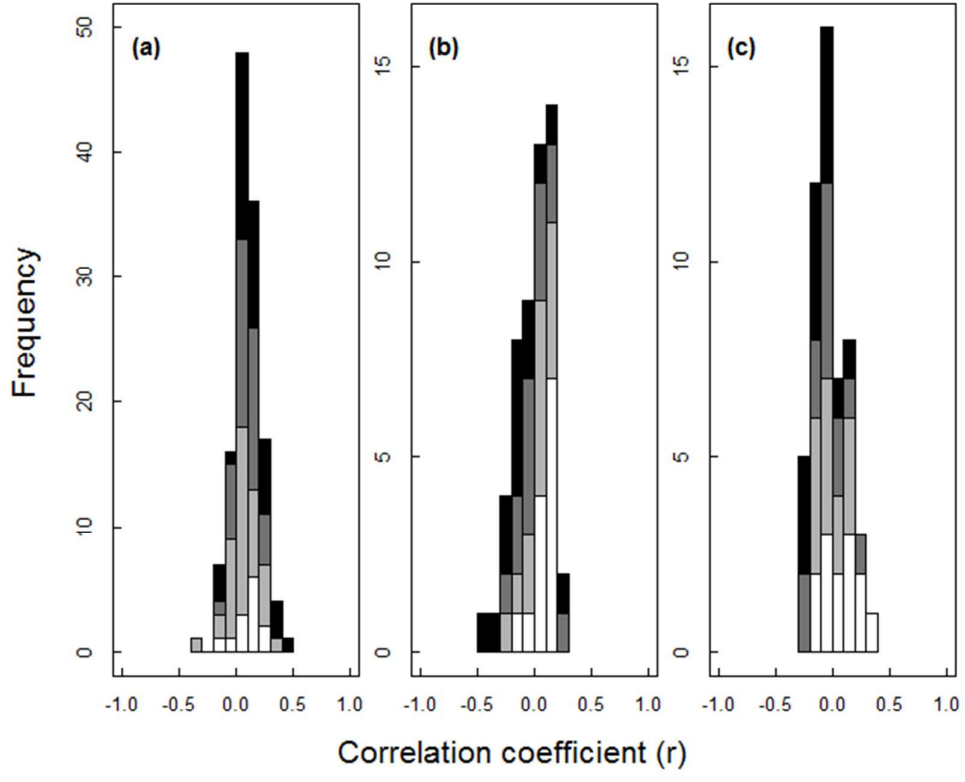


Fig. 5

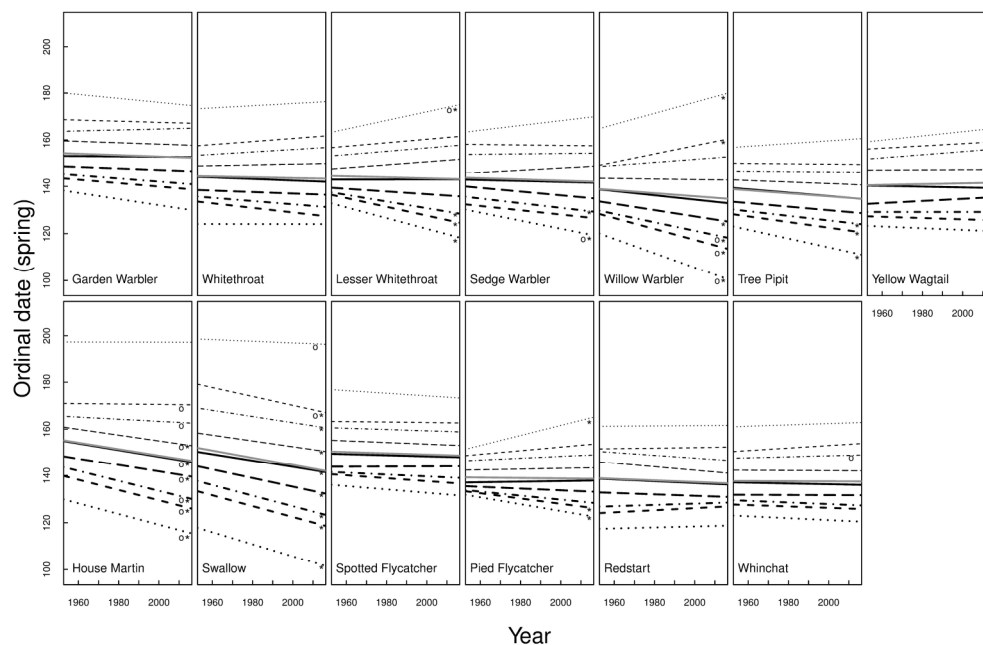


Fig. 1 Summary of modelled spring migration phenology across 60 years (1955-2014) for 13 species of trans-Saharan migrant bird, measured using ten metrics for each species. Lines represent linear regressions of each metric on year. Metrics are first date (bold dotted line), 5th percentile date (bold short dashes), 10th percentile date (bold dash-dot), 25th percentile date (bold long dashes), median date (bold solid black), mean date (bold solid grey), 75th percentile date (long dashes), 90th percentile date (dash-dot), 95th percentile date (short dashes), last date (dotted). \*  $p < 0.05$  for the linear regression. o  $p < 0.05$  for the season by year interaction.

