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Pre-Print Version

Quantifying the robustness of first arrival dates as a measure of avian migratory phenology

Summary

As the climate changes, many long-term studies have shown that the timing of bird migration is shifting, increasing the need for reliable measures of migratory phenology. Ideally, daily counts of birds at a site are used to calculate the Mean Arrival Date (MAD) but, as this approach is not always possible and is very labour-intensive, simpler metrics such as First Arrival Date (FAD) have commonly been used. Here, we examine the relationship between FAD and MAD in 31 summer migrant bird species over a 42-year period at Portland Bird Observatory, UK. While significant correlations between FAD and MAD were detected, relationships were weak (particularly in long-distance migrants) and no clear patterns in the FAD-MAD relationship were apparent within taxonomic groups: we conclude that First Arrival Date is a poor metric of migratory phenology, and that Mean Arrival Date is preferred wherever possible.

Introduction

Recent climatic change has led to increasing interest in avian phenology (Rubolini *et al*., 2007). Studies of breeding phenology have shown advances in egg laying for many species (Crick and Sparks, 1999; Dunn and Winkler, 1999). Climatic change can also affect migration phenology and there is some evidence that migrants are arriving earlier at breeding grounds (e.g. Sokolov *et al*., 1998; Gordo, 2007; Rubolini *et al*., 2007). This is true particularly for short-distance migrants, which usually display greater adaptability to temperature changes at breeding grounds than do long-distance migrants (Tryjanowski *et al*., 2002; Butler, 2003; Lehikoinen *et al*., 2004; Tøttrup *et al*., 2006). Phenological change (or lack of change) in part of the annual cycle can affect scheduling of other seasonal activities; for example, migratory phenological inertia can constrain adjustment of breeding phenology (Both and Visser, 2001; Goodenough *et al*., 2010a).

Most avian phenological research uses long-term datasets, for example, from longitudinal research projects (Both and Visser 2001), national surveys (Crick and Sparks, 1999), long-term site records, (Goodenough *et al*., 2010b) and bird observatories (Browne and Aebischer, 2003). However, whilst research on breeding phenology typically uses lay dates from multiple clutches per year, the most common metric of migration phenology is first arrival dates (FADs) – the date when the first individual of a given species is observed (Lehikoinen *et al*., 2004). FADs have a long history (e.g. White, 1789) and provide an easily discernible phenological measure. However, because FADs are based on just one record per year, they are sensitive to misidentifications and outliers. By contrast, mean arrival dates (MADs), which are based upon arrival dates of multiple individuals should provide a more robust and accurate phenological measure that is less sensitive to misidentification or outlier bias (Lehikoinen *et al*., 2004).

Calculation of MADs is only possible when arrival dates of multiple individuals are known for a particular site or when birds are on passage (e.g. data from bird observatories). Accordingly, whilst numerous studies use FADs to examine migration phenology (e.g. Crick and Sparks 1999; Butler 2003; Cotton 2003; Sparks *et al*., 2007; Goodenough 2010a), there has been little consideration of how well FADs actually correlate with MADs, such that their robustness as a proxy for migratory phenology is uncertain. The only direct analysis was undertaken by Sparks *et al*. (2005), which indicated FADs and MADs correlated only weakly. However, as analysis was based on three species over a short period, the generality of this pattern is unclear. An indirect analysis, undertaken by Tøttrup *et al*. (2006), found that species usually showed similar temporal change over a given time period regardless of whether FAD or MAD was correlated against year, but, importantly, that change magnitude often differed. No FAD-MAD correlations were reported. More generally, in analyses of simulated data, Moussus *et al*. (2010) found phenological measures of first appearance/arrival highly inaccurate and concluded that their use in scientific research might generate erroneous results.

Here, we examine migration phenology using data collected by Portland Bird Observatory, UK. We quantify the strength of the relationship between FADs and MADs for 31 species over a 42-year period and examine whether life-history traits or population demographics affect the strength of the FAD-MAD relationship. Finally, we discuss whether FADs are a robust proxy for MADs and a suitable metric for timing of migration in phenological research.

Methods

Portland Bird Observatory (PBO) is situated at the southern tip of the Isle of Portland, Dorset, UK (50.55°N, 2.44°W) . Daily bird counts have been undertaken and recorded in paper-based logs (number of individuals per species per day) since PBO became an active observatory in 1961.

