



UNIVERSITY OF
GLOUCESTERSHIRE

This is a peer-reviewed, post-print (final draft post-refereeing) version of the following published document:

Goodenough, Anne E ORCID: 0000-0002-7662-6670, Hart, Adam G ORCID: 0000-0002-4795-9986 and Stafford, Richard (2010) Is adjustment of breeding phenology keeping pace with the need for change? Linking observed response in woodland birds to changes in temperature and selection pressure. *Climatic Change*, 102 (3-4). pp. 687-697. doi:10.1007/s10584-010-9932-4

Official URL: <http://dx.doi.org/10.1007/s10584-010-9932-4>

DOI: <http://dx.doi.org/10.1007/s10584-010-9932-4>

EPrint URI: <https://eprints.glos.ac.uk/id/eprint/3369>

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT.

This is a peer-reviewed, post-print (final draft post-refereeing) version of the following published document:

Goodenough, Anne Elizabeth and Hart, Adam G. and Stafford, Richard (2010). *Is adjustment of breeding phenology keeping pace with the need for change? Linking observed response in woodland birds to changes in temperature and selection pressure.* Climatic Change, 102 (3-4), 687-697. ISSN 0165-0009

Published in Climatic Change, and available online at:

<http://link.springer.com/article/10.1007%2Fs10584-010-9932-4>

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

The URL for the published version is <http://dx.doi.org/10.1007/s10584-010-9932-4>

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT

**Is adjustment of breeding phenology keeping pace with the
need for change? Linking observed response in woodland birds
to changes in temperature and selection pressure**

Anne E Goodenough*, Adam G. Hart, Richard Stafford

Department of Natural and Social Sciences, University of Gloucestershire, Cheltenham, UK, GL50 4AZ

Corresponding author: Department of Natural and Social Sciences

Francis Close Hall Campus

University of Gloucestershire

Swindon Road

Cheltenham, UK, GL50 4AZ

aegoodenough@glos.ac.uk

+44 (0)1242 714669

Despite the recent plethora of studies investigating biotic implications of climate change, most research has been undertaken without the need for change being quantified. Failure to link observed responses to selection pressure is a fundamental omission because whether change is appropriate cannot then be determined. We use almost 7,000 records to analyse long-term (1974-2004) changes in breeding phenology for six co-occurring woodland birds at a site with significantly increasing spring temperatures. We link observed change to changes in selection for early laying (calculated using differential breeding success as the season progresses) to determine whether change is: (1) necessary, (2) appropriate, and (3) sufficient. Three (resident) species – blue tit, great tit, and nuthatch – started clutches significantly earlier over time without selection for early laying becoming stronger over the same period. This suggests that observed advancements are appropriate, and sufficient, to track climate change. For another species – coal tit – there was no change in lay date, and although there was always selection to lay early, selection intensity did not change over time. For this, the earliest-laying species, bet-hedging to prevent maladaptation (laying too early) or stabilising selection may be acting to maintain phenological inertia, even when phenological change could be adaptive. For the final two (migratory) species – pied flycatcher and redstart – there was no temporal change in lay date, despite selection for early laying becoming significantly stronger over time. This study indicates that some species are tracking climate change successfully while ecologically-similar species, at the same study site, are failing to do so.

16

Keywords: climate change; selection differentials; lay date; clutch initiation; passerines; global warming

1. INTRODUCTION

20 Quantifying temporal trends in phenology has become an increasingly important research area as ecologists seek to understand the biotic implications of, and responses to, accelerated climate change. The initial seminal papers in this field (e.g. Beebee 1995 for amphibians; Crick 1997 for birds) simply described long-term phenological changes. More recent studies have linked change not to year itself, but long-term environmental changes such as spring temperatures and the North Atlantic Oscillation (see reviews by Walther et al. 2002; Parmesan 2006). However, most analyses are still undertaken without simultaneous quantification of change in selection pressures. This is a fundamental omission as it means that the adaptive nature of phenological change (or lack thereof) cannot be determined (Visser and Both 2005).

28 Avian phenological changes are particularly well-studied, especially with regard to the timing of migration (arrival and departure dates) or breeding (lay dates). Such research often uses multi-site data from national surveys, for example, the British Trust for Ornithology's Nest Record Scheme (NRS) or Cornell's North American Nest Record Card Program (Crick and Sparks 1999; Dunn and Winkler 1999). However, while these studies have given a valuable overview of general patterns of change at a national level, phenological change needs to be quantified in relation to an appropriate yardstick (Visser and Both 2005) to determine whether it is: (1) necessary, (2) appropriate, and (3) sufficient. The need for such studies has recently been highlighted as a priority in climate change research (Visser 2008).

