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**Goodenough, Anne E ORCID logoORCID: <https://orcid.org/0000-0002-7662-6670>, Hart, Adam G ORCID logoORCID: <https://orcid.org/0000-0002-4795-9986> and Elliot, Simon L (2010) What prevents phenological adjustment to climate change in migrant bird species? Evidence against the “arrival constraint” hypothesis. *International Journal of Biometeorology*, 55 (1). pp. 97-102. doi:10.1007/s00484-010-0312-6**

Official URL: <http://dx.doi.org/10.1007/s00484-010-0312-6>

DOI: <http://dx.doi.org/10.1007/s00484-010-0312-6>

EPrint URI: <https://eprints.glos.ac.uk/id/eprint/3341>

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**Goodenough, Anne E and Hart, Adam G and Elliot, Simon L (2010). *What prevents phenological adjustment to climate change in migrant bird species? Evidence against the “arrival constraint” hypothesis*. International Journal of Biometeorology, 55 (1), 97-102. ISSN 0020-7128**

Published in International Journal of Biometeorology, and available online at:

<http://link.springer.com/article/10.1007%2Fs00484-010-0312-6>

We recommend you cite the published (post-print) version.

The URL for the published version is: <http://dx.doi.org/10.1007/s00484-010-0312-6>

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# **What prevents phenological adjustment to climate change in migrant bird species? Evidence against the “arrival constraint” hypothesis**

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Short title: Phenological adjustment in migrant birds

## Summary

Phenological studies have demonstrated changes in the timing of seasonal events across multiple taxonomic groups as the climate warms. Some northern European migrant bird populations, however, show little or no significant change in breeding phenology, resulting in synchrony with key food sources becoming mismatched. This phenological inertia has often been ascribed to migration constraints (i.e. arrival date at breeding grounds preventing earlier laying). This has been based primarily on research in The Netherlands and Germany where time between arrival and breeding is short (often as few as nine days). Here, we test the arrival constraint hypothesis over a fifteen year period for a U.K. pied flycatcher (*Ficedula hypoleuca*) population where lay date is not constrained by arrival as the period between arrival and breeding is substantial and consistent (average 27 days  $\pm$  4.57 days SD). Despite increasing spring temperatures and quantifiably stronger selection for early laying on the basis of number of offspring to fledge, we found no significant change in breeding phenology, in contrast with co-occurring resident blue tits (*Cyanistes caeruleus*). We discuss possible non-migratory constraints on phenological adjustment, including limitations on plasticity, genetic constraints and competition, as well as the possibility of counter-selection pressures relating to adult survival, longevity or future reproductive success. We propose that such factors need to be considered in conjunction with the arrival constraint hypothesis.

Keywords: Phenology, migration, breeding, lay date, pied flycatcher, *Ficedula hypoleuca*.

## 20 Introduction

The past decade has seen considerable interest in the biotic implications of, and responses to, climate change. Numerous studies of plants, animals and fungi have demonstrated advances in spring phenology across multiple taxonomic groups (reviewed by Parmesan and Yohe 2003). However, despite this overall pattern, 24 differences between species, and between populations of the same species, are common (Visser et al. 2003).

A recent (and concerning) finding is the absence of change in the breeding phenology of many migrant birds in northern Europe, including the pied flycatcher (*Ficedula hypoleuca*) (e.g. Laaksonen et al. 2006). Although in some populations, particularly those in Scandinavia, phenological inertia is due to lack of local warming (i.e. 28 no stimulus for earlier laying) (Both et al. 2004), it also occurs where co-occurring resident species are laying earlier, seemingly in response to increasing spring temperatures (Crick and Sparks 1999). Even where migrant lay dates are advancing, as they are in 36% of European pied flycatcher populations (Both et al. 2004), advancement often appears insufficient given the substantial shift in the timing of peak food sources, which 32 is leading to phenological mismatches between trophic levels (Both et al. 2006; Laaksonen et al. 2006). Such mismatching is seen in a range of bird species (e.g. Buse et al. 1999; Reuter and Breckling 1999; Stenseth and Mysterud 2002), but population-level consequences appear particularly severe for migrants (Both et al. 2009).

