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

Running head: DIVERGENT CHANGES IN MIGRATION TIMING

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Abstract

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

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

Introduction

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

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

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

Quantifying changes in the timing of seasonal biological events requires appropriate phenological metrics to be enumerated for key traits. Previous studies have often measured phenological change using just one or two metrics, commonly the first date or mean date on which an event was observed each year (Tryjanowski & Sparks, 2001; Lehikoinen et al., 2004; Knudsen et al., 2007; Miller-Rushing et al., 2008). Such studies have demonstrated considerable changes across recent decades (e.g. Walther et al., 2002; Hüppop & Hüppop, 2003; Sparks et al., 2005; Both et al., 2009; Ibáñez et al., 2010). However, it has been repeatedly highlighted that such restricted metrics might provide limited or misleading information regarding the dynamics of full phenological event distributions (Leopold & Jones, 1947; Sparks et al., 2001; Tryjanowski & Sparks, 2001; Mason, 1995; Sparks et al., 2005; Miller-Rushing et al., 2008; Newton, 2008; Knudsen et al., 2011). It remains unclear whether single metrics, such as first or mean date, are reliable proxies. If they are not, the conclusions of some previous studies, and hence our current view of the overall phenological consequences of environmental change, might be partially invalidated. Full understanding of long-term phenological dynamics, and evaluation of existing evidence, therefore requires multi-faceted analyses of comprehensive data that quantify entire seasonal distributions of key biological events spanning many years.

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

Migration constitutes one major biological response to natural seasonal environmental change (Newton, 2008; Alerstam, 2001; Milner-Gulland & Fryxell, 2011). Up to half of bird species migrate annually, and migration also occurs in reptiles, fish, mammals and insects (Alerstam et al., 2003; Robinson et al., 2009; Newton, 2008). Appropriate migration timing is crucial if populations are to maximise utilisation of geographically discrete seasonally abundant resources yet avoid seasonally inhospitable environments (Alerstam et al., 2003; Newton, 2008). However, migratory life-histories might be particularly susceptible to disruption caused by spatially-structured climatic and environmental changes, because such changes can rapidly cause temporal asynchrony between migration and spatio-temporal variation in resource availability (Newton, 2004; Dingle, 2006). For example, the considerable climatic changes occurring across Western Europe are rapidly changing the phenologies of key seasonal resources for migrant species that breed in this region (Cotton, 2003; Hüppop & Hüppop, 2003; Seneviratne et al., 2006; Araújo et al., 2011).

In birds, there is evidence that short-distance migrant species that both breed and winter within Western Europe can shift their migration timing in response to environmental changes that affect both the breeding and wintering habitats (Both & Visser, 2001; Hüppop & Hüppop, 2003; Newton, 2008). However in long-distance (trans-continental) migrants, such phenological plasticity may be hampered by the greater separation between breeding and wintering areas and relatively independent environmental conditions. Such species are potentially vulnerable to rapidly developing asynchrony between current migration and resource phenologies (Sokolov et al., 1998; Both & Visser,, 2001; Tryjanowski et al., 2002; Alerstam et al., 2003; Hüppop & Hüppop, 2003; Newton, 2008). Long-distance migration timing in birds is also influenced by endogenous physiological changes triggered by day-length thresholds, meaning that phenotypic plasticity allowing rapid responses to changing environmental conditions may be limited (Visser et al., 1998; Both & Visser, 2001; Møller, 2002). However, long-distance migrants that breed at northern latitudes but utilise stop-over sites further south could potentially adjust their migration timing on route. Consequently, even if departure timing was inflexible due to strong endogenous control, departure from stop-over locations and hence arrival at final destinations could potentially still be modulated to match environmental conditions encountered during initial migration phases. Furthermore, such species could potentially adjust autumn departure timing to match northern environmental conditions, even if spring migration phenology is set endogenously and/or influenced by southern environments. Large-scale climate or environmental change could then cause major structural changes to species' life-histories, for example because earlier spring migrations and later autumn migrations mean that individuals spend more time in northern environments, impacting physiology and numerous dimensions of population and community ecology. Alternatively, a species' current life-history could be more simply shifted forward in time, if migration occurred earlier in both spring and autumn. Quantifying such divergent or parallel seasonal phenological dynamics requires the degrees to which spring and autumn long-distance migration timings have changed, and the degree to which phenological variation in one season is associated with variation in the other season within or across years, to be quantified.

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

Materials and methods

Study site and data collection

Fair Isle (768ha) is located midway between the Shetland and Orkney archipelagos (59°54′N, 01°62′W), and is used by birds migrating via north-westernmost routes within the Western Palaearctic-Afrotropical migration system (Newton, 2008). Each year during 1955 to 2014, in April to June and August to October inclusive (hereafter the 'core' census periods), three professional ornithologists from Fair Isle Bird Observatory (FIBO) carried out simultaneous daily observational censuses of migrant birds, across three standardised areas that collectively covered the whole of Fair Isle. Each observer walked routes within each census area that encompassed all key areas of foraging habitat and cover for migrant birds, taking a minimum of approximately three hours per area per day. All migrants encountered were identified to species and counted, and daily count totals across the three areas were compiled. Fair Isle's predominant vegetation is grass and heather, with cliffs, gardens and small areas of crop around croft houses providing the only areas of cover. Hence, while it is unlikely that all individual migrants that were present on Fair Isle each day would be observed, observation probability is high and observations are likely to provide a representative sample of the migrant species populations that were present and visible on passage on any day. The same census regime was also implemented in March, July and November each year. However, since the full staff of three ornithologists was not always present during these months, daily coverage was sometimes less comprehensive. This overall census regime spanning March to November each year was maintained unchanged throughout 1955-2014 (Figure S1). There was therefore no major systematic change in observer effort across years. Censuses were carried out in all weathers except particularly severe storms. During 1955 to 2014, the number of core period days per year on which no counts were made averaged 1.0 ± 1.0 SD in spring (April-June) and 0.1 ± 0.3 SD in autumn (August-October) and did not change across the 60 years in either season (Spring: linear regression slope $\beta_{58} = -0.03 \pm 0.03$ SE, $p = 0.22$; Autumn: $\beta_{58} = -0.02 \pm 0.03$ SE, $p = 0.39$).

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

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

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

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

Least squares linear regression models were fitted to quantify overall changes in metrics of spring and autumn migration phenologies across the 60 year study period. Separate models were fitted for each of the ten phenology metrics for each species in spring and autumn. Negative and positive slopes show that migration timing advanced and delayed respectively. Separate models were also fitted for each of the two migration duration metrics for each species in spring and autumn. Here, negative and positive slopes show that the migration duration shortened and lengthened respectively. The model-estimated total numbers of days by which migration timing advanced or delayed and by which migration duration shortened or lengthened during 1955-2014 were calculated as 60x the regression slopes. To test whether the overall change in spring migration timing across the study period differed from the overall change in autumn timing, we additionally tested for season by year interactions for each of the ten metrics for each species. This analysis tests for divergent changes in spring and autumn phenologies in the same metric, but does not test for direct linkage in metrics across consecutive seasons. Further models showed no evidence of substantial non-linear (i.e. quadratic) changes in any species-season-metrics (zero significant quadratic terms). Results remained quantitatively similar when models were refitted after excluding the very small number of seasons with <5 observations of a particular species.

