Warmer springs lead to mistimed reproduction in great tits (*Parus major*)

M. E. Visser[1]*, A. J. van Noordwijk[1], J. M. Tinbergen[2] and C. M. Lessells[1]

[1]*Netherlands Institute of Ecology, PO Box 40, 6666 ZG Heteren, The Netherlands*
[2]*Zoological Laboratory, Groningen University, PO Box 14, 9750 AA Haren, The Netherlands*

In seasonal environments, the main selection pressure on the timing of reproduction (the ultimate factor) is synchrony between offspring requirements and food availability. However, reproduction is initiated much earlier than the time of maximum food requirement of the offspring. Individuals should therefore start reproduction in response to cues (the proximate factors), available in the environment of reproductive decision making, which predict the later environment of selection. With increasing spring temperatures over the past decades, vegetation phenology has advanced, with a concomitant advancement in the reproduction of some species at higher trophic levels. However, a mismatch between food abundance and offspring needs may occur if changes in the environment of decision making do not match those in the environment of selection. Date of egg laying in a great tit (*Parus major*) population has not advanced over a 23-year period, but selection for early laying has intensified. We believe that this is the first documented case of an adaptive response being hampered because a changing abiotic factor affects the environment in which a reproductive decision is made differently from the environment in which selection occurs.

Keywords: timing of reproduction; laying date; *Parus major*; phenotypic plasticity; climate change; selection

1. INTRODUCTION

Over the past decade, the phenology of the vegetation has advanced owing to higher spring temperatures (Myneni *et al*. 1997). This will affect the time at which arthropod populations start to increase in spring (Ellis *et al*. 1997). For insectivorous species, the abundance of arthropods at the time of maximum food requirement of their young is a crucial determinant of reproductive success (Lack 1968). We would therefore expect the timing of reproduction of these species to advance as well. Recently, it has been shown that many bird species in the UK have advanced their date of egg laying over the past 25 years (Crick *et al*. 1997). This pattern is confirmed by long-term studies of a few bird populations (Winkel & Hudde 1997; McCleery & Perrins 1998). It is tempting to conclude that increases in spring temperature will therefore not result in a mismatch between the time of reproduction of birds and the time of food abundance. It has, however, not been shown that the date of egg laying and the food peak advance to the same degree. Moreover, it is not expected that this will generally be the case. Often, individuals make decisions about the timing of reproduction well before their offspring's need for food is at its maximum and will have to rely on cues that act as predictors of this food peak. Photoperiod is an important cue (Rowan 1926), but other cues are needed for 'fine tuning' (Wingfield 1980). As photoperiod is independent of spring temperatures, it cannot account for short-term variation in laying date, and therefore we concentrate

on the 'fine-tuning' cues. With increasing spring temperatures, these cues might change to a different extent compared with the food peak. Furthermore, production of eggs requires nutrients and energy. The source for these might advance to a lesser extent than the peak in the food for the offspring, thereby constraining the advancement of the timing of reproduction. This potential problem of a differential change in the environment of selection and the environment of the initiation of reproduction is exemplified using a long-term study on a Dutch population of the great tit (*Parus major*). We will first show that there has been no advancement of date of egg laying, but that the main ultimate factor, caterpillar abundance, has advanced. Next, we show, by calculating the selection differentials for laying date, that selection for early laying has intensified. Finally, we explore whether this is due to a lack in shifts of the main cues (the proximate factors) or to more severe resource constraints at the time of egg formation.

2. MATERIALS AND METHODS

(a) *Study area and methodology*

We used 23 years of data (1973 to 1995) from a long-term study of a population of great tits on the Hoge Veluwe (The Netherlands). The study area covers a mixed pine–deciduous wood of 171 ha ($1\,ha = 10^4\,m^2$) in which there are about 400 nest-boxes. Nest-boxes are checked weekly to determine laying date and clutch size, and daily during the days immediately before hatching to determine hatching date of the young. When the young are 7 days old, they are ringed and their parents identified. From these measurements, the laying date of the first clutch and the number of