The most frequently-cited cause of this problem has been migratory constraint of lay dates (i.e. arrival date at 36 the breeding grounds preventing a trend towards earlier laying). Evidence for this “arrival constraint” hypothesis includes: (1) that females cannot begin laying until they have arrived at the breeding site, selected a mate and built a nest (Coppack and Both, 2002); (2) population-level correlations between arrival and lay dates in some migrants (Sparks et al. 2001); and (3) individual-level correlations between arrival and lay dates in ringed 40 pied flycatchers (Moore et al. 2005). However, almost all research has been conducted in The Netherlands, Germany and Sweden where time between first arrival date and first lay date is very limited (sometimes as few as nine days: Both and Visser, 2001). Here, we test the arrival constraint hypothesis for a U.K. pied flycatcher 44 population where local spring temperatures are increasing and the period between arrival and breeding is substantial, such that lay date is not constrained *de facto* by migration. We discuss possible non-migratory constraints on phenological adjustment, including limitations on plasticity, genetic constraints and competition, and briefly relate findings to changes in lay date by co-occurring resident blue tits (*Cyanistes caeruleus*).

## 48 Materials and Methods

### **Study area**

Work was undertaken at Nagshead Nature Reserve (Gloucestershire, UK, 2°34'0"W, 51°47'0"N), a broadleaf woodland site that supports a regionally-important population of nestbox-breeding pied flycatchers. The site is managed by the Royal Society for the Protection of Birds (RSPB). The pied flycatcher population at this site has been in decline since the late 1980s, decreasing from 86 pairs nesting in a constant resource of 295 nestboxes in 1990, to 23 pairs nesting in those same boxes in 2004 (Goodenough et al. 2009a).

### 56 **Datasets**

Data on migratory phenology were obtained from county annual bird reports (Gloucestershire Ornithological Co-ordinating Committee, 1990-2004) and RSPB annual records. Together, these provided First Arrival Dates (FADs) – the date of arrival of the first male at the study site for each year between 1990 and 2004.

60 Data in the county bird reports were collected primarily by a local ornithologist, who has worked intensively on pied flycatchers at Nagshead since the early 1980s, and rings both adults and nestlings on the reserve. Migrant arrival data from local groups has been found to be reliable in previous phenological studies (Both and Visser, 2001; Cotton 2003; Sparks et al. 2007). Data in the RSPB records were from standardised point counts and roving records (methods as per Bibby et al. 2000). These records were typically of territorial males (i.e. those defending a territory, usually by singing), such that potential transient males should not be a confounding factor. Effort was relatively consistent between years. It is recognised that the first arrival date variable is based on just one individual bird, but it was not possible to use other measures of arrival date (such as the date when 50% of territories were occupied) as the pied flycatcher is variably polyterritorial (Lundberg and Alatalo, 1992). Moreover, FADs correlate positively with mean arrival date for species where the latter can be calculated (Sparks et al. 2005; Tøttrup et al. 2006) and have been widely used to determine temporal change in migration (e.g. Sparks, 1999; Both and Visser, 2001; Butler, 2003; Cotton 2003; Sparks et al. 2007). Analysis of FADs is particularly robust for analysing temporal change for the same population (as here) (Tryjanowski et al. 2005). It should also be noted that for pied flycatchers at this study site, the majority of birds arrive very quickly (3-4 days) after the arrival of the first (*pers. obs.*), with the first female usually arriving a couple of days after the first male (and occasionally simultaneously).

76 Data on breeding phenology (date of clutch initiation for each nest) were obtained from the RSPB for each year between 1990 and 2004 – the latest year for which data were available – inclusive. First Egg Dates (FEDs) were determined from weekly counts of eggs in incomplete clutches as per Perrins and McCleery (1989). As lay dates are influenced by spatially-varying factors such as habitat, only data from the 295 nestboxes maintained in the same position were analysed. Unfinished clutches (those where incubation was

not started) and rare second clutches were excluded (total  $n = 709$  in 15 years). For each year, the minimum FED (the date on which the first egg of the first clutch of that year was laid) and the mean FED (the mean of all clutch initiation dates in that particular year) were calculated. It should be noted that although the number of nests was not consistent between years (maximum of 86 in 1990, minimum of 23 in 2004), there were sufficient nests in all years to ensure that mean FEDs were representative. We also obtained equivalent phenological data for blue tits ( $n = 1495$  nests in 14 years; no significant temporal trends in population size) and calculated annual minimum and mean FEDs as detailed above. It should be noted that there were only 14 years of phenological data for blue tits owing to statutory restrictions on data collection early in 2001 because of an outbreak of foot and mouth disease.