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

To quantify associations in migration phenology between consecutive springs and autumns, we implemented three further sets of analyses for each species. These analyses were designed to provide a multi-faceted assessment of phenological links between seasonally paired life-history events that does not rely entirely on any single phenological metric for either season. First, to quantify whether spring migration phenology was associated with analogous phases of autumn phenology within the same year, we quantified the correlations between the spring and autumn values of each of the ten phenology metrics within each calendar year (e.g. spring and autumn first dates, spring and autumn 5th percentile dates, etc.). Second, to quantify whether migration phenology in late spring was associated with migration phenology in early autumn within the same year, we quantified the correlations between each species' last date in spring and first date in autumn, 95th percentile date in spring and 5th percentile date in autumn, 90th percentile date in spring and 10th percentile date in autumn, and 75th percentile date in spring and 25th percentile date in autumn. Third, to quantify whether migration phenology in late autumn was associated with migration phenology in early spring in the following year, we quantified the correlations between each species' last date in autumn and first date in the following spring, 95th percentile date in autumn and 5th percentile date in the following spring, 90th percentile date in autumn and 10th percentile date in the following spring, and the 75th percentile date in autumn and 25th percentile date in the following spring. The first two sets of analyses used 60 years of within-year comparisons, while the third set of analyses used 59 available pairs of between-year comparisons. Positive correlations would show that phenology in consecutive seasons varied synchronously, for example that delayed spring migration was followed by delayed autumn migration. Such correlations could arise even if there were no overall changes in spring or autumn migration phenology across the 60-year study period for any species, simply reflecting among-year variation that was correlated across seasonally paired events.

Standard checks showed no inadequacies in model fit; residuals were approximately normally distributed with minimal temporal autocorrelation. In principle, hypothesis tests could be further validated by bootstrapping, thereby allowing uncertainty in focal percentile values to be estimated and incorporated into regression analyses. However, appropriate bootstrapping is not readily feasible because the most appropriate resampling unit would be individual birds, but individuals are not generally recognisable across days in migration census data. Rather, the common synchronized arrival of multiple individuals of any focal species means that core period percentiles are directly estimated with little uncertainty. All analyses were implemented in R version 2.15.0 (R Core Team, 2015). Due to the large number of non-independent analyses we view results holistically and do not focus primarily on the statistical 'significance' of estimated effects in any one species. Rather than apply explicit corrections for multiple testing, we summarise general patterns emerging across the 13 focal species. Throughout, we use the term ‘significant’ to mean ‘nominally significant’ at $p < 0.05$.

Abundance

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

Results

Spring migration phenology

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

However, despite the widespread advancements in early phase migration, the core phase of species' spring migration distributions (i.e. 25th, 50th and 75th percentile dates and mean date) changed relatively little across years (Fig. 1). Specifically, regression slopes on year were non-significant for 43 (83%) of 52 species-metrics, comprising 33 (77%) negative slopes and ten (23%) positive slopes. Indeed, in five species the estimated change in 50th percentile (median) date was less than one day across 60 years (Fig. 1, Table S1). Regression slopes were significant for nine (17%) species-metrics involving three species, all demonstrating advancements in core phase migration timing (Fig. 1, Table S1).

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

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

Autumn migration phenology

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

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

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

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

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

Season by year interactions

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

Cross-correlations between phenological metrics

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

Between-season associations

The analogous spring and autumn values of each individual percentile metric and the mean were generally weakly correlated within each year. Specifically, the distribution of correlation coefficients was approximately centred on zero (mean 0.09 ± 0.12 SD, Fig. 5a, Table S6). The absolute correlation coefficients never exceeded 0.5, and only ten (8%) of 130 values were nominally significant. Similarly, there were no strong or consistently positive or negative correlations between metrics describing the late phase of spring migration and those describing the early phase of autumn migration within the same year (Figure 5b, Table S6). Five (10%) of 52 correlations were significant, and the distribution of correlation coefficients was again centred on zero (Fig. 5b, Table S6). Furthermore, there were no strong or consistently positive or negative correlations between metrics describing the late phase of autumn migration and those describing the early phase of spring migration in the following calendar year (Fig. 5c, Table S6). One of 52 correlations was significant, and the distribution of correlation coefficients was again centred on zero (Fig. 5c, Table S6). Overall, therefore, the timing of any one migration season was not strongly or consistently correlated with the timing of the preceding season.

Abundance

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

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

Discussion

Dynamics of spring and autumn migration phenologies

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

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

However, despite the predominant temporal stability of the core migration phase, the timing of the early and late phases of species' migration distributions commonly changed across years. In 12 species in spring and/or autumn, the early phase got earlier across years, or the late phase got later, or both changes occurred. Consequently, there was a widespread pattern of lengthening of spring and autumn migration periods during 1955-2014, as shown by the 'fan-shaped' patterns of changes across the ten phenological metrics across years. In many cases the magnitude of change in phenology measured by individual metrics was considerable. For example advancements and delays in autumn migration timing exceeding 20 days occurred in Swallow and Lesser Whitethroat respectively. Overall, these patterns suggest that migration timing in long-distance migrants is not completely constrained, but is somewhat flexible.

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

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

Quantifying phenological change

Our analyses showed that the form of phenological change across years can be complex, and this complexity is only revealed if multiple metrics encompassing full seasonal event distributions are quantified. Specifically, there were no consistently strong positive correlations between the annual values of different metrics of migration timing, except among immediately adjacent metrics (e.g. adjacent percentiles). Consequently, no one metric could have been used as an accurate proxy for all the others. For example, simply quantifying changes in first date would have indicated advancing migration timing in multiple species, but would not have revealed the temporal stability and delays in the core and late phases of species' migration. Similarly, quantifying mean date would have indicated temporal stability in migration timing in most species, but would not have revealed the advancements and delays in the early and late phases. Many studies have used just one or a few metrics to quantify phenological change, commonly first arrival date and mean date, often because data are sparse or otherwise limiting (Sparks et al., 2001, 2005; Miller-Rushing et al., 2008; Goodenough et al., 2014). Our analyses imply that reported phenological changes measured using only one or two metrics should be interpreted with caution, because such metrics do not necessarily comprehensively describe phenological dynamics and can fail to detect complex phenological changes occurring simultaneously. Indeed, small or negative correlations between percentiles located on opposite sides of the mean or median of an event distribution could generally arise if the mean changes little across years but the variance increases. However, more complex correlation structures might arise given more complex changes in distribution shapes, involving altered skewness or kurtosis, or multimodality or other irregularities. Overall, future studies must therefore strive to measure phenology using multiple metrics that collectively quantify the full biological event distribution of interest.

