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Contrasting temporal changes in lay date distributions in co-occurring Blue and Great Tits

Suggested running title: Lay date distributions

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Capsule: Phenological change differs in co-occurring populations of Blue Tits (adaptive advancement in mean First Egg Date (FED) throughout the population) and Great Tits (increasing variance of FED, with some individuals laying earlier but others laying later and becoming maladapted).

Recent interest in phenology has prompted numerous studies into temporal changes in the timing of avian reproduction, usually using First Egg Dates (FEDs) as the phenological measure (see review by Crick 2004). Such research tends to focus on the relationship between year and the average timing of breeding, typically regressing multiple FEDs (e.g. Dunn & Winkler 1999) or mean annual FEDs (e.g. Both *et al.* 2004) against year. This has shown that 37% of British species advanced their lay date between 1971 and 1995 (Crick *et al.* 1997), while over 50% showed advancement over the period 1939-1995 (Crick & Sparks 1999). Consideration of temporal change in lay date distribution parameters other than just the mean, for example variability and skewness, would offer insight into within-population phenological changes. However, although such changes might be crucial in terms of evolution, this is a topic that we know little about (Laaksonen *et al.* 2006). There have been a few studies comparing between-year phenological variability in different populations (e.g. Testka 2004; Menzel *et al.* 2006) but we could only locate two comparing temporal trends in within-year phenological variability for the same population, for birds or any other taxa (Winkler *et al.* (2002) on Tree Swallows *Tachycineta bicolor* in America and Laaksonen *et al.* (2006) on Pied Flycatchers *Ficedula hypoleuca* in Finland).

In many avian datasets, analysing phenological variability is problematic as few nests are found early enough for the FED to be known with certainty, such that studies often necessarily use the mid-point between the earliest and latest possible FEDs, reducing accuracy to ± 5 days (Baillie *et al.* 2007). Use of the mid-point is likely to reduce within-year variability in complex and unclear ways. At the very least, outliers (first and last FEDs) might not be encapsulated within the dataset and skewness may be affected by all dates being set to the midpoint. This means that while national data might be sufficient for studying mean change, they are not necessarily ideal for analysis of trends in variability. Moreover, national or multi-site analyses do not usually account for second breeding attempts, the influence of temporally-changing site-specific factors, or unequal photoperiod and warming at different sites (Crick & Sparks 1999); all factors that can influence FED variability (Lambrechts *et al.* 1997; Visser *et al.* 2003). Although recent studies into individual-level phenotypic plasticity in FED have provided valuable insights into relative adaptability of specific individuals (e.g. Nussey *et al.* 2005; Charmentier *et al.* 2008), these have been undertaken without reference to changes in underlying lay date distributions, or, in many cases, selection for early laying. Further analysis of FED variability and skewness would be useful to determine whether these change temporally, and, if so, if they co-vary with change in mean FEDs.

Here, we study change in annual mean FEDs, as well as variability and skewness, for two co-occurring parid species (Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major*) and relate findings to selection for early laying and local spring temperature. We also test for temporal changes in FED kurtosis and modality parameters, apparently for the first time. Our study was based at Nagshead Nature Reserve (Gloucestershire, UK, 2°34'0"W,

51°47'0"N.), a 308 ha woodland dominated by Pedunculate Oak *Quercus robur*. The Royal Society for the Protection of Birds (RSPB) manage the site and provide nestboxes in super-abundance (about 28% of boxes remain unused each year). The site is subject to increasing spring temperatures (mean of March, April and May temperatures combined: $r = 0.601$, $n = 31$, $P < 0.001$; annual increase = 0.067°C ; Goodenough et al. 2010).

Nest data were obtained from the RSPB for the years 1990 to 2004 (excluding 2001 when monitoring was prohibited due to Foot and Mouth Disease). FEDs were calculated as per Perrins & McCleery (1989) (1 = 1st April). To avoid spatial factors confounding analyses, only data from the 295 standard nestboxes that were in the same position throughout the study period were analysed. The populations were not double brooded but likely re-lay records (second breeding attempts after initial failure) were excluded and although it remains possible that unidentified re-lay records could be included in analysis, this would have only a very limited effect given the very low numbers involved. The final sample sizes were 1,495 Blue Tit nests and 490 Great Tit nests.