Daily count data for 31 summer migrants were digitized for 1970-2011, giving 42 consecutive years of reliable data for spring migration (26,871 daily records covering 330,430 individual birds). Species recorded as presence-only or in abundance categories were excluded, as were rarer species (<100 records or seen in <30% of years). Although records were held, for some species, for 1961-1969, these were not used since: (1) data were usually presence-only or estimated with no record of estimate confidence; and (2) there was little substantive change in sample effort in 1970-2011 whereas effort in 1961-1969 was both lower and more variable. Discarding pre-1970 data also followed the recommendation for long-term phenological studies (Rubolini *et al*. 2007) given that most contemporary climatic change has occurred since 1970 (Griggs and Noguer, 2002). For terrestrial species, data combined ringing records and daily sightings of non-captured individuals. For seabirds, data came from estimated sea passage counts. Spring arrival period was defined as 1st March to 31st May as per Sokolov *et al*. (1998), Cotton (2003) and van Buskirk *et al*. (2009). This was necessary to avoid autumn migration records or occasional over-wintering birds skewing the data. For each species, arrival dates were converted to an ordinal scale whereby 1 = 1st Jan with leap years accounted for as necessary (non-leap-years days 60-151; leap years days 61-152). FADs and MADs were calculated for each species in each year.

Birds were classified as per British Ornithologists' Union (2006) taxonomy: gulls/terns (Charadriiformes), birds of prey (Strigiformes/Falconiformes) and songbirds (Passeriformes). Songbirds were subdivided into family: warblers (Sylviidae), thrushes (Turdidae), flycatchers (Muscicapidae), pipits/wagtails (Moracillidae) and buntings (Emberizidae). Migration strategy was classified as short-distance (non sub-Saharan) or long-distance (sub-Saharan) (Table 1). Because life-history strategy could affect migratory phenology, the position of each species on the r/K strategist continuum was quantified by running a Principal Components Analysis on four key correlates of r/K strategy identified by Pianka (1970): (1) lifespan; (2) adult weight; (3) broods per year; (4) clutch size (data from BTO BirdFacts and Birdguides 2009). Finally, because population size can affect migratory phenology, and potentially the accuracy with which it can be recorded (Tryjanowski *et al*., 2005; Sparks *et al*., 2007), the average number of individuals of each species to pass through PBO per year was quantified.

For each species, MAD was regressed against FAD to produce 31 significance values and 31 regression coefficients. The sample size for each analysis was the number of years for which there was data. Fisher's exact tests were used to determine if there was an association between the number of species with statistically significant FAD-MAD relationships and either (1) migration strategy or (2) taxonomic group.

To establish whether any life-history or population demographics explained significant variation in the strength of the FAD-MAD relationship (rather than simply whether relationships were statistically significant), a new estimated dependent variable (EDV) was created using the regression coefficients generated from the species-specific regressions of FAD and MAD. The EDV was regressed against the species traits discussed above (taxonomic group, migration strategy and r/k strategy, PBO population size) using stepwise Multiple Linear Regression. Undertaking regression on an EDV generated using outcomes of previous analyses is statistically valid (Borjas 1982, Lewis & Linzer 2005). The approach is ideally suited to identifying factors influencing relationships between variables (as here) rather than the variables themselves (Gelman 2005; Jusko & Shively 2005) and has been used previously to analyze avian phenology (Tryjanowski *et al*., 2005; Goodenough *et al*., 2009). All MLR assumptions (normality, homoscedasticity, orthogonality) were met and the case:variable ratio exceeded 3:1 (Tabachnick and Fidel 1989). Stepwise criteria were as per Field (2000): entry $\alpha = 0.05$; subsequent removal $\alpha = 0.10$.

Finally, to establish whether there was any link between the strength of the FAD-MAD relationship and phenology itself, two bivariate regression analyses were undertaken. To test whether the reliability of FAD as a proxy of MAD differed for early- or late-arriving species, the EDV was regressed against average MAD. Then to test whether FADs and MADs were better correlated in species with a bunched arrival date distribution or a dispersed arrival date distribution, the EDV was regressed against the number of days between average FAD and average MAD. These analyses were undertaken separately due to high colinearity between the independent variables. All analyses were undertaken using SPSS v.19 or GraphPad 2013.