Between-season phenological associations

Spring and autumn migration are seasonally paired events. Cross-season linking of such events could potentially drive or constrain year-round phenological dynamics in many species, but has rarely been quantified (Gallinat et al., 2015). However, we found little evidence that migration timing was correlated across analogous metrics for spring and autumn in the same year, between late spring and early autumn in the same year, or between late autumn and early spring in the following year. Such decoupling might be expected if individual migrants recorded in spring and autumn on Fair Isle are from different breeding populations. However, our focal species breed across much of western Scandinavia and ringing recoveries suggest that at least some individuals recorded on Fair Isle in spring and autumn are from the same breeding populations (Wernham et al., 2002). Furthermore, ringing recoveries have shown that the same individuals have migrated via Fair Isle in consecutive spring and autumn periods (Fair Isle Bird Observatory annual reports, 1955-2014). Overall, therefore, our results suggest that spring and autumn migration timings occur largely independently across consecutive seasons. In contrast, Van Buskirk et al. (2008) found that changes in spring migration timing were correlated with changes in autumn migration timing in long- and short-distance migrant North American passerine birds.

Mechanisms of observed phenological change

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

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

Advances and delays in migration timing at a single location such as Fair Isle can result from changes in departure timing from the wintering or breeding quarters, changes in migratory speed and/or changes in route, reflecting evolution or phenotypic plasticity (Berthold, 1996; Møller et al., 2008; Newton, 2008). Although there is evidence that initial departure timing among trans-Saharan migrant birds is influenced by endogenous processes, weak connectivity between climatic conditions in Africa and Europe has been recently demonstrated (Gordo et al., 2005; Saino & Ambrosini, 2008). Migrants may consequently be able to judge conditions at long range and adjust departure in both spring and autumn in response to inter-continental climatic flux. Additionally, since Fair Isle lies approximately 60° north and 2° west, migrants moving to northerly breeding locations must traverse relatively long distances across Western Europe. The observed changes in migration phenology might therefore stem from changes in migration speeds and/or routes in response to climate change or other factors such as food availability within Europe, as demonstrated in other systems (e.g. Visbeck et al., 2001; Hüppop & Hüppop, 2003; Bearhop et al., 2005).

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

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

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WTSM and JMR designed and undertook analyses, wrote the paper and contributed to data collection and compilation, MB contributed to analysis and editing, all other authors oversaw and undertook data collection and compilation and contributed to editing.

References

Alerstam T (2001) Detours in bird migration. Journal of Theoretical Biology, **209**, 319-331.

Alerstam T, Henderström A, Åkesson S (2003) Long distance migration: evolution and determinants. Oikos, **103**, 247-260.

Araújo, MB, Alagodor D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. Ecology Letters, **14**, 484-492.

Barbet-Massin M, Walther BA, Thuiller W, Rahbek C, Jiguet F (2009) Potential impacts of climate change on the winter distribution of Afro-Palaearctic migrant passerines. Biology Letters, **5**, 248–251.

Bearhop S, Fiedler W, Furness RW, et al. (2005) Assortative mating as a mechanism for rapid evolution of a migratory divide. Science, **310**, 502-504.

Beebee TJC (1995) Amphibian breeding and climate change. Nature, **374**, 219-220.

Both C, van Asch M, Bijlsma RG, van den Berg A, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology, **78**, 73-83.

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature, **411**, 296-298.

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature, **441**, 81–83.

Butchart SHM, Walpole M, Collen B, et al. (2010) Global Biodiversity: indicators of recent declines. Science, **328**, 1164-1168.

Chazal J, Rounsevell MDA (2009) Land-use change within assessments of biodiversity change: A review. Global Environmental Change, **19**, 306-315.

Chuine I (2010) Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B, **365**, 3149-3160.

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends in Ecology & Evolution, **22**, 357-365.

Cotton PA (2003) Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences, **100**, 12219-12222.

Crick HQP (2004) The impact of climate change on birds. Ibis, **146**, 48-56.

Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. Nature, **388**, 526.

Dingle H (2006) Animal migration: is there a common migratory syndrome? Journal of Ornithology, **147**, 212-220.

Forchhammer MC, Post E, Stenseth NC (1998) Breeding phenology and climate. Nature, **391**, 29-30.

Forrest J, Miller-Rushing AJ (2010) Towards a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B, **365**, 3101-3112.

Gallinat AS, Primack RB, Wagner DL (2015) Autumn, the neglected season in climate change research. Trends in Ecology and Evolution, **30**, 169-176.

Goodenough AE, Fairhurst SM, Morrison JB, Cade M, Morgan PJ, Wood MJ (2014) Quantifying the robustness of first arrival dates as a measure of avian migratory phenology. Ibis, **157**, 384-390.

Gordo O, Brotons L, Ferre X, Comas P (2005) Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? Global Change Biology, **11**, 12-21.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution, **15**, 56-61.

Hüppop O, Hüppop K (2003) North Atlantic Oscillation and timing of spring migration in birds. Proceedings of the Royal Society London B, **270**, 233-240.

Ibáñez I, Primack RB, Miller-Rushing AJ, Ellwood E, Higuchi H, Lee SD, Kobori H, Silander JA (2010) Forcasting phenology under global warming. Philosophical Transactions of the Royal Society B, **365**, 3247-3260.

Jenni L, Kery M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society B, **270**, 1467-1471.

Jonzén N, Lindén A, Ergon T, et al. (2006) Rapid advance of spring arrival dates in long-distance migratory birds. Science, **312**, 1959-1961.

King DA (2004) Climate change science: adapt, mitigate or ignore? Science, **303**, 176-177.

Knudsen E, Lindén A, Ergon T, Jonzén N, Vik JO, Knape J, Røer JE, Stenseth NC (2007) Characterising bird migration phenology using data from standardized monitoring at bird observatories. Climate Research, **35**, 59-77.

Knudsen E, Lindén A, Both C, et al. (2011) Challenging claims in the study of migratory birds and climate change. Biological Reviews, **86**, 928-946.

Lehikoinen E, Sparks TH, Zalakevicius M (2004) Arrival and departure dates. Advances in Ecological Research, **35**, 1–31.

Leopold A, Jones SE (1947) A phenological record for Sauk and Dane Counties, Wisconsin, 1935–1945. Ecological Monographs, **17**, 81–122.

MacMynowski DP, Root DL (2007) Climate and the complexity of migratory phenology: sexes, migratory distances and arrival distributions. International Journal of Biometeorology, **51**, 361-373.

Mason CF (1995) Long-term trends in the arrival dates of spring migrants. Bird Study, **42**, 182–189.

McCleery RH, Perrins CM (1998) …temperature and egg-laying trends. Nature, **391**, 30-31.

Menzel A, Fabien P (1999) Growing season extended in Europe. Nature, **397**, 659.

Miller-Rushing AJ, Inouye DW, Primack RB (2008) How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. Journal of Ecology, **96**, 1289–1296.

Miller-Rushing AJ, Høye TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B, **365**, 3177-3186.

Milner-Gulland EJ, Fryxell JM (2011) *Animal migration: a synthesis*. Oxford University Press, Oxford.

Møller AP (2001) Heritability of arrival date in a migratory bird. Proceedings of the Royal Society B, **268**, 203-206.

Møller AP (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. Journal of Animal Ecology, **71**, 201-210.

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences, **105**, 16195-16200.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern latitudes from 1981 to 1991. Nature, **386**, 698-702.

Newton I (2004) Population limitation in migrants. Ibis, **146**, 197-226.

Newton I (2008) *The Migration Ecology of Birds*. Elsevier Ltd., London.