Regression was used to establish temporal change in mean FEDs and within-year variation (standard deviation; SD) for both species. Regression was weighted by the number of nest records to prevent annually-variable sample sizes affecting analysis (especially for Blue Tits where sample size and year were positively correlated). Lay date distribution parameters were also quantified to examine temporal change in: (1) kurtosis (distributions becoming more platykurtic (flattened) or leptokurtic (peaked)); (2) skewness; and (3) modality (becoming more bi- or multi-modal). The first possibly was tested by regressing kurtosis values against year. The second possibly was tested initially by examining Fisher's skewness values (g_1), which were standardised to create z-scores by dividing skewness by the standard error of skewness (Field 2000). As skewness can be strongly influenced by a single outlier (Brys et al. 2004), tendencies for (positive) skew were confirmed by regressing the percentage of birds initiating clutches within the first 10% of the total FED range in each specific year, against year itself. This prevented one or two very early nests in given years biasing results and causing a type II error, making our analysis more robust. The third possibility, of increasingly bi- or multi-modal distributions, was tested using annual Hartigan's dip test statistics (Hartigan & Hartigan 1985) regressed against year. As it was not possible to use dip statistics directly (as these are dependent on sample size, which varied in different years), a bootstrapped dip test statistic was calculated in R (version 2.9.0) using 10,000 test iterations per year. In order to obtain sufficient samples, each iteration used a random subset of 15 nests (below the lowest sample size of 20 nests to ensure that there was variation in dip test bootstrap calculations in all years). A positive correlation between annual dip test scores (now sample size independent) and year would indicate an increasing tendency to bi- or multi-modality.

The strength of selection for early laying on the basis of breeding success was quantified for each species using standardised annual selection differentials. The differentials were calculated using the mean lay date weighted by the number of offspring to fledge from each nest, divided by the standard deviation of lay date (Falconer and MacKay 1996). Fledging numbers were used as the weighting parameter in the absence of recruitment data in this unringed population; an approach used in previous research (e.g. Ahola et al. 2009; Smallegange et al. 2010).

The overall (i.e. non year-specific) mean lay date for Blue Tits across the 15-year study period was 2nd May; four days earlier than for Great Tits on 6th May, but there was substantial overlap in laying periods in each year. Selection differentials were negative (i.e. favouring early laying rather than late laying) in all years (Blue Tit = -5.36 mean \pm 1.16 SD; Great Tit = -5.24 mean \pm 1.25 SD) (although note that these were calculated using fledging numbers, not recruits, such that first-year offspring survival was not accounted for).

Mean FED advanced for Blue Tits by five days between 1990 and 2004 ($F_{1,12} = 20.067$, $P = 0.001$; Fig. 1a), a relationship that was unchanged when the very early mean lay date in 2002 was removed. There was no temporal change in mean FED for Great Tits ($F_{1,12} = 0.023$, $P = 0.882$; Fig. 1b); removal of the 2002 outlier did not alter this result. Within-year variability in FEDs did not change for Blue Tits ($F_{1,12} = 2.065$, $P = 0.176$; Fig. 1c) but there was a significant increase over time for Great Tits ($F_{1,12} = 6.405$, $P = 0.026$; Fig. 1d). This was strengthened when one extreme outlier (in 1996), which was over seven standard deviations from the mean, was removed ($F_{1,11} = 10.433$, $P = 0.008$). For Great Tits, increasing variability in FEDs occurred, in the absence of change in the mean, because distributions became significantly more positively skewed over time ($F_{1,12} = 6.106$, $P = 0.029$; Fig. 1f). This suggested that a greater proportion of individuals were laying earlier but that other individuals appeared to be laying later relative to the mean in later years, such that the right-hand tail of the lay date distribution increased over time (thereby explaining the lack of change in the mean). This was reinforced by a significant increase in the percentage of birds initiating clutches within the first 10% of the total lay date range in that year (percentage in 1990 = 14%; percentage 2004 = 34%; $F_{1,12} = 9.544$, $P = 0.009$; Fig. 1h) and a borderline significant increase in the FED of the latest nest ($F_{1,12} = 4.389$, $P = 0.058$; Fig. 1j), suggesting that the end of the breeding season was pushed back in later years. There was no change in either measure of skewness for Blue Tits (Fig. 1e and g), as was expected given the advancement of mean FED and lack of change in variability, but the FED of the latest nest decreased ($F_{1,12} = 6.960$, $P = 0.022$; Fig. 1i). The smaller skewness values, on average, for Great Tits compared to Blue Tits is unlikely to be due to the smaller sample sizes involved as randomly selecting a subset of Blue Tit nest records (to mirror Great Tit sample sizes) gave results that were very similar to those obtained using the full nest record dataset. There was no evidence that the FEDs of either Blue or Great Tits were becoming increasingly platykurtic or bimodal as kurtosis values and dip test values, respectively, did not change significantly over time ($P > 0.565$ in all cases; graphs not shown).