Fig. 1  
197x133mm (300 x 300 DPI)



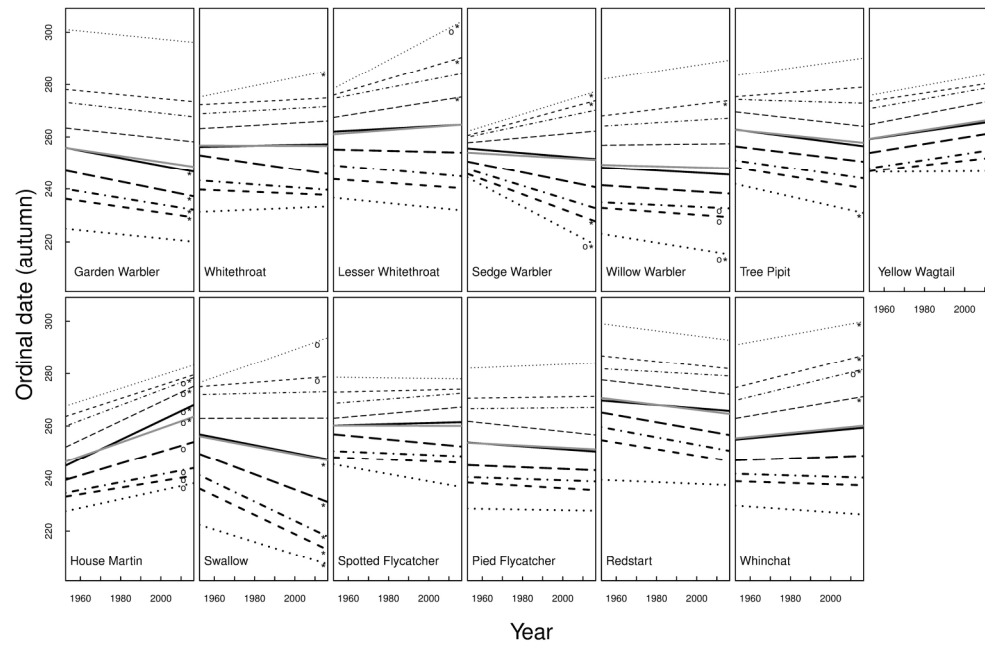


Fig. 2 Summary of modelled autumn migration phenology across 60 years (1955-2014) for 13 species of trans-Saharan migrant bird, measured using ten metrics for each species. Lines represent linear regressions of each metric on year. Metrics are first date (bold dotted line), 5th percentile date (bold short dashes), 10th percentile date (bold dash-dot), 25th percentile date (bold long dashes), median date (bold solid black), mean date (bold solid grey), 75th percentile date (long dashes), 90th percentile date (dash-dot), 95th percentile date (short dashes), last date (dotted). \*  $p < 0.05$  for the linear regression. o  $p < 0.05$  for the season by year interaction.