Nolan V, Ketterson ED (1990) Timing of autumn migration and its relation to winter distribution of dark-eyed juncos. Ecology, **71**, 1267-1278.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics, **37**, 637-669.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature, **421**, 37-42.

Perrins CM (1970) The timing of birds' breeding season. Ibis, **112**, 242-255.

R Development Core Team. 2015. R: A language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing, Austria. Available: http://www.R-project.org/.

Robinson RA, Crick HQP, Learmonth JA, et al. (2009) Travelling through a warming world: climate change and migratory species. Endangered Species Research, **7**, 87-99.

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. Global Change Biology, **6**, 407-416.

Saino N, Ambrosini R (2008) Climatic connectivity between Africa and Europe may serve as a basis for phenotypic adjustment of migration schedules of trans-Saharan migratory birds. Global Change Biology, **14**, 250-263.

Seneviratne SI, Lüthi D, Litschi M, Schär C (2006) Land-atmosphere coupling and climate change in Europe. Nature, **443**, 205-209.

Snow DW, Perrins CM (Eds.) (1998) *The Birds of the Western Palaearctic concise edition. Vol. 2*. Oxford University Press, Oxford.

Sparks TH, Mason CF (2004) Can we detect change in the phenology of winter migrant birds in the UK. Ibis, **146**, 58-61.

Sparks TH, Menzel A (2002) Observed changes in seasons: an overview. International Journal of Climatology, **22**, 1715-1725.

Sparks TH, Roberts DR, Crick HQP (2001) What is the value of first arrival dates of spring migrants in phenology? Avian Ecological Behaviour, **7**, 75-85.

Sparks TH, Bairlein F, Bojarinova JG, Hüppop O, Lehikoinens EA, Rainos K, Sokolov LV, Walker D (2005) Examining the total arrival distribution of migratory birds. Global Change Biology, **11**, 22-30.

Sparks TH, Huber K, Bland RL, et al. (2007) How consistent are trends in arrival (and departure) dates of migrant birds in the UK? Journal of Ornithology, **148**, 503-511.

Sparks TH, Tryjanowski P (2007) Patterns of spring arrival dates differ in two hirundines. Climate Research, **35**, 159-164.

Sokolov LV, Markovets MY, Shapoval AP, Morozov YG (1998) Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. Avian Ecology & Behaviour, **1**, 1-21.

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliot JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology, **16**, 3304-3313.

Tryjanowski P, Sparks TH (2001) Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. International Journal of Biometeorology, **45**, 217–219.

Tryjanowski P, Kuźniak S, Sparks T (2002) Earlier arrival of some farmland birds in western Poland. Ibis, **144**, 62-68.

Van Buskirk J, Mulvihill RS, Leberman RC (2009) Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. Global Change Biology, **15**, 760-771.

Visbeck MH, Hurrell JW, Polvani L, Cullen HM (2001) The North Atlantic Oscillation: past, present and future. Proceedings of the National Academy of Sciences, **98**, 12876-12877.

Visser ME, van Noordwijk AJ, Tinberg JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (Parus major). Proceedings of the Royal Society B, **265**, 1867-1870.

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B, **272**, 2561-2569.

Walther GR, Post E, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature, **416**, 389-395.

Wernham CV, Toms MP, Marchant JH, Clark JA, Siriwardena GM, Baillie SR (2002) *The Migration Atlas: movements of the birds of Britain and Ireland*. T. & A. D. Poyser, London.

Wilson JR, Thomas CD, Fox R, Roy DB, Kunin WE (2004) Spatial patterns in species distributions reveal biodiversity change. Nature, **432**, 393-396.

Wuethrich B (2000) How climate change alters rhythms of the wild. Science, **287**,793-795.

Zalakevicius M, Bartkeviciene G, Raudonikis L, Janulaitis J (2006) Spring arrival response to climate change in birds: a case study from eastern Europe. Journal of Ornithology, **147**, 326-343.

Supporting Information

Figure S1. Species cumulative count distributions.

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

Table S1. Summary statistics for spring migration phenology.

Table S2. Summary statistics for spring migration duration.

Table S3. Summary statistics for autumn migration phenology.

Table S4. Summary statistics for autumn migration duration.

Table S5. Summary statistics for season by year interactions.

Table S6. Summary statistics for between-season associations.

Appendix S1. Stop-over duration analyses.

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

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

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

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

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

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

Table 1 Study species and summary of mean total migration period[a], mean total bird days[b] and regression coefficients (ß) of total bird days on year across 60 years (1955-2014) for 13 species of trans-Saharan migrant birds in spring and autumn. SE = standard error. * denotes p < 0.05.

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

[a] For each species in each season the total migration period was calculated as the number of days from the first record to the last record. The mean length of this period was computed across the 60 study years.

[b] For each species in each season total bird days was calculated as the sum of all counts on all days. The mean total bird days was computed across the 60 study years.

Figure captions

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. 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. 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. 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. 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).

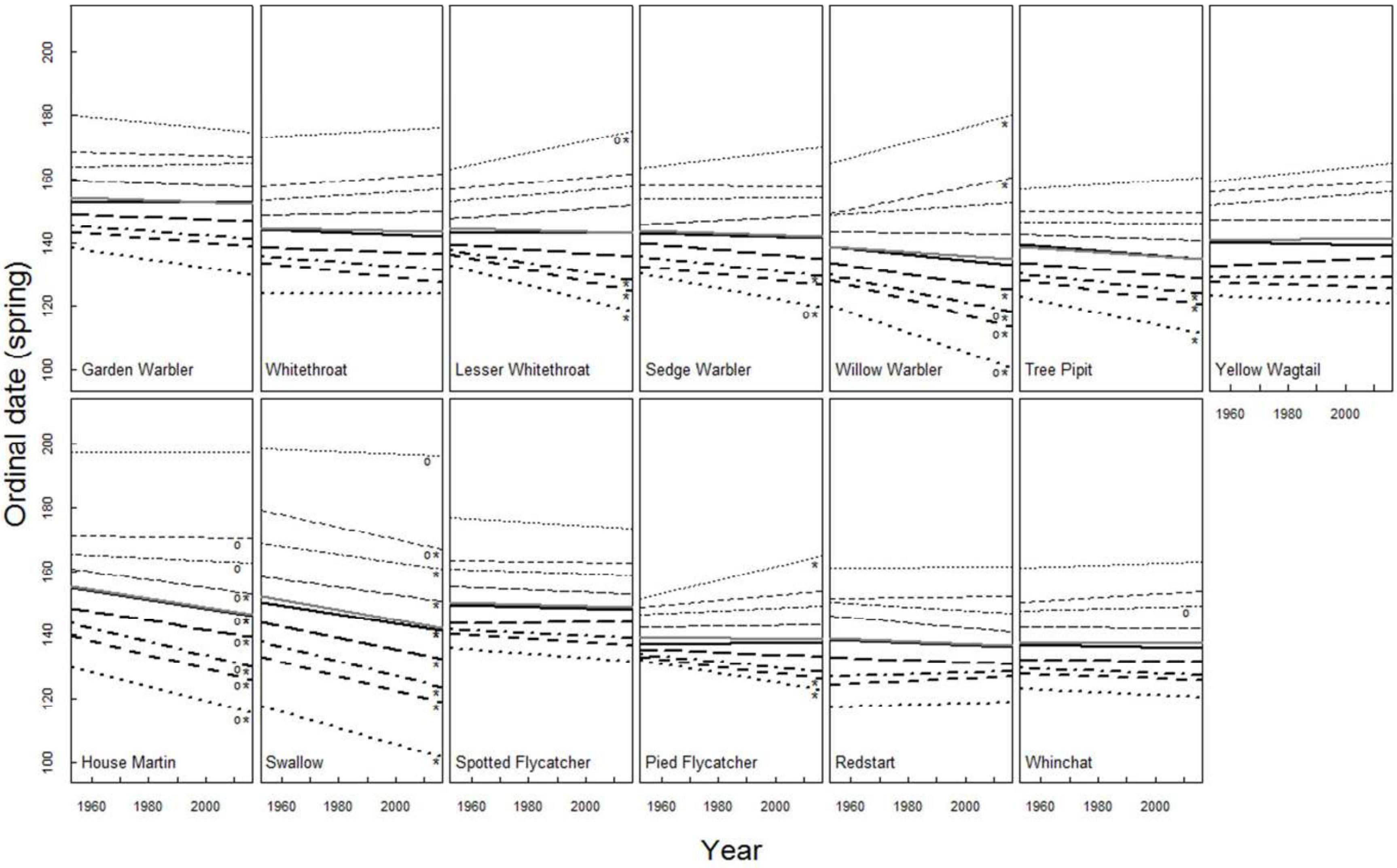
Ordinal date (spring)
200
180
160
140
120
100
Garden Warbler
Whitethroat
Lesser Whitethroat
Sedge Warbler
Willow Warbler
Tree Pipit
Yellow Wagtail
House Martin
Swallow
Spotted Flycatcher
Pied Flycatcher
Redstart
Whinchat
1960
1980
2000
Year

