Immense plasticity of timing of breeding in a sedentary forest passerine, *Poecile palustris*

Tomasz Wesołowski, Marta Cholewa, Grzegorz Hebda, Marta Maziarz and Patryk Rowiński

Numerous bird species have advanced their breeding seasons in response to climate warming. These changes were mostly brought about by phenotypic plasticity, i.e. flexible reactions of individual birds, rather than by microevolutionary change. Knowing the limits of plasticity is thus of paramount importance in any attempt to predict possible reactions of birds to climate warming. However, the breeding performance of the same individuals in contrasting environmental conditions, necessary to answer this question, is rarely observed. Here, we provide data on the flexibility in timing of egg-laying of individual marsh tit *Poecile palustris* females breeding in an extremely late (2013) and early (2014) spring in Białowieża National Park (Poland). In both years the birds stayed in the same places in the primeval old-growth forest, free of direct human influences (no nest-boxes, no additional food). The weather variation was within the range of conditions observed during 40 yr in the study area, and no climate warming occurred in the marsh tit’s pre-breeding period. Females (*n* = 16) shifted the onset of laying by 13–23 (median = 20) days between the seasons. This range of individual flexibility encompasses almost the whole latitudinal range of the breeding dates found across Europe. Such a buffer of plasticity would probably be sufficient for marsh tits to adjust the onset of egg-laying to the forecasted range of climate change. A combination of temperature and photoperiod appears to be involved in fine tuning of the birds’ breeding times with spring conditions, but how the birds assess and integrate this information remains poorly understood.

The impact of climate warming (Stocker et al. 2013) on birds’ timing of breeding has been studied extensively (reviewed by Sparks and Menzel 2002, Parmesan and Yohe 2003, Dunn 2004, Wesołowski and Cholewa 2009). Many species have advanced their breeding seasons in response to warmer springs, although this was not always the case (Visser et al. 2003, Both et al. 2004, Dunn 2004, Wesołowski and Cholewa 2009). Occurrence of phenological shifts posed a question of the mechanisms by which such adjustments were accomplished, whether these were brought about by individual plasticity, flexible behavioural and physiological responses of birds to varying weather conditions, or – additionally – by selection and microevolutionary (genetic) change. It seems that, despite numerous claims in the literature, the role of microevolutionary changes has not been demonstrated convincingly (reviewed by Gienapp et al. 2008, Charmantier and Gienapp 2014, Merilä and Hendry 2014). Thus, as phenotypic plasticity plays a central role in tracking the warming springs, understanding the limits of plasticity should become an important research goal (Charmantier et al. 2008). However, to quantify the relative importance of plastic versus evolutionary responses, data are required on the performance of the same individuals in contrasting environmental conditions (Charmantier and Gienapp 2014). If extrapolation of individual plasticity to the population level can explain temporal trends in mean values, then plasticity might be considered a sufficient explanation for the population trend (Merilä and Hendry 2014). Unfortunately, within the abundant literature on climate change effects on the phenology of wild birds, only a small fraction of studies are based on replicate observations of individuals (reviewed by Charmantier and Gienapp 2014). Therefore, additional information on this point would be worthwhile.

Here we report observations on reactions of individual marsh tit *Poecile palustris* females to extreme variations in spring weather conditions, gathered in the Białowieża National Park (Poland) within an ongoing long-term study of individually marked birds (Wesołowski 1998, 2013, 2015). Marsh tits are strictly site-tenacious in our study area, staying in the same forest patch all year round, and they do not switch locations between the years (Wesołowski 2006, 2015). This allows for the recording of variation in the behaviour of the same bird, breeding in the same forest patch, in consecutive years.

It so happened that an unusually late breeding season, one of the three latest during the forty years of study, was immediately followed by the earliest season on record (Wesołowski 1998, Wesołowski and Cholewa 2009, unpubl.). This created
a natural experiment allowing for comparisons of egg-laying dates and assessment of the range of phenological flexibility of the individual birds.

**Study area and methods**

Detailed descriptions of the study area and field methods are given in the earlier papers (Wesołowski 1998, 2000, 2002). Here we give only a brief overview of points immediately relevant for the current communication. The study was carried out in the fragments of primeval old-growth forests strictly preserved in the Białowieża National Park (BNP hereafter). Marsh tits occupied mostly multi-storey, mixed-species, high stature deciduous stands of oak–lime–hornbeam (*Tilio-Carpinetum*) or swampy forest (Wesołowski 1996, 1998).

The data were collected in 2013–2014. Intensive searches for nests, aimed at finding the holes of all breeding pairs, were carried out in four plots in deciduous old-growth areas (Wesołowski 2015), where marsh tits bred exclusively in tree-holes and relied on natural food. No nest boxes, or additional food were available (Wesołowski 2007).