Temperature data were obtained from the Ross-on-Wye Meteorological Office weather station, 13km north of Nagshead. Spring temperature was quantified as the mean of April, May and June temperatures (i.e. the temperatures experienced during the laying period (May-June) and the preceding month: Crick and Sparks, 1999).

### Analysis

To analyse temporal change in arrival and laying, FADs and FEDs were converted to days after 31<sup>st</sup> March (i.e. 1 = 1<sup>st</sup> April) and correlated with year. To determine whether within-year variability in lay date changed over time, annual lay date interquartile ranges (IQR) and standard deviations (SD) were correlated with year. Analysis of IQR quantified variation in the phenology of the most typical 50% of nests (thus excluding the outliers prevalent in protracted breeding seasons). Analysis of SD allowed consideration of the entire laying period, including outliers (Laaksonen et al. 2006). Mean lay dates and between-year variability in the period 1990-2004 were compared with those at the same site during 1948-1963 (Lack 1966) using a two-sample  $t$ -test and an  $F$ -test, respectively.

To analyse change in the selection for early laying, standardised annual selection differentials were calculated and correlated with year. Selection differentials were calculated by subtracting the mean lay date from the mean lay date weighted by the number of offspring to fledge from each nest, and dividing the result by the SD of lay date (Falconer and MacKay, 1996). A similar approach (using the number of young to return as breeding adults) has been used previously to determine selection for early laying in pied flycatchers (Both and Visser, 2001). The number of fledglings was used here in the absence of ringing (and thus recruitment) data. Temporal change in temperature data was quantified using correlation analysis.

## Results

### Baseline data

The overall mean FAD was 11<sup>th</sup> April (range 4<sup>th</sup>-23<sup>rd</sup> April in individual years), while the overall minimum FED was 5<sup>th</sup> May (range 1<sup>st</sup>-14<sup>th</sup> May in individual years). The mean period between FAD and minimum FED was 27 days ( $\pm 4.57$  days SD). The minimum time between FAD and minimum FED was 20 days (2002). The mean FED was 12<sup>th</sup> May (range 8<sup>th</sup>-22<sup>nd</sup> May in individual years).

### Spring temperature and migratory phenology

There was an increase in the local spring (mean of April, May and June) temperatures over the 15 year study period, which was borderline-significant ( $r = 0.406$ ,  $n = 15$ ,  $P = 0.066$ ; annual increase =  $0.057^{\circ}\text{C}$ ; Fig. 1a), which was set within a period of significant increase in spring temperatures at the same site over the longer period of 1974-2004 ( $r = 0.601$ ,  $n = 31$ ,  $P < 0.001$ ; annual increase =  $0.067^{\circ}\text{C}$ ; Goodenough 2008). No significant change was found for FADs during the 1990-2004 study period ( $r = 0.162$ ,  $n = 15$ ,  $P = 0.549$ ; Fig. 1b).

### Breeding phenology

There was no temporal change in minimum FEDs ( $r = 0.206$ ,  $n = 15$ ,  $P = 0.461$ ; Fig. 1c) or mean FEDs ( $r = 0.152$ ,  $n = 15$ ,  $P = 0.588$ ; Fig. 1d). Between-individual variability in breeding phenology also remained consistent, both in terms of annual lay date IQR ( $r = 0.255$ ,  $n = 15$ ,  $P = 0.359$ ; Fig 1e) and SD ( $r = 0.420$ ;  $n = 15$ ;  $P = 0.119$ ; Fig. 1f). Annual mean FEDs have not changed significantly between 1990-2004 (this study) and 1948-1963 (Lack 1966): 12<sup>th</sup> May ( $\pm 1.16$  days SD) in both cases ( $t = -0.054$ , d.f. = 29,  $P = 0.957$ ). Similarly, between-year variation in lay date during 1990-2004 was not significantly different from the between-year variation in 1948-1963 ( $F = 1.466$ , d.f.<sub>1</sub> = 15, d.f.<sub>2</sub> = 14,  $P = 0.240$ ).

The time between FADs and minimum FEDs remained static between 1990 and 2004 ( $r = -0.016$ ,  $n = 15$ ,  $P = 0.995$ ; Fig. 1g), even though the selection differential for early laying became stronger (i.e. increasingly negative) over this period ( $r = -0.639$ ,  $n = 15$ ,  $P = 0.010$ ; Fig. 1h).