Fig. 1

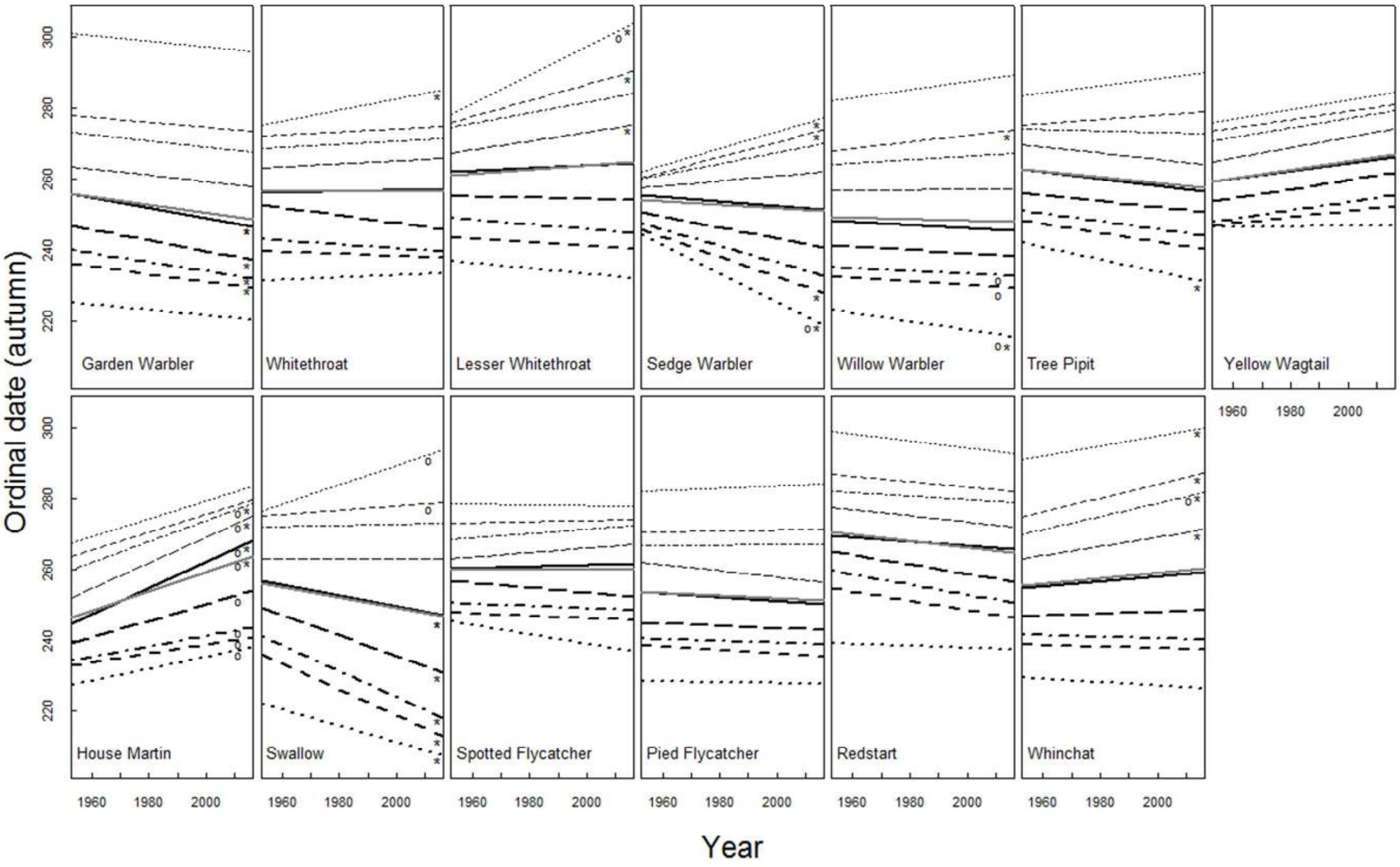
Ordinal date (autumn)
300
280
260
240
220
Garden Warbler
Whitethroat
Lesser Whitethroat
Sedge Warbler
Willow Warbler
Tree Pipit
Yellow Wagtail
House Martin
Swallow
Spotted Flycatcher
Pied Flycatcher
Redstart
Whinchat
1960
1980
2000
Year