In this study, we use almost 7,000 breeding records to analyse long-term changes in breeding phenology for six co-occurring passerines breeding in mature oak woodland at Nagshead Nature Reserve (Gloucestershire, UK) between 1974 and 2004. Because a single site is being examined, it is possible to relate phenological change to local change in temperature and the timing of peak caterpillar abundance, as well as the direction of selection pressure for the timing of laying and, more importantly, change in the intensity of that selection pressure (Both and Visser 2001). Selection pressure can be calculated on the basis of differences in breeding success as the breeding season progresses. For example, if birds laying earlier have higher success relative to late-laying individuals, there is a selection pressure to lay early, with the intensity of this pressure being linked to the magnitude of the seasonal difference. We predict that birds that have tracked changes in local spring temperature successfully by altering their phenology appropriately will not experience increasing selection for early laying, while species that have not adjusted (or not adjusted enough) will be subject to increasingly strong selection for early laying as the penalty for laying late relative to the timing of spring (decreasing reproductive success) becomes increasingly severe. Although a couple of studies have analysed changes in increased directional selection pressures for individual avian species (e.g. Cresswell and McCleery 2003; Charmantier et al. 2008), this would appear to be the first time that observed phenological change has been related to temporal change in selection pressure directly for multiple species. This simultaneous analysis of co-occurring species means that it is possible to use a comparative approach to explore findings and establish whether there are species-specific differences in phenological change (actual change or selection for such change) in response to the same abiotic stimulus at the same study site over the same time period. This approach has recently been used effectively to give insights into demand for, and mechanisms of, phenological change (Smallegange et al. 2010).

52

2. METHODS

Analysis was undertaken for four resident species – blue tit (*Cyanistes caeruleus*), great tit (*Parus major*), coal tit (*Periparus ater*) and nuthatch (*Sitta europaea*) – as well as the migratory pied flycatcher (*Ficedula hypoleuca*) and

56 redstart (*Phoenicurus phoenicurus*). Breeding records were obtained from the Royal Society for the Protection of Birds
and lay dates (the date on which the first egg of each clutch was laid) were calculated as per Perrins and McCleery
(1989). Records were discounted if: (1) lay dates could not be calculated accurately due to missing data or very small
60 clutch sizes; (2) clutches remained incomplete; or (3) second/replacement clutches were involved. The final sample size
was 6,839 nests (see Table 1 for full details of sample sizes).

To quantify selection for early or late laying in each year, standardised annual selection differentials were
calculated by subtracting the annual mean lay date for the population from the mean lay date of the population divided
by the number of offspring to fledge per nest. This result was then divided by the population standard deviation of lay date
64 in that year (Falconer and MacKay 1996; Both and Visser 2001). Differentials close to zero suggest that there is little
selection pressure. Negative values suggest pressure for early laying and positive values indicate pressure for late laying,
with selection pressure intensity increasing the further a differential is from zero. The number of young to fledge was used as
the weighting parameter in the absence of recruitment data (Ahola et al., 2009; Smallegange et al. 2010; Goodenough et al.
68 2010). Change in selection pressure was established for each species by correlating annual differentials with year. Actual
change in phenology was quantified using annual mean lay dates. The intensity of selection pressure was related to observed
phenological adjustment and to whether the species was an 'early' breeder (early mean lay date compared to other species) or
'late' (late mean lay date compared to other species).

72 Change in spring temperature over time was established using data from the Ross-on-Wye Meteorological Office
weather station, 13km north of Nagshead. Spring temperature was quantified as the mean of daily temperatures
experienced in March, April and May combined (i.e. the temperatures experienced during the laying period and the
preceding month(s): Crick and Sparks 1999). Because it was not possible to calculate degree-day or warmth-sum
76 benchmarks (e.g. Strode 2003; Charmantier et al. 2008) without daily temperature readings, temporal change was also
quantified for each of these months individually to allow for the fact that two years with the same average temperature
could have very different spring temperature profiles. Temporal change in the timing of peak arthropod food abundance,
and its relationship to local spring temperature, were ascertained using caterpillar half-fall dates from Wytham Woods
80 (Oxfordshire, UK), which is 50km due east of our study site. These data, provided in Charmantier et al. (2008) for 19
years between 1975 and 2004, give the date by which 50% of the total number of caterpillars in a given year descend
from trees to pupate, this being an excellent proxy for the timing of peak caterpillar biomass (van Noordwijk et al. 1995).
The two sites are comparable both botanically, being dominated by Pedunculate Oak (*Quercus robur*), and in terms of
84 the main caterpillar species, winter moth (*Operophtera brumata*) (Goodenough, 2008).