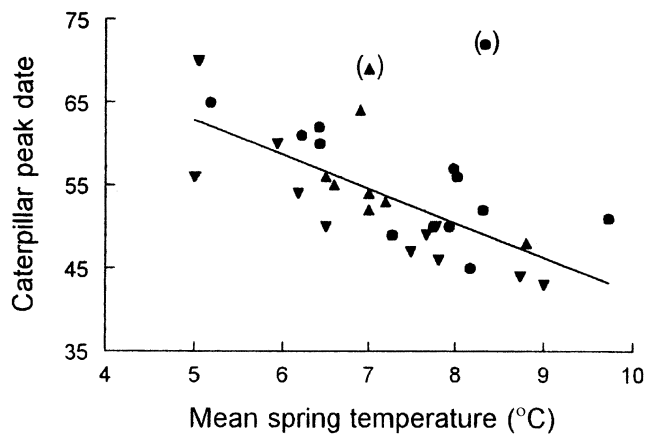*Author for correspondence (m.visser@cto.nioo.knaw.nl).

Figure 1. Caterpillar peak dates (1 = 1 April) against spring temperatures (mean daily temperature from 21 February to 10 May) for 30 years of data on caterpillar peaks from our study populations on the Hoge Veluwe (1985–1997, filled circles), Vlieland (1988–1995, filled upright triangles) and Oosterhout (1958–1968, filled inverted triangles). Biomass peak is well predicted by spring temperature (peak date = 83.5 − 4.1 × temp, $r = 0.73$, excluding 1991 (the points between brackets) when a late frost damaged all oak leaves).

fledglings recruited into the breeding population the following year (our measure of fitness) are known for each breeding pair.

(b) Laying dates

For the analysis of annual mean laying date, only first clutches with a known laying date were used (this excludes 1.7% of the clutches). To assess whether laying has advanced over the 23-year study period, the annual mean laying date was regressed against year.

(c) Annual peak dates of caterpillar biomass

Annual peak dates of caterpillar biomass are calculated from a regression model based on caterpillar peaks determined from frass-fall samples on the Hoge Veluwe (1985–1997), Vlieland (1988–1995) and Oosterhout (1958–1968) (van Balen 1973; Verboven *et al.* 1998; M. E. Visser, unpublished data). The caterpillar peak is well predicted by the mean daily temperature from 21 February to 10 May ($F_{1,26} = 52.3$, $p < 0.0001$; figure 1; see also van Balen 1973). The regression model allows us to predict the date of peak caterpillar biomass each year over the period 1973–1995 using temperature data supplied by the KNMI (Royal Dutch Meteorological Institute) in De Bilt.

(d) Selection differentials

Selection differentials estimate the amount of directional selection on a trait (Falconer 1981; Endler 1986; Schluter & Smith 1986; van Noordwijk *et al.* 1995). We calculated the selection differential for laying date as the difference between the mean date of laying of first clutches, weighted for the number of recruits produced per female over the entire season, and the unweighted mean laying date of first clutches. By including all recruits produced in a season, the fact that early-laying pairs are more likely to produce a second clutch is taken into account. Negative selection differentials indicate that early-laying birds produce on average more recruits than those birds laying later.