Advancement of lay date for Blue Tits is due to consistent change at an individual level across the majority of individuals in the population. Given the strongly negative selection for early laying in this population, this would appear to be adaptive as it probably allows retention of synchrony with caterpillar food supplies (Cresswell & McCleery 2003). The magnitude of temporal change in Blue Tit phenology at our site is a reflection of the national trend for this species (Baillie *et al.* 2007). The absence of change in the mean FED of Great Tits is contrary to the change seen in other UK populations (e.g. Wytham Woods; Charmantier *et al.* 2008) and nationally (Baillie *et al.* 2007), but is certainly not unusual. Indeed, 8/13 populations studies across Europe between 1979 and 1998 did not show significant advancement in mean FEDs (Visser *et al.* 2003), while Sanz (2002) also found between-site differences in temporal lay date changes species.

The increased FED variability for Great Tits is evidence that the breeding season is becoming more protracted in more recent (warmer) years, something that is contrary to the absence of change in lay date variability in migratory Pied Flycatchers in areas of increasing temperature (Laaksonen *et al.* 2006). This trend is a result of some individuals laying earlier (both in absolute terms and relative to the mean), but others laying later in relation to the rest of the population. Thus differential phenological change is occurring between individuals in a given year. This supports work done on lifetime inter-individual variability in the plasticity of FED for Great Tits in The Netherlands (Nussey *et al.* 2005). As at our study site, this is occurring without phenological change being observable at a population level (Visser *et al.* 2003).

As early laying typically constitutes a fitness advantage, there must be a fundamental reason why Great Tits are not advancing their lay dates *en masse* in a similar way to the sympatric Blue Tit population, especially given that selection consistently favours early FEDs and local temperatures are warming. One possible explanation is that a shortage of food prevents some females laying early in the season, such that plasticity of FED is constrained in some cases. That some females can obtain sufficient food to begin their clutch before others is likely to reflect individual fitness and foraging skills (Perrins 1996), together with their age, dominance and experience. However, unless competition for maternal food is intense, this would only explain why some individuals lay early and not why others are laying later, both relative to the mean (increase in variability) and in absolute terms (end of the breeding season being delayed in more recent years). The possibility that individuals that are unable to lay early strategically delay breeding to reduce competition for offspring food is improbable; birds are unlikely to be able to predict competition for food some four weeks after clutches are started. Instead, the increasing incidence of laying late (absolutely and relative to the mean) in Great Tits, taken in tandem with the strong selection to lay early, suggests that some individuals are becoming increasingly maladapted. If this is the case, it would seem to stem directly from individual failure to maintain synchronicity with environmental cues (Cresswell & McCleery 2003), since increased competition for nest sites early in the breeding season, a potential indirect cause of maladaptation (Dunn & Winkler 1999), is unlikely given that the study population is not nest site limited. It should, however, be noted that temporal change in the population structure might be occurring; for example, the presence of fewer young – typically late-laying – birds in later years might have resulted in increasing positive skew in the lay date distribution. This cannot be tested directly as the Great Tit population is not ringed. However, this probability seems unlikely since again it would only explain why more individuals are laying early, not why other individuals are laying later.

In summary, analysis of a comparatively short data time-series has shown that mean FEDs are changing (temporal advancement) for Blue Tits, while the FEDs of co-occurring Great Tits are only changing in terms of variance and positive skew (temporal increases). These species-specific trends are all the more interesting as the species are closely related and ecologically similar. This study thus underlines the need to consider variability and skewness when analysing temporal phenological patterns; something that is particularly relevant for research into climate change effects. Restricting analysis to quantification of mean trends does not allow for differential change between individuals and can mask temporal patterns that are important in terms of evolutionary ecology.

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Figure 1 – Temporal change in lay date parameters for Blue and Great Tits. Trend lines show significant or borderline significant relationships at α 0.05. Outliers discussed in the Results are shown using open circles.