Fig. 2

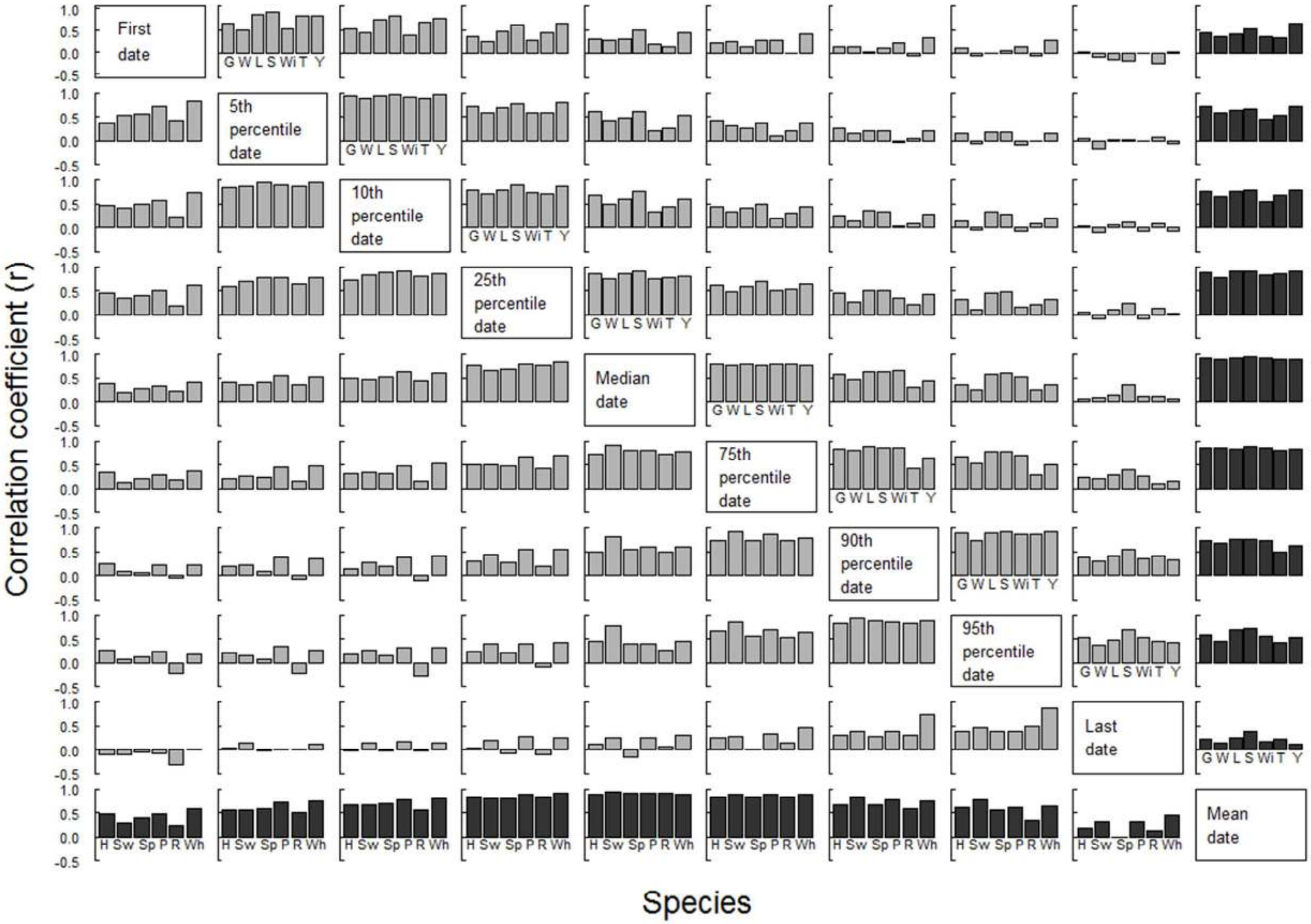
Correlation coefficient (r)
1.0
0.5
0.0
-0.5
First date
5th percentile date
10th percentile date
25th percentile date
Median date
75th percentile date
90th percentile date
95th percentile date
Last date
Mean date
G W L S Wi T Y
H Sw Sp P R Wh
Species

Fig. 3

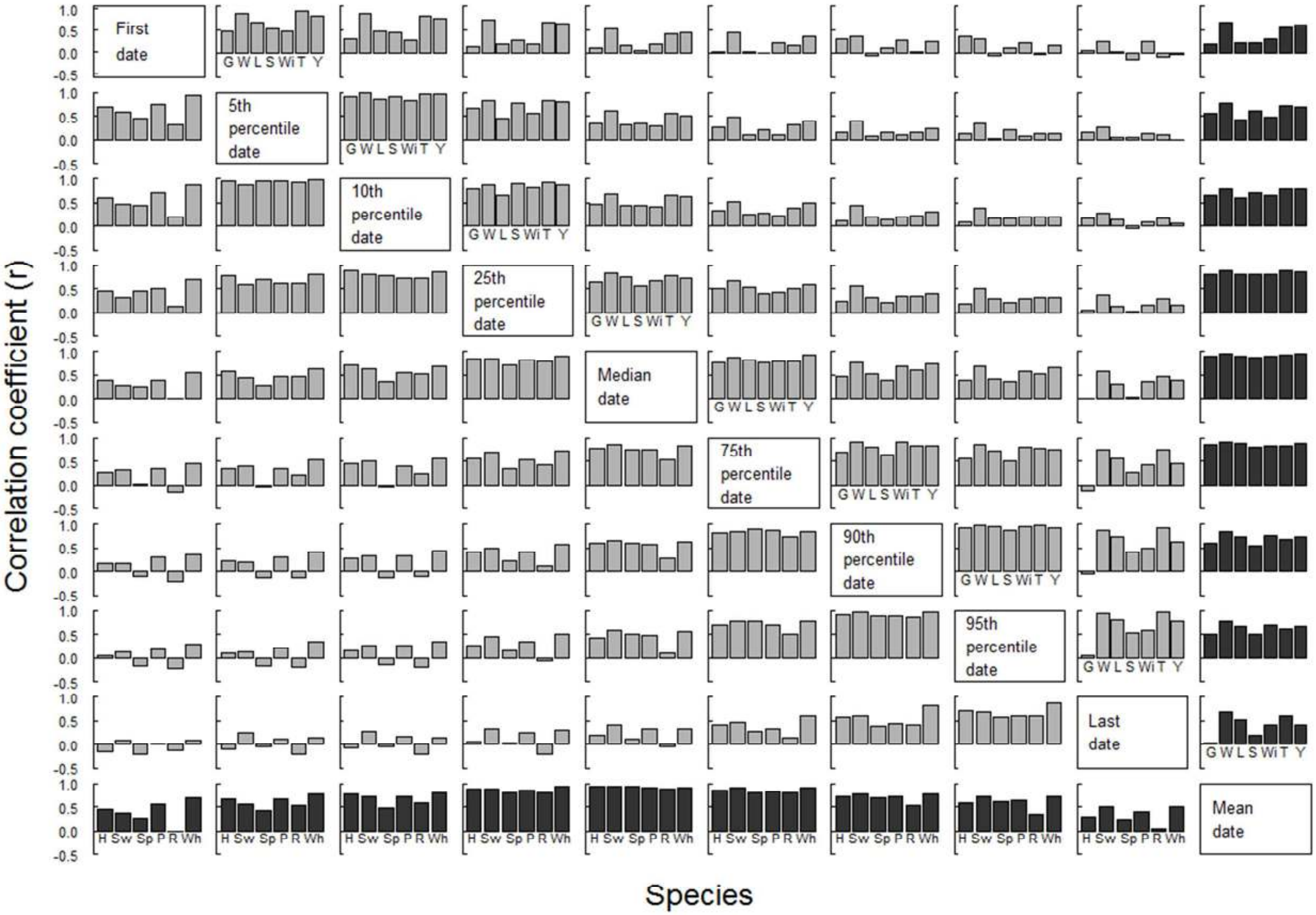
Correlation coefficient (r)
1.0
0.5
0.0
-0.5
First date
5th percentile date
10th percentile date
25th percentile date
Median date
75th percentile date
90th percentile date
95th percentile date
Last date
Mean date
G W L S Wi T Y
H Sw Sp P R Wh
Species