Results

There was considerable variability in FADs and MADs between species and between years. The overall (non-year specific) mean values for each species are shown in Table 1, together with annual variability (standard deviations calculated from annual data). FADs were generally more variable than MADs (5 species; 16.1%) or variability was similar (24 species; 77.4%). Only for two species, Grey Wagtail (*Motacilla cinerea*) and Stonechat (*Saxicola rubicola*), were MADs more variable than FADs. The lag between FAD and MAD differed from 7 days for Black Tern (*Chlidonias niger*) and Little Tern (*Sternula albifrons*) to 36 days for Chiffchaff (*Phylloscopus collybita*) (Table 1). This was due to arrival of individuals being clustered for some species and highly variable in others (see Appendix 1 for illustrative figure). Of the 31 species analysed, 24 (77.4%) showed a significant ($P < 0.05$) positive relationship between FAD and MAD. However, model fit was generally low with FADs explaining just 23.4% of variability in MAD on average. FADs explained >50% of variability in MAD in only four species (12.9%): Mediterranean Gull (*Ichthyaetus melanocephalus*), Short-eared Owl (*Asio flammeus*), Nightingale (*Luscinia megarhynchos*) and Stonechat (*Saxicola rubicola*) (Table 1).

There were significant positive relationships between FAD and MAD in all taxonomic groups (Fig. 1) and the number of significant relationships was not associated with taxonomy (Fisher's exact test: $P = 0.546$). However, there was an association between the number of significant FAD-MAD relationships and migration strategy, with more significant relationships for short-distance migrants (100%) compared to long-distance migrants (65%) (Fisher's exact test: $P = 0.030$).

When considering the strength of the FAD-MAD relationship in relation to species traits, migration strategy was important (stepwise regression analysis: $F_{1,29} = 6.558$, $R^2 = 0.190$, $P = 0.016$). This was because the FAD-MAD relationship was much stronger for short-distance migrants (Fig. 1). No other species-specific trait (taxonomy, r-K strategy, PBO population size) was significant. However, there was a negative relationship between average MAD and the strength of the correlation between FAD and MAD ($F_{1,29} = 4.882$, $R^2 = 0.144$, $P = 0.035$; Fig. 2a), such that FAD was a better proxy for MAD in early-arriving species. This was likely driven by short-distance migrants tending to arrive earlier than long-distance migrants (short-distance migrants mean MAD 11 April ± 13 days SD; long-distance migrants mean MAD 28 April ± 10 days SD; independent t-test: t = 2.345, d.f = 29, P = 0.026). There was also a significant negative relationship between the number of days lag between average FAD and average MAD and the strength of the FAD-MAD relationship ($F_{1,29}$ = 4.902, R^2 = 0.145; P = 0.035; Fig. 2b), such that FAD was a better proxy for species with a clustered arrival date distribution compared to those with a dispersed distribution (see Appendix 1 for illustrative figure). Lag did not differ significantly according to migratory strategy (independent t-test t = -0.449, d.f. = 29, P = 0.657).

Discussion

This study of the metrics of migration phenology has demonstrated that significant relationships between First Arrival Dates (FADs) and Mean Arrival Dates (MADs) occur for most species but are usually weak (FAD typically explaining <50% of variability in MAD). Accordingly, although they might be correlated, FAD is generally a poor proxy for the preferable MAD. This agrees with work on simulated data (Moussus *et al*., 2010), which found first arrival/emergence dates to be a poor measure of overall phenology and suggests that the weak FAD-MAD correlations quantified previously for three species – Pied Flycatcher, Willow Warbler and Chiffchaff – is typical (Sparks *et al*., 2005). This is probably because FADs are based on just one record per species per year and are highly variable. It is possible, indeed likely, that the earliest bird (an outlier by definition) might respond differently to external stimuli than the population norm. There is no simple relationship between taxonomy and FAD-MAD relationships.

The number of significant relationships between FAD and MAD is higher for short-distance migrants than for long-distance migrants. Migration strategy also affects the strength of the FAD-MAD relationship, with stronger relationships for short-distance (early-arriving) migrants than for long-distance (late-arriving) migrants. This makes intuitive sense, since there is likely to be less inter-individual variation in migratory schedules for short-distance migrants. Accordingly, the first individual is generally not as much of an outlier relative to the mean as in long-distance migrants (for whom individually-variable stop-over strategies might add further complexity). Moreover, short-distance migrants typically winter in a more spatially restricted area (e.g. part of the Mediterranean) compared to long-distance migrants (large parts of sub-Saharan Africa). This raises the possibility that, for long-distance species, the individuals coming through a single bird observatory represent many different populations at different wintering sites with different migratory schedules (as speculated previously for certain species – e.g. pied flycatcher: Hope-Jones *et al*., 1977). If this is true, the first individual (and thus FAD) might be representative of MAD for the individuals from that one wintering site, but not the MAD for the overall species. Differences in temperatures along different migratory routes might also be important (Ahola *et al*., 2004) and there is more potential for this in long-distance migrants. It should also be noted that short-distance migrants are generally tracking climate change better (Tryjanowski *et al*., 2002; Butler, 2003; Cotton, 2003; Lehikoinen *et al*., 2004; Tøttrup *et al*., 2006). This consistent change due to directional selection could tighten the FAD-MAD relationship for short-distance migrants whereas differential change at the level of the individual could weaken links FAD-MAD links for long-distance migrants (as seen previously for breeding phenology: Goodenough *et al*., 2011).