To establish the distribution of colour-ringed marsh tits in the plots, every spring the birds were followed and their movements noted on field maps just before the onset of breeding (they usually stayed in the same patch as in the previous year or moved to a neighbouring area, Wesołowski 2006). Birds carrying nest material were followed to locate the tree-hole being occupied, and the position of the hole was marked on the map. Nests (29 of 32) were mostly found at building/egg-laying stages but the dates of the first egg could seldom be directly recorded. This is because marsh tit females regularly cover eggs with woolly hair during the egg-laying period, which causes difficulties with ascertaining if egg-laying had already commenced (Wesołowski 1998, 2013). Therefore it was necessary to wait until the onset of incubation (to determine this, the holes were checked, mostly from a distance, every two days) and to back-calculate the first egg dates from nest checks carried out immediately after incubation has already begun. During calculations it was assumed that one egg is laid per day and incubation commenced with laying the last egg. This assumption was tested on a subsample of nests (cavities situated close to the ground) in which the exact first egg dates could be directly established. In 2013 six of seven females commenced incubation on the laying of the ultimate egg and one before the clutch completion. In 2014, eight of 12 females commenced incubation on the laying of the last egg, one before completing the clutch, and three females took short (1–2 d) pauses between laying of the ultimate egg and onset of incubation. For checking the nest contents a small bulb on a pliable wire and a small mirror were used.

Meteorological data were obtained from the local weather station at Białowieża village, which is situated <1 km from the southern edge of BNP.

**Results**

Weather patterns in the two years were strikingly different. In 2013, sub-zero temperatures prevailed, during the whole of March. It got warmer only in the first half of April (Table 1), and snow cover disappeared on 12 April. In 2014, on the other hand, snow had disappeared already by 14 February, and temperatures in March were much higher than in 2013 (Table 1).

Marsh tits in BNP commenced egg laying much later in 2013 (population median = 25 April) than in 2014 (6 April, Table 1), a 19 days’ difference. The same pattern was apparent at the individual level. Sixteen individually marked females bred both in 2013 and 2014. In 2013, females presumed to be in their first year of breeding (previously unringed, n = 6) and older females (n = 10) commenced breeding at the same time (Mann–Whitney test, Z = 1.30, p = 0.16). Nest building was observed on 11 April and the earliest clutch was initiated on 21 April, and the median first-egg date fell on 24 April. In 2014 the birds commenced breeding significantly earlier (Fig. 1; median = 6 April, Wilcoxon matched pairs test Z = 3.52, p < 0.001). The nest building was observed already on 25 March and the earliest clutch was initiated on 2 April. All individual females advanced breeding in 2014, they started egg-laying from 13 to 23 (median 20)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean temperature (°C)</th>
<th>Egg laying commencement (1 = 1 April)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2013 (late)</td>
<td>2014 (early)</td>
</tr>
<tr>
<td>March (first half)</td>
<td>−1.9</td>
<td>3.0</td>
</tr>
<tr>
<td>March (second half)</td>
<td>−5.1</td>
<td>7.1</td>
</tr>
<tr>
<td>April (first half)</td>
<td>2.9</td>
<td>5.8*</td>
</tr>
<tr>
<td>Median</td>
<td>25</td>
<td>6</td>
</tr>
<tr>
<td>25–75%</td>
<td>24–27</td>
<td>5–10</td>
</tr>
<tr>
<td>Range</td>
<td>21–32</td>
<td>2–15</td>
</tr>
<tr>
<td>n</td>
<td>54</td>
<td>51</td>
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</tbody>
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*temperatures in this period could not influence marsh tits’ decisions on commencement of laying, as most females had already begun laying in the first days of April.

Figure 1. Laying dates of individual marsh tit females in two consecutive years (dots connected by line), as well as, medians (squares), 25–75% percentiles (boxes) and ranges (whiskers) of their laying dates in the two seasons.
days earlier than in 2013, and half of them advanced by 17–21 d. However, individual females advanced their onset of laying at different rates (Fig. 1). There was no relationship between laying order by the individual females in the two years ($r_s = -0.006$, $p = 0.80$), and those birds which were earliest in 2013 did not necessarily remain so in 2014. In both years, however, all females bred highly synchronously, with 50% initiating egg laying within three (2013) to four (2014) days.

Discussion

The impact of changes in the local weather on bird behaviour is easier to study in sedentary species than in migrants, as performance of the latter could also be affected by weather conditions in places away from the breeding areas (reviewed by Gordo 2007, Saino et al. 2007). The extremely site-tenacious marsh tits in BNP are thus very convenient in this respect.

Individual marsh tit females in BNP demonstrated enormous flexibility in decisions about when to start reproduction. They were able to shift their timing of breeding by more than three weeks between the two consecutive years, which means that the same bird would be able to breed in synchrony with Swedish birds in one year (Nilsson and Smith 1988) and along with the Italian (Minelli et al. 1995) or Croatian (Dolenec 2006) birds in the other. A single individual is, thus, flexible enough to encompass (almost) the entire latitudinal range of marsh tit breeding dates in Europe. Therefore, the enormous inter-annual variation of breeding dates observed in BNP across years (30 d between extremes, Wesolowski and Cholewa 2009) could be accounted for by individual plasticity, and invoking additional mechanisms would be superfluous (Merillä and Hendry 2014).