Fig. 2  
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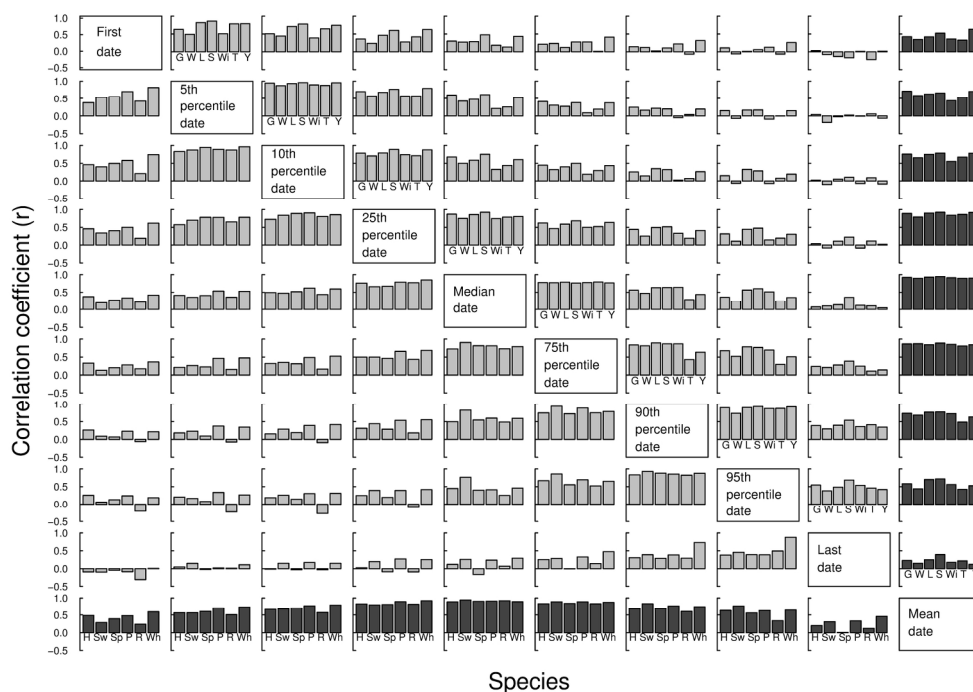


Fig. 3 Pairwise correlation matrix for 10 metrics of spring migration phenology measured across 60 years (1955-2014), for 13 species of trans-Saharan migrant bird. Grey bar heights represent within-species pairwise Pearson correlation coefficient values among first, percentile and last dates. Black bar heights represent within-species pairwise correlation coefficient values between first, percentile and last dates and mean date. Y-axes span -0.5 to 1.0. Each bar represents one species, denoted (G) Garden Warbler; (W) Common Whitethroat; (L) Lesser Whitethroat; (S) Sedge Warbler; (Wi) Willow Warbler; (T) Tree Pipit and (Y) Yellow Wagtail above the leading diagonal, and (H) House Martin; (Sw) Swallow; (Sp) Spotted Flycatcher; (P) Pied Flycatcher; (R) Redstart and (Wh) Whinchat below the leading diagonal.

Fig. 3

197x140mm (300 x 300 DPI)