Fig. 4

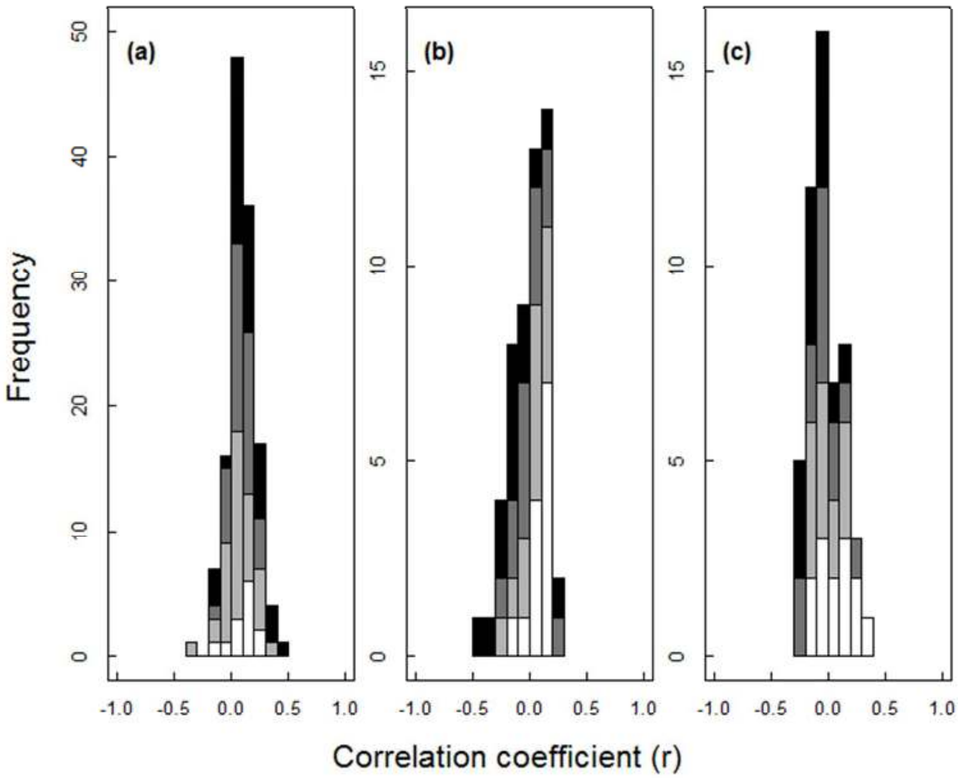
(a)
(b)
(c)
Frequency
0
10
20
30
40
50
0
5
10
15
-1.0
-0.5
0.0
0.5
1.0
Correlation coefficient (r)

Fig. 5

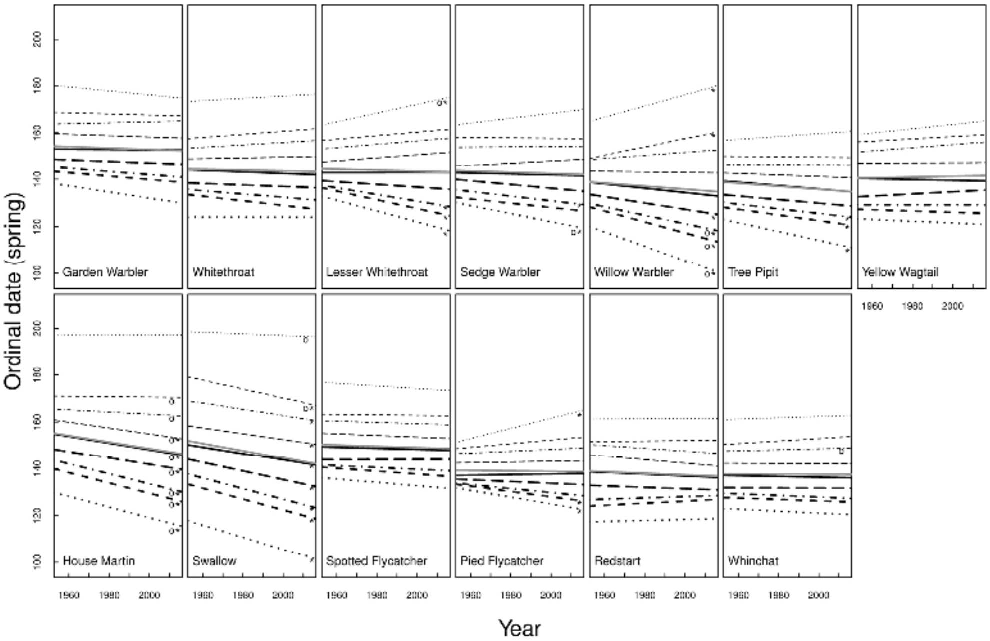

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Fig. 1

197x133mm (300 x 300 DPI)

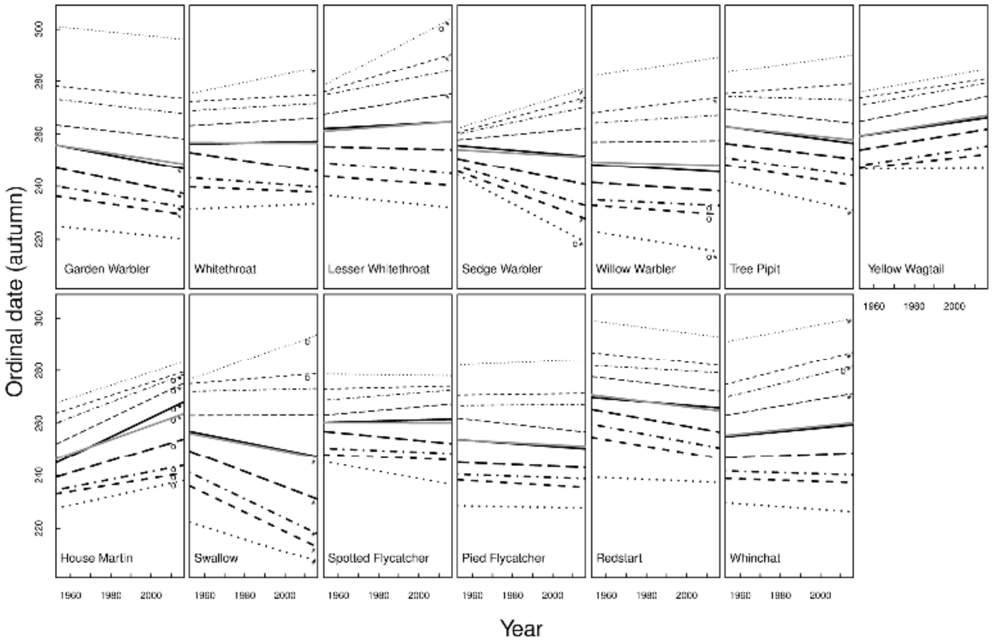

Fig. 2 Summary of modelled autumn migration phenology across 60 years (1955-2014) for 13 species of trans-Saharan migrant bird, measured using ten metrics for each species. Lines represent linear regressions of each metric on year. Metrics are first date (bold dotted line), 5th percentile date (bold 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

197x133mm (300 x 300 DPI)