3. RESULTS

3.1 Local change in temperature and caterpillar phenology

88 Local spring temperature increased significantly over the 31-year study period (correlation analysis: $r = 0.601$,
 $n = 31$, $P < 0.001$; increase per year = 0.067°C ; Fig1a). Temperatures also increased significantly when each month was
analysed separately ($P < 0.004$ in all cases; tests not shown). There was no change in the variability (standard deviation)
of overall spring temperature ($r = 0.174$, $n = 31$, $P < 0.350$). Caterpillar half-fall date at nearby Wytham woods advanced

92 significantly over the study period ($r = 0.748$, $n = 19$, $P < 0.001$; advance = 0.696 of a day per year; Fig. 1b) and correlated
almost perfectly with local spring temperature ($r = 0.956$, $n = 19$, $P < 0.001$; Fig. 1c) and month-specific temperatures
($P < 0.025$ in all cases; tests not shown).

96 3.2 Linking observed phenology to the need for change

Annual mean lay date became increasingly early for three of the six species: blue tit, great tit and nuthatch (Fig. 2
a-b, d). The magnitude of adjustment varied from 5.4 days adjustment in 31 years in blue tits, to 7.4 days for great tits
and 8.8 days for nuthatch over the same period. Annual mean lay dates for the remaining three species (coal tit, pied
100 flycatcher and redstart) did not change over time (Fig. 2 c, e-f). Selection differentials, calculated as a proxy for the
intensity of selection pressure for early laying, varied considerably between years and between species, but were negative
for all species in all years (i.e. there was never selection for later laying). Mean selection differentials (across all years)
ranged from -5.44 (blue tit) to -13.27 (redstart), but did not vary consistently with mean lay date (i.e. later-breeding species
104 did not always have high mean selection differentials: Table 1). Selection for early laying did not change significantly
over time for any of the four resident species (Fig. 2g-j) but did become increasingly strong for the two migrant species
(Fig. 2 k-l). Thus change in selection pressure occurred without associated change in observed phenology in two species
(pied flycatcher and redstart), while change in actual breeding phenology occurred without intensifying selection
108 pressure in three species (blue tit, great tit and nuthatch).

When the (negative) selection differentials were correlated with annual earliest lay dates, a negative correlation
resulted for all species, such that when the absolute date at start of the breeding season was late, there was very strong
selection pressure for laying early relative to other individuals. Thus the cost of being late compared to other birds in a
112 'late' year was greater than the cost of being late compared to others in an 'early' year. This pattern was significant for
all species except redstart, when border-line significant result was returned (Table 1).

4. DISCUSSION

116 Generally, selection for early laying in single-brooded birds occurs because early-laying birds have greater
reproductive success. This is because late clutches tend to be smaller (Lack 1966) and relative fledging success is usually
lower, mainly due to maximum food demand missing peak caterpillar numbers (Buse et al. 1999), although other factors such
as female age (Järvinen, 1991) and competition (Goodenough et al. 2009) can also have an effect. Selection differentials vary
120 between years but means may either be consistent over time (van Noordwijk et al. 1995), or may change, either positively
(selection for early laying becoming weaker) or negatively (selection for early laying becoming stronger) (Both and Visser 2001).

4.1 Temporally-consistent selection pressures for early laying

124 There are four scenarios under which the selection pressures acting on an organism might be expected to be
consistent between years: (1) all environmental factors (abiotic and biotic) are stable, or at least comparatively so; (2)
environmental factors are subject to variability but there is no long-term change in a given direction; (3) there is considerable
variability in selection pressures (direction or magnitude) between years (Merilä et al. 2001); and (4) at least one

128 environmental parameter is undergoing change that can be tracked successfully by that organism, either through phenotypic plasticity (Charmantier et al. 2008) or evolutionary change (Visser 2008).