The lack of significant change in breeding phenology for the migratory pied flycatcher is in contrast to significant lay date advancement by co-occurring resident blue tits. In blue tits, minimum FEDs have become progressively earlier ( $r = -0.527$ ,  $n = 14$ ,  $P = 0.043$ ), while mean FEDs have advanced by five days in 15 years ( $r = -0.773$ ,  $n = 14$ ,  $P = 0.001$ ) (Goodenough, 2008). The significance of these findings was unchanged when analysis was repeated on a random sub-sample of blue tit nests to ensure equal sample sizes (i.e. when the number of nests included per year was directly comparable with the number of pied flycatcher nests).

144 Discussion

Despite increasing spring temperatures and quantifiably-increasing selection for early laying, we found no significant change in pied flycatcher breeding phenology (minimum or mean FEDs) over a 15-year period from 1990 to 2004. Moreover, lay dates in 1990-2004 were not significantly different from those of pied flycatchers  
148 breeding at the same site in 1948-1963 (Lack, 1966). Although our dataset is relatively short for studying longitudinal trends, the apparent lack of phenological adjustment is intriguing, especially as it contrasts with significantly earlier laying in co-occurring resident blue tits over the same period.

One of the most discussed explanations for the lack of reproductive phenological adjustment in migrant  
152 species is migratory constraint (Sanz et al. 2003; Both et al. 2004). This could occur because the endogenous rhythms that determine the phenology of migration are based upon photoperiodic stimuli (Gwinner 1996), which are independent of climate, and change therein. This explanation is supported in populations with a short period between arrival and breeding (Both and Visser, 2001). In stark contrast to  
156 previous studies, however, the lack of phenological adjustment in our study population does not appear to be due to migratory constraint. The time between arrival and breeding (FADs and minimum FEDs) is consistently around 27 days (minimum 20 days), whereas in continental European populations, this period can be as short as nine days for the pied flycatcher (Both and Visser, 2001). This difference is due primarily to U.K. birds  
160 arriving at their breeding grounds earlier: the median FAD at Nagshead is 11<sup>th</sup> April, while the median FAD at Hoge Veluwe in The Netherlands is 24<sup>th</sup> April (calculated from data presented by Both and Visser, 2001). The fact that there is such a large gap between arrival and breeding suggests that some constraint other than migration, either direct or indirect, is acting to prevent phenological adjustment in our UK population.

164 As phenotypic plasticity appears to be the most likely mechanism by which breeding parameters change with climate, as demonstrated in the closely-related collared flycatcher (*Ficedula albicollis*), and also in great tits (Przybylo et al. 2000; Charmantier et al. 2008), the most likely direct constraint is some limitation on phenotypic plasticity (Pigliucci, 2005). Although, at first sight, a limitation on plasticity seems unlikely given the substantial  
168 variation in lay dates (Fig 1e-f), it is possible that it is constrained because environmental stimuli for phenotypic change are either unavailable for migrants (e.g. if the cue is temperature at the breeding ground before arrival) or unsuitable (e.g. photoperiod) (DeWitt et al. 1998). There could also be lag effects or a genetic constraint compounded by the low heritability of lay dates (van der Jeugd and McCleery, 2002). Moreover, as the  
172 magnitude of migratory phenological change is negatively related to decreases in population size (i.e. declining species changing least) (Tryjanowski et al. 2005), with species that have been in decline during the period 1990-2000 showing a fundamental lack of migratory phenological adjustment (Møller et al., 2008), population trends could likewise be important for breeding phenology. Crucially, this could mean that rather than

176 population decline in The Netherlands being caused by insufficient phenological change (as suggested by Both  
et al. (2006)), decline there and at our U.K. site might, to some extent, be the cause of this insufficient change.  
The other possibility that needs to be considered is that of a counter-selection pressure. We have quantified a  
selection pressure for early laying on the basis of the number of young to fledge. However, although Lack (1954)  
180 famously suggested that behaviour should be modified to maximise the number of surviving young from each  
breeding attempt, it remains possible that there is a counter-selection pressure for later laying (or at least for  
phenological inertia), either related to the fitness of offspring, which would not be accounted for in a simple  
count of fledging numbers but which would have a large impact on offspring survival and recruitment, or the  
184 fitness of adult birds (this could be linked to immediate survival, longevity, or future reproductive success). If  
this were the case, there would be a trade-off between selection pressures relating to number of offspring and  
other aspects of fitness (Nilsson and Svensson, 1996; Dhondt, 2001). Further work needs to be done to  
research these possibilities.