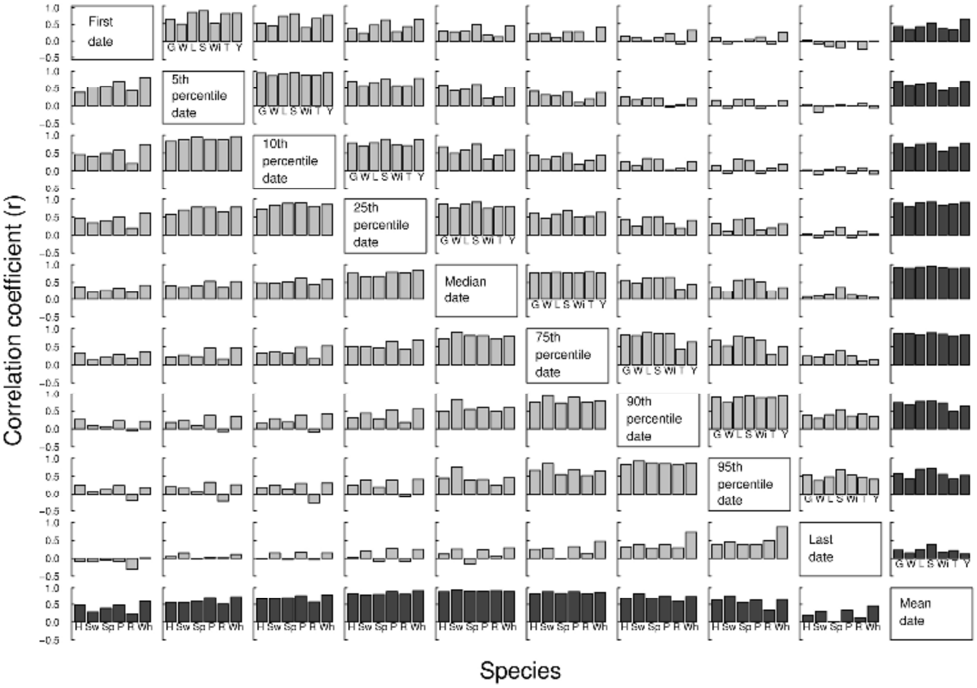

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Fig. 3

197x140mm (300 x 300 DPI)

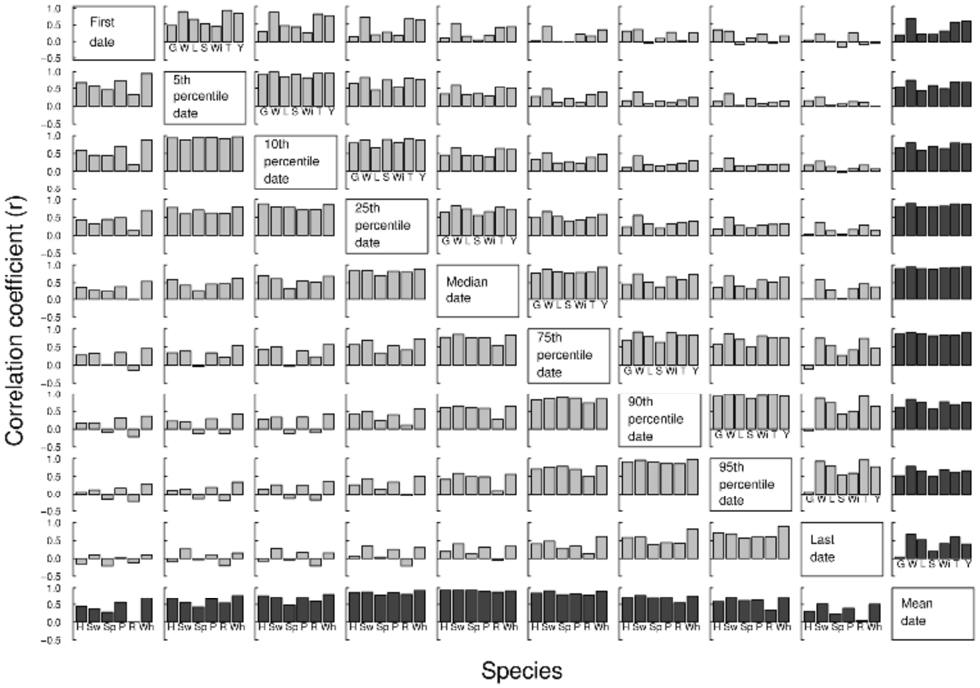

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Fig. 4

197x140mm (300 x 300 DPI)

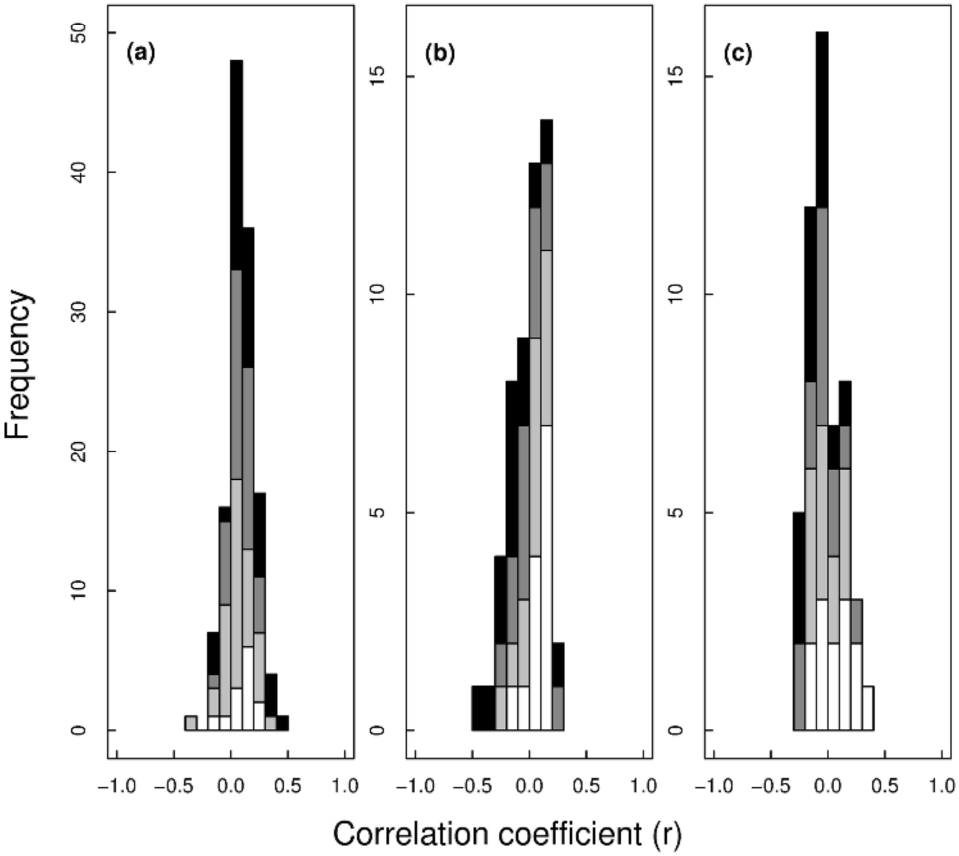

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Fig. 5

168x161mm (300 x 300 DPI)