Increasing spring temperature often causes phenological change in the first trophic level and organisms in subsequent trophic levels must remain in synchrony if mis-matching is to be avoided (Stenseth and Mysterud 2002). Here, temperature, one of the most important factors influencing breeding phenology (van Noordwijk et al. 1995) and recently shown to be a direct cue for clutch initiation (Visser et al. 2009), is increasing significantly. Tree phenology is directly dependent on spring temperature, with temperatures during March, April and May all being positively correlated with bud burst in trees such as those at the study site (Chmielewski and Rötzer 2001). More importantly in terms of avian ecology, the timing of peak caterpillar biomass relates to both temperature and tree phenology (as well as other factors such as precipitation), and is advancing at the study site (Fig 1b and c). If birds are to remain in synchrony, maximum food demand from chicks must coincide with maximum caterpillar abundance (Perrins 1991; Both et al. 2006), such that intensifying pressure for earlier laying and/or observed phenological advancement might be expected for some species (Buse et al. 1999).

140

4.1.1. When change is sufficient: blue tit, great tit and nuthatch

In line with national trends (Baillie et al., 2010), and as might be expected given local changes in temperature and peak caterpillar numbers, three of the four resident species studied here (blue tit, great tit and nuthatch) are laying earlier. However, calculation of selection pressures shows that there is no change in the intensity of selection for early laying in these species over the same time period (selection for early laying exists, but the magnitude of this selection pressure is not increasing). Consistency among years in the strength of selection for early laying most likely suggests that birds are tracking climate change successfully by altering their breeding phenology (Charmantier et al. 2008; Smallegange et al. 2010). This in turn means that the alteration of breeding phenology (advancement of lay dates by 5-8 days over 31 years) is appropriate in direction and magnitude to the temperature changes at the study site, as per scenario four.

Given that the few studies previously linking change in phenology to the need for phenological adjustment have found observed change is usually either too strong (3/11 studies) or too weak (5/11 studies) – see cross-taxonomic review by Visser and Both (2005) – documentation of where phenological adjustment is both appropriate and sufficient is comparatively uncommon. However, the apparent tracking of climate change during the study period does not preclude the possibility that current phenological advancement is occurring within a selection window (within which selection pressure is constant). If this is the case and the threshold of this window is reached in the future, lay date advancement might no longer keep pace with the need for change, resulting in selection for earlier laying increasing after that time.

156

4.1.2 When selection intensity is variable: coal tit

The fourth resident species, coal tit, is also showing no significant change in selection pressure, but for this species neither is there advancement in lay date. The negative selection differentials in all years suggest that coal tits should be laying earlier, although the magnitude of selection (and thus the strength of the stimulus for individuals to adapt) is variable. As this selection consistency and phenological inertia is occurring against a background of temperature change and change in the timing of the vital caterpillar food source (thus eliminating scenarios one and two), it is logical that this is occurring because

160

164 there is considerable variability in selection pressure between years (scenario three). Indeed coal tit selection differentials
are much more variable than for other species (coal tit standard deviation is 8.8 selection units versus 2.1 for all other
species combined; Table 1, Fig. 2c). This variability might be related to coal tits being the smallest and earliest-laying
species (Table 1) and thus most at risk of laying too early (Perrins 1970; Stevenson and Bryant 2000). This may, therefore,
168 be an example of where conservative bet-hedging in order to prevent maladaptation (Slatkin 1974; Olofsson et al. 2009) –
in this case laying too early – is acting to maintain phenological inertia, even when phenological change could be adaptive.
Alternatively, the absence of phenological change, and directional selection therefore, might be the result of stabilising
selection acting to favour an intermediate lay date. Stabilizing selection has been suggested previously as the explanation
172 for why avian breeding date does not shift **within** seasons despite earliest-laying females having increased fecundity (Price
et al. 1988) and extending this might explain why coal tits are not shifting breeding date **between** seasons (although the
fact that coal tit lay dates are the most variable of any species studied here might be regarded as counter-evidence for this
explanation). It is also possible that stabilising selection and bet-hedging are occurring in tandem, with factors that would
176 encourage bet-hedging (such as the increased risk of inclement weather early in the season) being the cause of stabilising
selection for intermediate lay dates. More research is needed to disentangle these concepts.

4.2 Temporally-changing selection pressures for early laying

180 There two non mutually-exclusive scenarios under which the selection pressures acting on an organism might be
expected to change significantly over time: (1) when at least one environmental parameter is changing to such an extent that
individual-based change (the plastic reaction norm slope) is not sufficient to track this change successfully (Charmantier et al.
2008); and (2) when at least one environmental parameter is changing too fast for population-level evolutionary change to keep
184 pace (Visser 2008). In either case, failure to track change successfully can be due to constraints, direct or indirect, acting to
prevent response, or limit the magnitude of response, such that stasis results in the species becoming increasingly less adapted to
its changing environment (Merilä et al. 2001).