The total number of recruits produced per year varied greatly between years. Because selection differentials for years
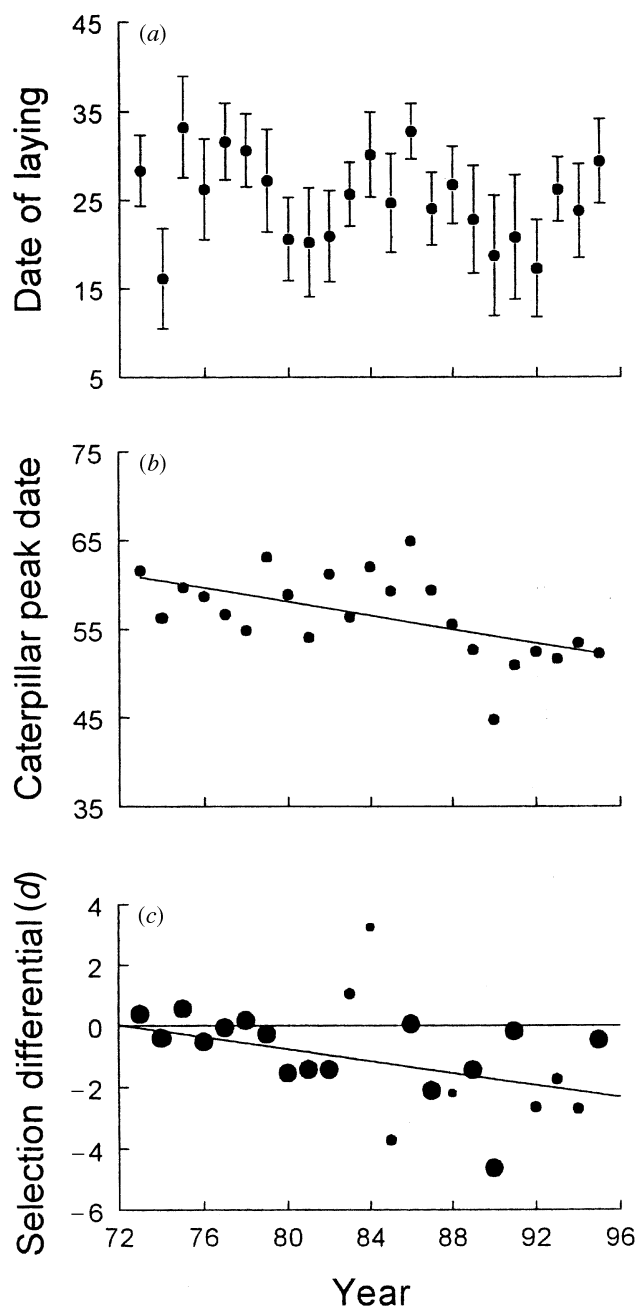

Figure 2. Timing of reproduction and food availability in great tits (*Parus major*) breeding on the Hoge Veluwe for the period 1973–1995. (*a*) Mean (±s.d.) laying date (1 = 1 April) of first clutches. (*b*) The estimated date of peak caterpillar biomass in oak (*Quercus robur*). (*c*) Selection differential for laying date, calculated as the difference between the mean laying date of first clutches, weighted for the number of recruits produced per female over the entire season, and the unweighted mean laying date of first clutches (large symbols, ⩾ 20 recruits; medium symbols, < 20 and ⩾ 10 recruits; small symbols, < 10 recruits produced from all broods in that year).

with only a few recruits are less reliable than those for years with many recruits, we weighted the selection differentials for the annual production of recruits against year.

3. RESULTS

Laying date has not advanced over the years 1973–1995 ($F_{1,21} = 1.00$, $p = 0.33$; figure 2*a*). However, the mean daily

temperature from 21 February to 10 May has increased over the 23 years ($F_{1,21}=9.50$, $p=0.006$), and hence the predicted date at which caterpillar biomass peaks has advanced by about nine days over this period ($F_{1,20}=7.86$, $p=0.01$; figure 2b), with perhaps the most rapid change occurring in 1988–1989.

Synchrony between the timing of reproduction and the availability of caterpillar food is the main selection pressure on laying date (van Noordwijk *et al*. 1995). The advance in the timing of the caterpillar peak without a concomitant advance in the timing of reproduction of the great tits is therefore expected to lead to increasingly negative selection differentials over the 23-year period. Selection for earlier laying has indeed become more intense over the 23-year period (regression weighted for the annual number of recruits, $F_{1,21}=6.54$, $p=0.018$; figure 2c).

Spring temperatures determine the date of peak caterpillar biomass. The effect of temperature is mediated both by the date of bud-burst of oak (*Quercus robur*) trees, before which the main caterpillar prey-species cannot grow (Holliday 1985), and by subsequent temperature-dependent caterpillar development (Topp & Kirsten 1991). Great tits are also phenotypically plastic in their timing of reproduction, laying earlier in warm springs (van Balen 1973). Why then has the date of egg laying not advanced in step with the peak caterpillar biomass over the years? One reason is that the environments of decision making and selection may have changed at different rates.