188 Indirect constraints could include competition for nest sites or the food necessary for egg production. In this  
population, the former can probably be discounted as nestboxes are provided in super-abundance (around  
28% are unoccupied each year, mainly in free territories: Goodenough et al. 2009b). The latter cannot be  
dismissed as food supplies have not been monitored. There seems sufficient food to enable resident blue tits to  
192 lay earlier (both in relative terms to pied flycatchers and in terms of the temporal trend towards earlier laying in  
this population), although these birds do not have to recover condition post-migration. Alternatively, the food  
supply at the wintering grounds could be important, since this determines migratory resources and will affect post-  
migratory recovery. As different pied flycatcher populations winter in different areas, this could account for inter-  
196 population differences in ability to advance breeding phenology (Moore et al. 2005). A study aimed at  
determining whether supplemental feeding results in advancement of lay date in pied flycatchers in the same way  
as it does for blue tits (Svensson and Nilsson, 1995) would be a useful first step in disentangling these issues.

For migrant populations with a short period between arrival and breeding, achieving significant change in  
200 breeding phenology requires changes in migratory phenology (Both et al. 2004), or acceleration of the  
migratory journey (Ahola et al. 2004), through phenotypic plasticity or selection on different genotypes  
(Przybylo et al. 2000; Coppack and Both, 2002). That such change is possible, at least to some extent, for  
pied flycatchers is suggested by temporal changes towards earlier arrival dates in around one-third of  
204 European populations (Both et al. 2004). However, given the evidence that we have presented here, we  
conclude that it should not be assumed that an absence of change in breeding phenology is always due to  
migratory constraint. We propose that analysis for other pied flycatcher populations (ideally over longer time  
periods than the 15 years possible here), and for other migrant bird species, should be undertaken to

208 establish how much support there is both for and against the arrival constraint hypothesis. In the meantime, we suggest that other factors, such as limited phenotypic plasticity and food-based constraints, need to be investigated in tandem with the arrival constraint hypothesis.

### Acknowledgements

212 We thank the RSPB and Nagshead nestbox monitors for providing data and the three individuals who reviewed an earlier draft of this paper for their helpful and constructive comments. This research was partially funded by the Gloucestershire Naturalists' Society and the British Trust for Ornithology.

216 References

- Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K, Lehikoinen E (2004) Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob Change Biol* 10: 1610-1617.
- Bibby CJ, Burgess ND, Hill DA, Mustoe SH (2000) Bird census techniques. 2<sup>nd</sup> edn. Academic Press, London.
- 220 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, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, Eeva T, Enemar A, Gustafsson L, Ivankina EV, Järvinen A, Metcalfe NB, Nyholm NEI, Potti J, Ravussin P-A, Sanz JJ, Silverin B, Slater FM, Sokolov LV, Torok J, Winkel W, Wright J, Zang H, Visser ME (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc R Soc B* 271:1657-1662.
- 224 Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81-83.
- 228 Both C, van Turnhout CAM, Bijlsma RG, Siepel H, van Strien AJ, Foppen RPB (2009) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc R Soc B*. In Press.
- Buse A, Dury SJ, Woodburn RJW, Perrins CM, Good JEG.(1999) Effects of elevated temperature on multi-species interactions: the case of pedunculate oak, winter moth and tits. *Funct Ecol* 13: 74-82
- 232 Butler CJ (2003) The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis* 145: 484–495
- Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320: 800-803.
- 236 Coppack T, Both C (2002). Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90: 369-378.
- Cotton PA. (2003) Avian migration phenology and global climate change. *P Acad Nat Sci Phila* 100: 12219-12222.
- 240 Crick HQP, Sparks TH (1999) Climate change related to egg-laying trends. *Nature* 399: 423-424.
- DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends Ecol Evol* 13: 77–81.
- Dhondt AA (2001) Trade-offs between reproduction and survival in tits. *Ardea* 89: 155-166.
- 244 Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4<sup>th</sup> edn. Longman, London.