188 4.2.1. When inertia occurs: pied flycatcher and redstart

In both migrants studied here, selection for early laying is intensifying, but there is no observed change in
phenology, suggesting that constraints are acting to prevent phenological adjustment occurring. Migrant species seem
particularly vulnerable to phenological inertia. This could be because of direct constraints imposed by late arrival dates (birds
192 being unable to breed earlier because they do not arrive at the breeding grounds until spring is well advanced: Both and Visser
2001; Sanz et al. 2003), or indirect constraints on phenotypic plasticity (Goodenough et al. 2010). Indirect constraints could
include environmental stimuli for phenotypic change being 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
196 genetic constraint compounded by the low heritability of laying dates (van der Jeugd and McCleery 2002), especially if
heritability is annually variable (Merilä et al. 2001). Differential changes in climate parameters experienced during different
parts of the migratory cycle (Fontaine et al. 2009) could also be important, especially if this affects the timing of food
abundance at stop-over sites or *en route*, as this might affect recovery time post-migration and thus ability to lay early. Such

200 constraints could explain why phenological adjustment is not apparent in these species, despite selection for early laying on the
basis of number of young to fledge becoming increasingly intense over time. There is also the possibility that there are
counter-selection pressures, not quantified here, acting on birds for later laying (or at least for phenological inertia), either
204 related to the fitness of offspring, which would not be accounted for in a simple count of fledgling numbers, or the fitness of
adult birds (immediate survival, longevity or future reproductive success). Notwithstanding this, in the long term, the fitness
consequences of phenological inertia in these species could have population-level implications, as already observed for pied
flycatchers in The Netherlands (Both et al. 2006). Importantly, decreases in population might cause a positive feedback loop as
declining populations appear less able to alter migratory (and thus possibly breeding) phenology (Tryjanowski et al. 2005).

208

4.3 Research implications and future directions

This work demonstrates the complex interactions between temperature change, selection pressure and phenological
adjustment. It demonstrates that, in some (resident) species, observed phenological change is necessary, appropriate, and
212 sufficient; while in other (migrant) species, absence of change in the presence of increasing selection pressure for such
change is resulting in maladaptation. It is also possible that, for coal tits, bet-hedging in order to prevent maladaptation and/or
stabilising selection is acting to maintain phenological inertia, even when change could be adaptive. This study highlights: (1)
that phenological adjustment/inertia needs to be considered in light of selection pressures in order to determine whether it
216 is adaptive or maladaptive; and (2) that substantial differences can occur between different species in response to the same
abiotic stimulus at the same study site, with some species tracking climate change successfully and others failing to do so.

References

- 220 Ahola MP, Laaksonen T, Eeva T, Lehikoinen E (2009) Great tits lay increasingly smaller clutches than selected for: a study of climate- and density-related changes in reproductive traits. *J Anim Ecol* 78: 1298-1306.
- Baillie SR, Marchant JH, Leech DI, Joys AC, Noble DG, Barimore C, Downie IS, Grantham MJ, Risely K, Robinson RA (2010) Breeding Birds in the Wider Countryside: their conservation status 2009. BTO Research Report No. 541. BTO, Thetford.
- 224 Beebee TJC (1995) Amphibian breeding and climate *Nature* 374: 219–220.
- 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, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296-298.
- 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 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.
- Chmielewski FM, Rotzer T. (2001) Response of tree phenology to climate change across Europe. *Agr Forest Meteorol* 108: 101-112.
- 236 Cresswell W, McCleery RH (2003) How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *J Anim Ecol* 72: 356-366.
- Crick HQP, Dudley C, Glue DE, Thomson DL (1997) U.K. birds are laying eggs earlier. *Nature* 388: 526.
- Crick HQP, Sparks, TH (1999) Climate change related to egg-laying trends. *Nature* 399: 423-424.
- 240 DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends Ecol Evol* 13:77–81
- Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proc R Soc B* 266: 2487-2490.
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edn. Longman, London.
- 244 Fontaine JJ, Decker KL, Skagen SK, van Riper C (2009) Spatial and temporal variation in climate change: a bird's eye view. *Climatic Change*, 97: 305–311
- 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.
- 248 Goodenough, A.E., Elliot, S.L., Hart, A.G. (2009) Annual variation in the relationship between lay date and clutch size in passerines. *Acta Ornithologica* 44: 27-36.
- Goodenough, AE, Hart AG, Elliot SL (2010) What prevents phenological adjustment to climate change in migrant bird species? Evidence against the "arrival constraint" hypothesis. *Int J Biomet.* in press.
- 252 Järvinen, A. (1991) A meta-analytic study of the effects of female age on laying-date and clutch-size in the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca*. *Ibis*, 133: 62-66.
- Lack DL (1966) Population Studies of Birds. London: Clarendon Press.