First, constraints on the timing of egg laying may not have changed in the same way as food availability for the young. The energetic demands of egg production may constrain timing of breeding (Perrins 1970). Great tits forage predominantly in different tree species during egg laying (larch (*Larix decidua*) and birch (*Betula pubescens*)) and chick rearing (oak). The bud-burst of the former species is much less temperature-dependent than that of oak. Based on dates of bud-burst predicted from observed spring temperatures (Kramer 1994), oak bud-burst has advanced over the 23-year period ($F_{1,21}=9.59$, $p=0.005$), but that of larch ($F_{1,21}=1.20$, $p=0.29$) and birch ($F_{1,21}=3.58$, $p=0.07$) has not. Thus the availability of resources needed to produce eggs advances only marginally compared with that needed for chick rearing.

Second, the predictors on which the decision to start breeding are based may not have changed over the years in the same way as the food availability for the young. Great tits lay at about the time that their caterpillar prey starts developing. If subsequent temperatures are high, the young hatch late relative to the caterpillar peak (van Noordwijk *et al*. 1995). The date of egg laying by great tits correlates well with the mean temperature between 1 March and 15 April (van Balen 1973), but this temperature mean has not increased significantly over the study period ($F_{1,21}=3.17$, $p=0.09$). In contrast, the mean temperature in the subsequent 30-day period, when caterpillars are growing, has increased ($F_{1,21}=6.98$, $p=0.015$). As these two periods start roughly at the same date, this difference must be due to a stronger increase in temperatures after the 15 April, that is, after and partly during the egg-laying period. Thus the relationship between the timing of peak caterpillar availability and the cues used to initiate laying may have changed over the study period. This interpretation is strengthened by
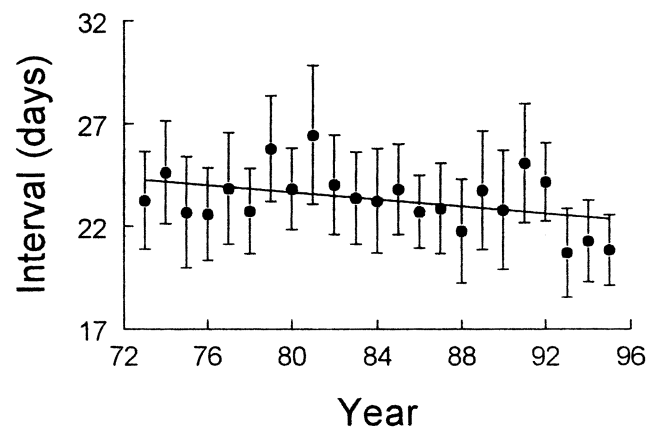

Figure 3. Mean (s.d.) interval between the laying date of the first egg and hatching date against year, for a great tit (*Parus major*) population on the Hoge Veluwe, 1973–1995.

the fact that in the early 1970s there was no correlation between annual mean laying date and selection differential, whereas in recent years a negative relationship exists (as indicated by a near-significant interaction between laying date and year (as a continuous variable) on the selection differential for laying date; $F_{1,19}=3.79$, $p=0.067$).

Laying date is not the sole determinant of hatching date, and thereby of the timing difference between offspring requirement and food availability. By laying smaller clutches, shortening the gap between the last egg and the onset of incubation (van Balen 1973), or reducing the duration of the incubation period, birds can reduce the interval between laying and hatching. The interval between the first egg and hatching (about 23 days) has indeed become two days shorter over the 23 years of this study ($F_{1,21}=4.32$, $p=0.05$, figure 3). This decrease is not due to changes in mean clutch size ($F_{1,21}=0.12$, $p=0.74$), and is thus most likely due to a reduction of the gap between clutch completion and incubation (of which we have no direct measurements). This observation can be explained in terms of both explanations outlined above. If the cues used for the start of egg production have not shifted as much as the peak in caterpillar biomass, the birds may detect that they are late from cues available closer to the nestling phase, and hence attempt to advance their hatching date. If constraints during egg laying have become more severe, the birds might trade-off the costs of producing eggs early against initiating incubation before clutch completion, with asynchronous hatching of the chicks as possible costs.