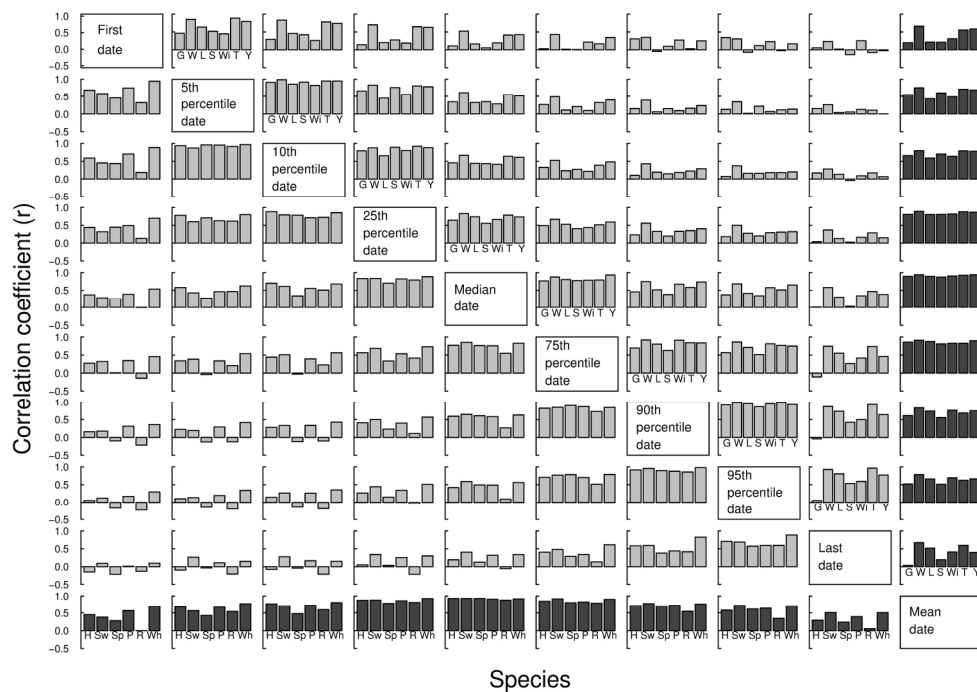


Fig. 4 Pairwise correlation matrix for 10 metrics of autumn migration phenology measured across 60 years (1955-2014), for 13 species of trans-Saharan migrant bird. Grey bar heights represent within-species pairwise Pearson correlation coefficient values among first, percentile and last dates. Black bar heights represent within-species pairwise correlation coefficient values between first, percentile and last dates and mean date. Y-axes span -0.5 to 1.0. Each bar represents one species denoted (G) Garden Warbler; (W) Common Whitethroat; (L) Lesser Whitethroat; (S) Sedge Warbler; (Wi) Willow Warbler; (T) Tree Pipit and (Y) Yellow Wagtail above the leading diagonal, and (H) House Martin; (Sw) Swallow; (Sp) Spotted Flycatcher; (P) Pied Flycatcher; (R) Redstart and (Wh) Whinchat below the leading diagonal.

Fig. 4

197x140mm (300 x 300 DPI)

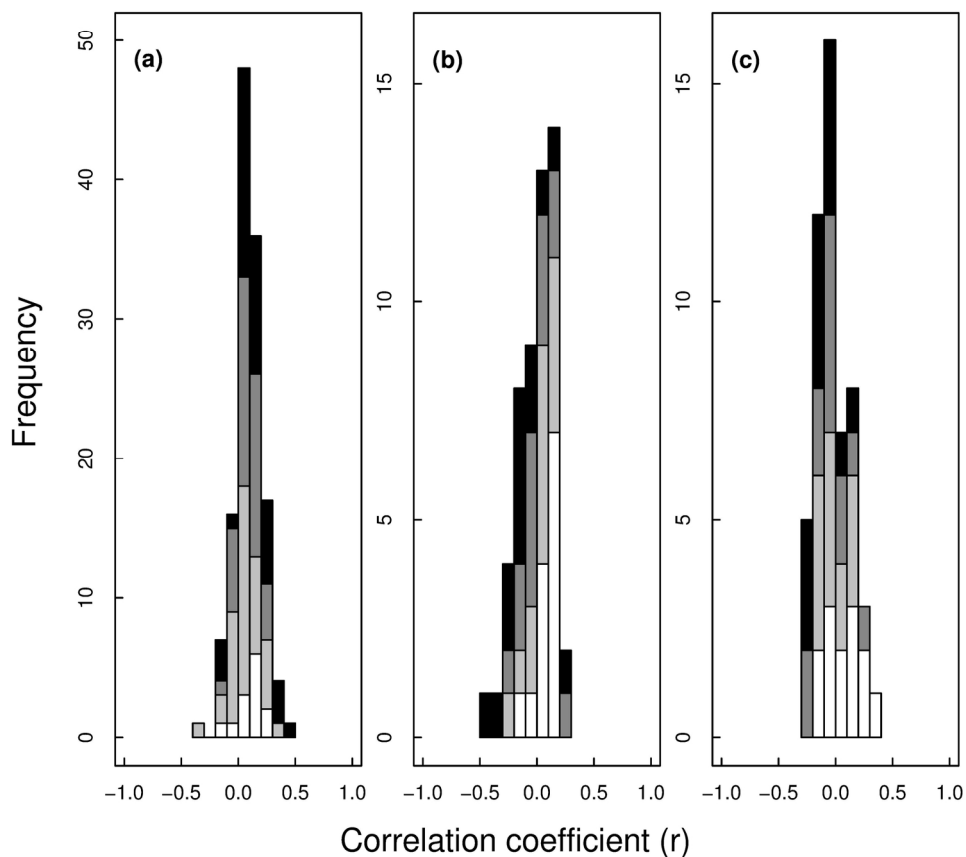


Fig. 5 Histograms summarising the between-season Pearson correlation coefficients among phenology metrics measured across 1955-2014, for 13 species of trans-Saharan migrant bird. a) Correlations between analogous early phase metrics (black), core phase metrics (dark grey) and late phase metrics (light grey) and mean date (white) in spring and autumn of the same year (130 tests). b) Correlations between last date in spring and first date in autumn (black), 95th percentile date in spring and 5th percentile date in autumn (dark grey), 90th percentile date in spring and 10th percentile date in autumn (light grey), and 75th percentile date in spring and 25th percentile date in autumn (white), of the same year (52 tests). c) Correlations between the last date in autumn and first date in the following spring (black), 95th percentile date in autumn and 5th percentile date in the following spring (dark grey), 90th percentile date in autumn and 10th percentile date in the following spring (light grey), and 75th percentile date in autumn and 25th percentile date in the following spring (white) (52 tests).

Fig. 5

168x161mm (300 x 300 DPI)