- 256 Merilä J, Sheldon B., Kruuk LEB (2001) Explaining stasis: microevolutionary studies in natural populations. *Genetica* 112: 199–222
- Olofsson H, Ripa J, Jonzén N. (2009) Bet-hedging as an evolutionary game: the trade-off between egg size and number. *Proc R Soc B* 276, 2963-29639.
- 260 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37: 637–669.
- Perrins CM (1970) The timing of birds' breeding seasons. *Ibis* 112: 242-255.
- Perrins CM (1991) Tits and their caterpillar food supply. *Ibis* 133: S49-S54
- Perrins CM, McCleery RH (1989) Laying dates and clutch size in the great tit. *Wilson Bull* 101: 236-253
- 264 Price T, Kirkpatrick M, Arnold SJ (1988) Directional selection and the evolution of breeding date in birds. *Science* 240: 798-799.
- 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
- 268 Slatkin M (1974) Hedging one's evolutionary bets. *Nature*, 250, 704-705.
- Smallegange IM, Fiedler W, Köppen U, Geiter O, Bairlein F (2010) Tits on the move: exploring the impact of environmental change on blue tit and great tit migration distance. *J Anim Ecol* 79: 350-357.
- 272 Stenseth NC, Mysterud A. (2002) Climate, changing phenology, and other life-history traits: non-linearity and match-mismatch to the environment. *Proc Nat Acad Sci USA* 99: 13379-13381.
- Stevenson IR, Bryant DM (2000) Climate change and constraints on breeding. *Nature*, 406: 366-367.
- Strode PK (2003) Implications of climate change for North American wood warblers (Parulidae). *Global Change Biol* 9: 1137–1144
- 276 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 Evol Biol* 15: 380–387
- 280 van Noordwijk AJ, McCleery RH, Perrins CM (1995) Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *J Anim Ecol* 64: 451-458.
- Visser M.E. (2008) Keeping up with a warming world: assessing the rate of adaptation to climate change. *Proc R Soc B* 275: 649–659
- 284 Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc R Soc B.* 272: 2561-2569.
- Visser ME, Holleman LJM, Caro SP (2009). Temperature has a causal effect on avian timing of reproduction. *Proc R Soc B* 276: 2323-2331.
- 288 Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416: 389-395.

Table 1 – Mean lay dates and selection differentials for early laying at Nagshead (Gloucestershire, UK) between 1974 and 2004, and the relationships between annual earliest lay date, a proxy for the timing of the breeding season, and selection for early laying (negative relationships mean selection is more intense in late-starting years; sample size used in analyses = N_{years}).

Status	Species	N_{nests}	N_{years}	Mean lay date (\pm S.D.)	Mean selection differential (\pm S.D.)	R	P
Resident	Blue tit	2721	29	4 th May (\pm 5.2 days)	-5.439 (\pm 1.128)	-0.686	<0.001***
	Great tit	1088	29	7 th May (\pm 5.1 days)	-5.474 (\pm 1.480)	-0.373	0.028*
	Coal tit	147	16	30 th April (\pm 4.3 days)	-9.495 (\pm 4.408)	-0.591	0.047*
	Nuthatch	281	20	3 rd May (\pm 4.9 days)	-7.968 (\pm 4.126)	-0.662	0.003**
Migrant	Pied flycatcher	1652	31	5 th June (\pm 3.7 days)	-7.287 (\pm 2.966)	-0.498	0.003**
	Redstart	50	15	6 th June (\pm 5.6 days)	-13.268 (\pm 2.836)	-0.480	0.080

296 Figure Legends

Figure 1: Relationship between year and (a) mean spring temperature (daily March-May temperatures °C) and (b) caterpillar half-fall date as a proxy for the phenology of maximum arthropod abundance (1 = 1 April), as well as (c) the relationship between temperature and caterpillar phenology.

300

Figure 2: Temporal change in selection differentials and lay dates for resident and migrant birds breeding at Nagshead (Gloucestershire, UK) between 1974 and 2004. Trendlines show relationships significant at α 0.05.

Figure 1