The relationship between FAD and MAD was better for species that had a clustered arrival distribution (short lag between FAD and MAD). This was not driven by migratory strategy (i.e. some short-distance migrants had widely-spread arrival distributions while some long-distance migrants had clustered distributions). Again, this makes intuitive sense given that birds with clustered distributions, and less arrival date variability, have less potential for de-coupling of FADs and MADs.

Interestingly, although past studies (e.g. Tryjanowski *et al*., 2005; Sparks *et al*., 2007) have suggested that FAD might be an especially weak migratory phenology proxy for species with small populations (since it is then harder to record the first bird reliably), population size was not related to the strength of the FAD-MAD relationship in this study. This could be due to the consistent observer effort for all species in a bird observatory situation (Sparks *et al*., 2007).

In conclusion, MADs should be used in preference to FADs wherever possible, and especially for long-distance migrants or species with wide arrival date distributions. When migratory phenology is considered for birds on passage (e.g. data from bird observatories) daily count data can and should be used to calculate MADs. For studies on breeding grounds, quantifying MADs is undeniably challenging, but it is possible for the majority of species using a combination of mapped bird censuses and song-based census indices. Where this is not feasible, or sampling effort is prohibitive, it might at least be possible to quantify the date by which, say, the first 10% of birds arrive, thereby reducing the effect of abnormally early individuals.

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Table 1. Phenology of 31 migrant species passing through Portland Bird Observatory, UK, (1979-2911) showing First Arrival Date (FAD), Mean Arrival Date (MAD) and the relationship between these parameters. Significant relationships ($P < 0.05$) are bolded, as are R^2 values >0.5. Species order follows British Ornithologists' Union (2006).

SPECIES	Migratory strategy	Average FAD ± annual SD	Average MAD ± annual SD	Lag FAD to MAD (days)	FAD-MAD Correlation	
					P value	R^2 value
Mediterranean Gull	Short	19 Mar ± 15	5 Apr ± 20	17	**<0.001**	**0.525**
Sandwich Tern	Long	22 Mar ± 04	21 Apr ± 08	30	0.567	0.008
Common Tern	Long	15 Apr ± 06	4 May ± 14	19	**0.047**	0.108
Arctic Tern	Long	1 Apr ± 12	3 May ± 16	32	**<0.001**	0.406
Little Tern	Long	27 Apr ± 08	4 May ± 08	7	**<0.001**	0.449
Black Tern	Long	28 Apr ± 07	6 May ± 08	7	**0.013**	0.153
Merlin	Short	14 Mar ± 11	4 Apr ± 21	21	**<0.001**	0.450
Hobby	Long	22 Apr ± 05	8 May ± 09	16	**0.001**	0.272
Short-eared Owl	Short	4 Apr ± 13	17 Apr ± 18	13	**<0.001**	**0.532**
Grasshopper Warbler	Long	12 Apr ± 04	17 Apr ± 06	13	**0.002**	0.211
Sedge Warbler	Long	15 Apr ± 04	6 May ± 06	21	0.849	0.001
Reed Warbler	Long	22 Apr ± 04	15 May ± 06	23	**0.031**	0.111
Willow Warbler	Long	30 Mar ± 05	24 Apr ± 06	25	**0.023**	0.122
Chiffchaff	Short	9 Mar ± 05	14 Apr ± 07	36	**0.021**	0.126
Wood Warbler	Long	9 Apr ± 09	27 Apr ± 09	18	**<0.001**	0.305
Blackcap	Short	24 Mar ± 05	24 Apr ± 10	32	**0.001**	0.243
Garden Warbler	Long	20 Apr ± 04	8 May ± 06	18	0.689	0.004
Lesser Whitethroat	Short	22 Apr ± 05	5 May ± 05	13	**<0.001**	0.302
Ring Ouzel	Short	28 Mar ± 06	13 Apr ± 08	16	**0.033**	0.109
Nightingale	Long	14 Apr ± 07	28 Apr ± 08	14	**<0.001**	**0.677**
Black Redstart	Long	10 Mar ± 07	4 Apr ± 08	25	**<0.001**	0.311
Redstart	Short	3 Apr ± 05	26 Apr ± 07	23	**0.014**	0.142
Whinchat	Long	17 Apr ± 04	5 May ± 05	18	0.312	0.025
Stonechat	Short	10 Mar ± 13	23 Mar ± 04	13	**0.034**	**0.516**
Wheatear	Long	11 Mar ± 05	15 Apr ± 05	35	0.078	0.076
Spotted Flycatcher	Long	27 Apr ± 03	16 May ± 07	19	0.169	0.047
Pied Flycatcher	Long	15 Apr ± 05	27 Apr ± 07	12	**0.006**	0.174