4. DISCUSSION

In great tits, the timing of reproduction has not advanced in step with early peak availability of food for the young over a 23-year period, leading to increased selection for early laying. We suggest that this results from greater changes in spring temperatures during the period of maximal food demands of the young than in the period of decision making over laying date, either because of constraints on egg laying or cues to initiate egg laying. These two factors have different long-term implications. If egg laying is constrained by energetic demands, the selection differentials displayed in figure 2c should be

modified to include detrimental effects on females attempting to lay earlier. There may then be no net selection on laying date, but climatic change will have caused an overall reduction in fitness by weakening the synchrony between the timing of peak food demands and availability. If, on the other hand, the relationship between food availability and a cue used for timing of breeding has changed, there will be selection on the reaction norm relating these two variables. However, the response to such selection may be slow (van Tienderen & Koelewijn 1994). Up until now, there has been no response to this selection in great tits (no significant interaction between spring temperature sum (1 March–15 April) and year on laying date; $F_{1,19} = 0.69$, $p = 0.42$).

Our findings differ from those of McCleery & Perrins (1998) for a UK great tit population. They find a clear advancement of laying date for the period 1970–1997 and conclude that this is solely due to increasing temperatures in spring. At present, it is unclear why the two great tit populations respond differently to increased spring temperatures. On the basis of the results of McCleery & Perrins (1998), and of the broader data set of Crick *et al.* (1997), it is tempting to conclude that climatic change may not have substantial adverse effects on reproductive success. Our results caution that climatic change may not always act uniformly on all parts of the breeding season, so that constraints and cues do not alter in step with selection pressures acting later in the breeding season. As a result, there may be a mismatch between timing of reproduction and food abundance, with shorter- or longer-term consequences for population viability.

REFERENCES

Crick, H. Q. P., Dudley, C. & Glue, D. E. 1997 Long-term trends towards earlier egg-laying by UK birds. *Nature* **388**, 526.

Ellis, W. N., Donner, J. H. & Kuchlein, J. H. 1997 Recent shifts in phenology of Microlepidoptera, related to climatic change (Lepidoptera). *Ent. Ber. Amst.* **57**, 66–72.

Endler, J. A. 1986 *Natural selection in the wild*. Princeton University Press.

Falconer, D. S. 1981 *Introduction to quantitative genetics*, 2nd edn. Harlow: Longman.

Holliday, N. J. 1985 Maintenance of the phenology of the winter moth (Lepidoptera: Geometridae). *Biol. J. Linn. Soc.* **25**, 221–234.

Kramer, K. 1994 A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in the Netherlands and Germany. *Pl. Cell Environ.* **17**, 367–377.

Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.

McCleery, R. H. & Perrins, C. M. 1998 . . . temperature and egg-laying trends. *Nature* **391**, 30–31.

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. 1997 Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698–702.

Perrins, C. M. 1970 The timing of birds' breeding season. *Ibis* **112**, 242–255.

Rowan, W. 1926 On photoperiodism, reproductive periodicity, and the annual migrations of certain birds and fishes. *Proc. Boston Soc. Nat. Hist.* **38**, 147–189.

Schluter, D. & Smith, J. N. M. 1986 Natural selection on beak and body size in the song sparrow. *Evolution* **40**, 221–231.

Topp, W. & Kirsten, K. 1991 Synchronisation of pre-imaginal development and reproductive success in the Winter Moth, *Operophtera brumata* L. *J. Appl. Entomol.* **111**, 137–146.

van Balen, J. H. 1973 A comparative study of the breeding ecology of the great tit *Parus major* in different habitats. *Ardea* **61**, 1–93.

van Noordwijk, A. J., McCleery, R. H. & Perrins, C. M. 1995 Selection of timing of great tit (*Parus major*) breeding in relation to caterpillar growth and temperature. *J. Anim. Ecol.* **64**, 451–458.

van Tienderen, P. H. & Koelewijn, H. P. 1994 Selection on reaction norms, genetic correlations and constraints. *Genet. Res. Camb.* **64**, 115–125.

Verboven, N., Tinbergen, J. M. & Verhulst, S. 1998 Multiple breeding and seasonal variation in food availability. In Verboven, N. 1998 Multiple breeding in a seasonal environment. PhD thesis, University of Utrecht, The Netherlands.

Wingfield, J. C. 1980 Fine temporal adjustment of reproductive functions. In *Avian endocrinology* (ed. A. Epple & M. H. Stenson), pp. 367–389. New York: Academic Press.

Winkel, W. & Hudde, H. 1997 Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and pied flycatchers *Ficedula hypoleuca*. *J. Avian Biol.* **28**, 187–190.