- Gloucestershire Ornithological Co-ordinating Committee (1990-2004) Gloucestershire Bird Report (annual publication). GOCC, Gloucester.
- 248 Goodenough (2008) Factors influencing nest-site choice and reproductive success in *Cyanistes caeruleus* (blue tit), *Parus major* (great tit) and *Ficedula hypoleuca* (pied flycatcher). PhD Thesis, University of Gloucestershire, U.K.
- 252 Goodenough AE, Elliot SL, Hart AG (2009a) The challenges of conservation for declining migrants: are reserve-based initiatives during the breeding season appropriate for the pied flycatcher *Ficedula hypoleuca*? Ibis 151: 429-439
- Goodenough AE, Elliot SL, Hart AG (2009b) Are nest sites actively chosen? Testing a common assumption for three non-resource limited birds. Acta Oecol 35: 598-602.
- Gwinner E (1996) Circannual clocks in avian reproduction and migration. Ibis 138: 47-63.
- 256 Laaksonen T, Ahola M, Eeva T, Väisänen RA, Lehikoinen E (2006) Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. Oikos 114: 277-290.
- Lack DL (1954) The natural regulation of animal numbers. Clarendon Press, Oxford.
- Lack DL (1966) Population studies of birds. Clarendon Press, London.
- 260 Lundberg A, Alatalo RV (1992) The pied flycatcher. T. and A.D. Poyser, London.
- Møller AP, Rubolini D, Lehikoinen E. (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. Proc Natl Acad Sci. USA 105: 16195–16200.
- 264 Moore FR, Smith RJ, Sandberg R (2005) Stopover ecology of intercontinental migrants: en route problems and consequences for reproductive performance. In Greenberg R and Marra PP (eds) Birds of two worlds: the ecology and evolution of migration Johns Hopkins University Press, Baltimore.
- Nilsson J-Å, Svensson E (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proc R Soc B 263: 711-714.
- 268 Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37-42.
- Perrins CM, McCleery RH (1989) Laying dates and clutch size in the great tit. Wilson Bull 101: 236-253.
- Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? Trends Ecol Evol 20: 481-486.
- 272 Przybylo R, Sheldon BC, Merilä J (2000) Climatic effects on breeding and morphology: evidence for phenotypic plasticity. J Anim Ecol 69: 395-403.

- Reuter H, Breckling B (1999) Emerging properties on the individual level: modelling the reproduction phase of the European robin *Erithacus rubecula*. *Ecol Model* 121: 199-219
- 276 Sanz JJ, Potti J, Moreno J, Merino S, Frías O (2003) Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Glob Change Biol.* 9: 461–472.
- Sparks TH (1999) Phenology and the changing pattern of bird migration in Britain. *Int J Biometeorol* 42:134–138.
- Sparks, TH, Bairlein F, Bojarinova JG, Hüppop O, Lehikoinen EA, Rainio K, Sokolov LV, Walker D (2005)
- 280 Examining the total arrival distribution of migratory birds. *Glob Change Biol* 11: 22–30.
- Sparks TH, Huber K, Bland RL, Crick HQP, Croxton PJ, Flood J, Loxton RG, Mason CF, Newnham JA, Tryjanowski P (2007) How consistent are trends in arrival (and departure) dates of migrant birds in the UK? *J. Ornithol.* 148: 503–511.
- 284 Sparks TH, Roberts DR, Crick HQP (2001) What is the value of first arrival dates of spring migrants in phenology? *Avian Ecology and Behaviour* 7: 75-85.
- Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life-history traits: non-linearity and match-mismatch to the environment. *Proc Natl Acad Sci USA* 99: 13379-13381.
- 288 Svensson E, Nilsson J-Å (1995) Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). *Ecology* 76: 1804-1812.
- Tøttrup AP, Thorup K, Rahbek C (2006) Patterns of change in timing of spring migration in North European songbird populations. *J Avian Biol* 37: 84–92.
- 292 Tryjanowski P, Kuzniak S, Sparks TH (2005) What affects the magnitude of change in first arrival dates of migrant birds? *J Ornithol* 146: 200-205.
- van der Jeugd HP, McCleery R (2002) Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *J Evolution Biol* 15: 380–387.
- 296 Visser ME, Adriaansen F, van Balen JH, Blondel J, Dhondt AA, van Dongen S, du Feu C, Ivankina EV, Kerimov AB, de Laet J, Matthysen E, McCleery RH, Orell M, Thomson DL (2003) Variable responses to large-scale climate change in European *Parus* populations. *Proc R Soc B* 270: 367-372.

300 **Figure legends**

**Figure 1:** Temporal change in climatic and phenological variables for a U.K. pied flycatcher population. Significant and borderline-significant relationships are shown by trend lines with *P* values. Migratory phenology is quantified using annual First Arrival Dates (FADs), breeding phenology is measured using  
304 annual First Egg Dates (FEDs) (minimum = earliest clutch of a year; mean = average of all clutches that year).