It is difficult to tell whether this immense plasticity is a unique feature of marsh tits (we have failed to find comparable figures in the literature), but it seems probable that similar plasticity ranges could exist in other sedentary forest species. At least they demonstrate an enormous inter-year variation of laying dates at a population level (Charmantier et al. 2008, Wesolowski and Cholewa 2009, Wesolowski and Rówiński 2012).

So far, temperatures in the pre-breeding period (March–first half of April), critical for marsh tit timing of breeding, have not risen in BNP and – accordingly – population level marsh tit breeding dates have varied widely but have not advanced there (Wesolowski 1998, Wesolowski and Cholewa 2009). Thus, in contrast to other studies at the individual level (reviewed by Charmantier and Gienapp 2014) the immense plasticity in the timing of egg-laying has not been induced by warming springs. However, even if springs would – as forecasted – finally become much warmer, the local marsh tits appear to already be ‘well prepared’, as they possess behavioural and physiological mechanisms allowing them to cope with this challenge. This ability to react to varying environmental conditions and to breed very early would appear superfluous, as such unusually warm early springs happen very infrequently (just twice in forty years: Wesolowski and Cholewa 2009, unpubl.), i.e. several generations of marsh tits in BNP do not experience them. This raises a question of proximate factors (cues) used by the birds to time their reproduction. As indicated by experiments on the impact of changes in day-length on food storing behaviour of marsh tits (Clayton and Cristol 1996), the breeding time of this species might be – similar to other birds of highly seasonal environments (Immelmann 1971, Murton and Westwood 1977, Lambrechts et al. 1996) – under strong photoperiodic control. Thus the birds probably used the increasing day-length as the first cue in preparations for breeding. If so, marsh tits in BNP were photoresponsive already at day lengths as short as 11 h (they could build nests in the last third of March).

Too short days, though, could not be responsible for much later breeding in the majority of years. It seems that low temperatures in the pre-breeding period could delay breeding in most years. In BNP the temperatures varied extensively across years and the onset of egg-laying in marsh tits was strongly negatively correlated with warmth-sums of the pre-breeding period (Wesolowski 1998, Wesolowski and Cholewa 2009). The same was also recorded in marsh tits breeding in Germany (Schmidt 1984) and Croatia (Dolenec 2006), as well as in other sedentary birds (Kluyver 1952, Perrins 1965, Van Balen 1973, Orell and Ojanen 1983, Nager 1990, Wesolowski and Cholewa 2009, Wesolowski and Rówiński 2012 and references therein).

Higher temperatures could affect the birds’ physiology directly, as well as indirectly, e.g. by speeding up the development of invertebrate food, or they could provide a cue helping the birds to predict future conditions (Nilsson 1994, Svensson and Nilsson 1995). However, if temperatures acted directly, then their thresholds of acceptance were not fixed. Much higher daily temperatures were necessary to induce marsh tits to breed early than late in the season (Wesolowski 1998, Wesolowski and Cholewa 2009). Similarly great Parus major and blue tits Cyanistes caeruleus produced eggs earlier in relation to leaf phenology during late springs (Nilsson and Källander 2006). This suggests that temperature has to be weighted (calibrated) against day length to trigger the breeding (Wesolowski 1998, Lambrechts and Perret 2000, Gienapp et al. 2005).

Marsh tits may also respond proximately to some correlate of increasing temperatures, e.g. increasing amounts of food (Perrins 1970). Svensson (1995) attempted to mimic this increase, by provisioning marsh tits with extra food in the pre-laying period. He managed to advance their egg-laying by only three days, though, a rather small gain in comparison with the three weeks’ shifts of laying dates observed in the current study. Similarly, although blue tits Cyanistes caeruleus may shift their breeding dates by as much as 30 d (Wesolowski and Cholewa 2009), offering them supplementary food usually advanced the start of laying by only few days, if at all (review of experiments in Svensson 1995). Thus, the availability of food, though not without influence, could not be the sole cue used by these birds to decide when to reproduce. It could be so, as well, that the experiments did not include important aspects of how birds perceive their environment. To reach decisions the birds could use a combination of cues, and weigh them against one another (e.g. day length vs temperature, see above), so it is not the level of a single factor, but the right combination of several causes that seems to be important (Wesolowski and Rówiński 2012).
Whatever the nature of environmental factors triggering reproduction, though, it seems that they are perceived and ‘interpreted’ the same way by the majority of marsh tits in BNP. The birds in all study areas (different habitat types, several kilometres apart) in BNP bred highly synchronously within a season, most females commenced laying just within a couple of days of each other (Wesolowski 1998, current study), even when their breeding dates in the consecutive years were three weeks apart. Such uniformity of reactions suggests that these perception and assessment mechanisms have developed in reaction to challenges posed by irregular year-to-year weather variability. It would, nevertheless, probably suffice to adjust birds breeding times to the forecasted climate changes. How the birds make decisions on when to breed, and how they assess and integrate information from surroundings, remains poorly understood, and would repay additional studies.

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References