Yellow Wagtail	Long	5 Apr ± 04	30 Apr ± 06	25	0.312	0.026
Grey Wagtail	Short	15 Mar ± 16	31 Mar ± 13	16	**<0.001**	0.473
Tree Pipit	Long	4 Apr ± 04	25 Apr ± 06	21	**0.007**	0.167
Reed Bunting	Short	15 Mar ± 10	31 Mar ± 10	16	**0.015**	0.142

Figure 1. The strength of the relationship between First Arrival Date (FAD) and Mean Arrival Date (MAD) quantified using species-specific regressions (n=31 species). The mean coefficient of determination (R^2) and mean significances values are shown in relation to (a, c) migratory strategy and (b, d) taxonomic group. Error bars show standard error and have been calculated where possible.

Figure 2. The strength of the relationship between First Arrival Date (FAD) and Mean Arrival Date (MAD) quantified using the correlation coefficient from species-specific regressions (n=31 species) plotted against: (a) arrival time (mean MAD); and (b) the lag between mean FAD and mean MAD (number of days).

Figure 1

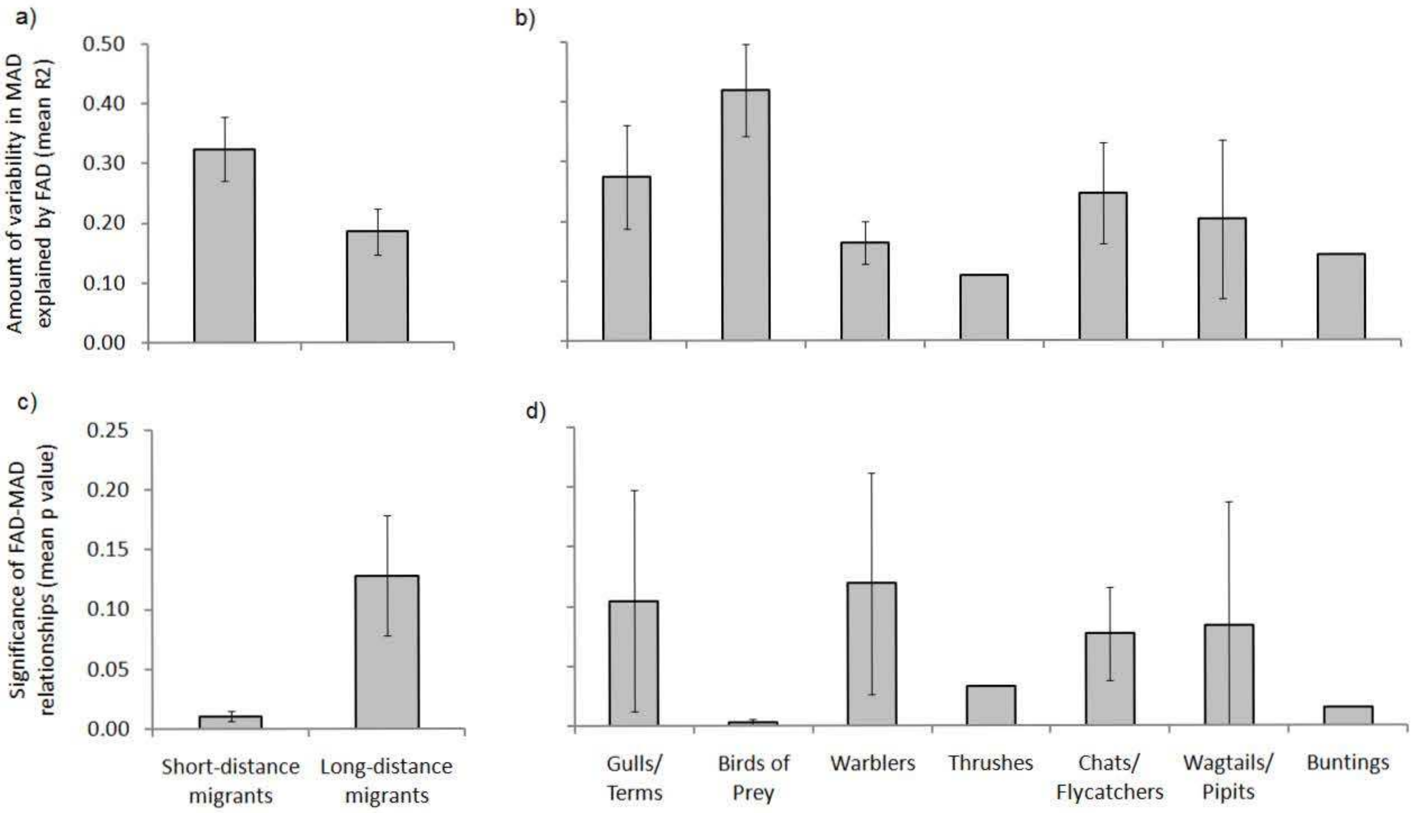
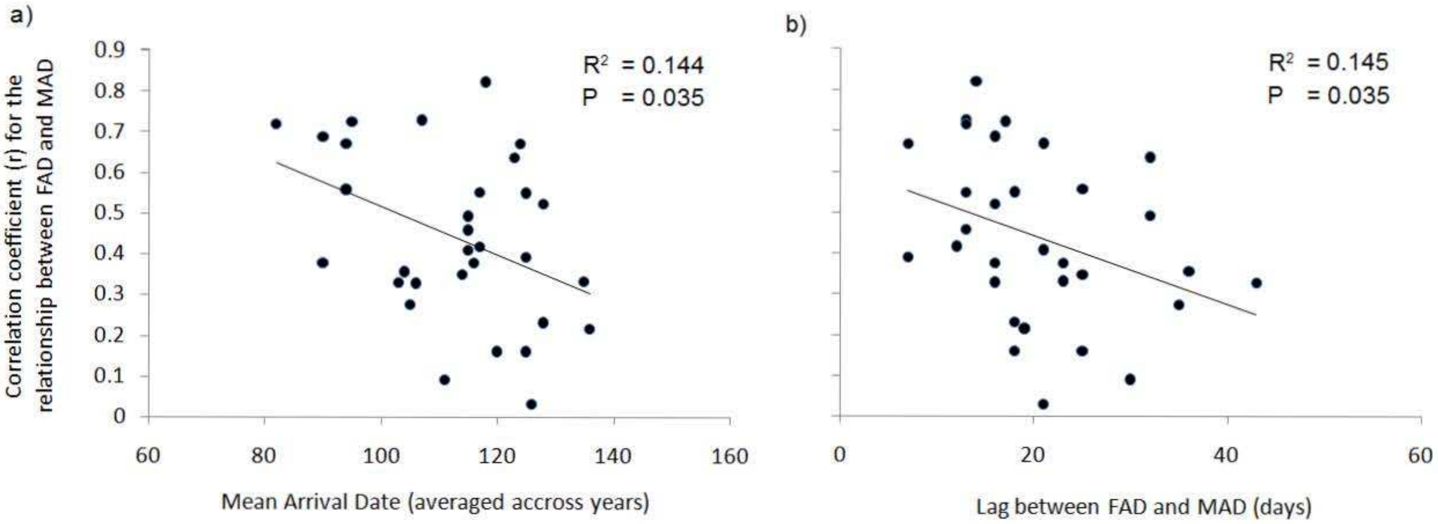

a)
b)
c)
d)
Amount of variability in MAD explained by FAD (mean R2)
0.50
0.40
0.30
0.20
0.10
0.00
Significance of FAD-MAD relationships (mean p value)
0.25
0.20
0.15
0.10
0.05
0.00
Short-distance migrants
Long-distance migrants
Gulls/ Terms
Birds of Prey
Warblers
Thrushes
Chats/ Flycatchers
Wagtails/ Pipits
Buntings

Figure 2


a)
Correlation coefficient (r) for the relationship between FAD and MAD
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
60
80
100
120
140
160
Mean Arrival Date (averaged accross years)
R² = 0.144
P = 0.035
b)
0
20
40
60
Lag between FAD and MAD (days)
R² = 0.145
P = 0.035