

Climate variation and bird breeding seasons in a primeval temperate forest

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ABSTRACT: We investigated evidence for climate warming in the primeval forest of Białowieża National Park (E Poland) over the last 33 yr (1975–2007). We examined whether local populations of 4 sedentary birds (*Sitta europaea*, *Poecile palustris*, *Cyanistes caeruleus*, *Parus major*) advanced their breeding phenology during that time, and how breeding phenology was affected by temperature variation during the period preceding egg laying. Mean yearly temperatures varied strongly across years, with a significant warming ($\sim 1^{\circ}\text{C}$) trend. Spring temperatures increased significantly solely in the second half of April. Only *P. major*, which breeds later than the other species, showed a significant advance (~ 9 d) in breeding. Breeding dates of *S. europaea* and *P. palustris*, which usually lay eggs before mid-April, did not significantly change over time. In all species, the onset of breeding was very variable across years (up to 30 d), as birds started breeding earlier in springs with higher temperatures in the pre-laying period. Such a wide range of phenological plasticity indicates that the birds already possess mechanisms enabling them to accelerate breeding in response to climate warming, provided that warming occurs in the pre-laying period. All species shifted their laying dates concurrently; thus, the order of egg laying (*S. europaea*, *P. palustris*, *C. caeruleus*, *P. major*) was retained irrespective of the spring earliness. This also indicates that mechanisms allowing birds to respond to their changing environments exist at the community level.

KEY WORDS: Climate change · Primeval forest · Timing of breeding · *Sitta europaea* · *Poecile palustris* · *Cyanistes caeruleus* · *Parus major*

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1. INTRODUCTION

During the last 100 yr, global temperatures have been increasing at an unprecedented rate, largely as a consequence of human activities (Walther et al. 2002, IPCC 2007). However, temperatures have not risen uniformly: they generally increased to a greater extent in the northern hemisphere (Easterling et al. 1997), and the greatest warming has occurred between 40° and 70°N (Wallace et al. 1996). Despite this general trend, some areas in the northern hemisphere showed no signs of warming or even recorded cooler temperatures than in earlier years (e.g. Schönwiese et al. 1993, Visser et al. 2003, Both et al. 2004). Similarly, warming did not uniformly affect all seasons, as temperatures increased mostly in winter and spring months (e.g. Menzel 2000, Sparks & Tryjanowski 2005).

The impact of climatic changes (particularly warm-

ing) on plants, animals and whole ecosystems were extensively researched in the last decades (reviewed by Sparks & Menzel 2002, Walther et al. 2002, Menzel et al. 2006). Especially well documented are phenological changes, such as the advancement of phenological phases in early spring (reviewed by Ahas et al. 2002, Walther et al. 2002, Menzel & Sparks 2006, Menzel et al. 2006). Birds were extensively studied in this respect. Numerous studies concern timing of important seasonal events, such as spring migration (Both & te Marvelde 2007, Gienapp et al. 2007, Pulido 2007 and other papers in the Climate Research Special 'Bird migration and climate') and breeding. Many species advanced their breeding seasons in response to warmer springs, although this was not always the case (reviewed by Sparks & Menzel 2002, Parmesan & Yohe 2003, Dunn 2004). Even within a species, local populations often behave in strikingly different ways, with

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some advancing their breeding seasons but not others (Visser et al. 2003, Both et al. 2004). This wide spread of phenological responses, both within and among species, appears to reflect the spatial patterns of climate variation (Visser et al. 2003, Both et al. 2004, Dunn 2004). Furthermore, such differences may also be due to variation in a whole array of other variables, such as food availability, predation, habitat quality, density, genetic differences, and invasion of alien species (e.g. Blondel et al. 1993, Perrins 1996, Dunn 2004). These variables could thus render the detection of a relationship between warming climate and advancement of breeding difficult. However, as the majority of these confounding factors are due to human activities, studying the effects of climate change in habitats with no direct human impact can clarify the exact role of temperature changes in the timing of reproduction.

The Białowieża Forest, situated on the Polish–Belarusian border, is one of the few pristine places left in temperate Europe. Here, fragments of primeval forests, which once covered European lowlands, have been strictly protected within the Białowieża National Park (BNP hereafter) (Tomiałojć & Wesołowski 2005, Wesołowski 2007a). Fauna and flora recorded in the BNP are expected to be living under conditions which prevailed in European forests before these were anthropogenically altered. Thus, such a primeval forest could provide us with an invaluable reference site for all studies in forest ecology and evolution (Tomiałojć et al. 1984, Stutchbury & Morton 2001, Wesołowski 2005, 2007b).

Organisms do not respond to global averages, but to local changes in climate. We therefore first investigated whether climate in the Białowieża Forest, particularly in the early spring months that are crucial for bird breeding, has become warmer in the past 33 yr (1975–2007).

Next, we examined long-term variation in avian breeding dates to test whether birds living in these primeval conditions, with no additional food or nest boxes for reproduction (Wesołowski 2007b), advanced their nesting periods. We analysed breeding data of 4 non-excavating hole-nesting passerines. Two of them—the nuthatch *Sitta europaea* and the marsh tit *Poecile palustris*—are totally sedentary and stay all year round in the forest (Wesołowski & Stawarczyk 1991, Wesołowski 2006). The 2 other species—the blue tit *Cyanistes caeruleus* and the great tit *Parus major*—spend most of their time in the forest, but emigrate in winter, most probably to the Białowieża region (although juveniles may migrate as far as NW Europe, reviewed by Glutz von Blotzheim et al. 1977). The fact that they are sedentary is important, as any relationships between changes in the local climate and bird behaviour would be easier to detect in such species

rather than in long-distance migrants, which could be also affected by climatic conditions in places far away (reviewed by Gordo 2007, Saino et al. 2007). The 4 bird species are also widespread and numerous in the BNP (Wesołowski et al. 2003, Wesołowski 2007b), produce large families, and are quite noisy. All these characteristics facilitate the detection of families shortly after fledging and thus allow the study of breeding phenology variation (Matthysen 1989). Finally, to assess the range of behavioural plasticity in breeding dates, we analysed bird responses to short-term (between-year) variation in spring weather. We used insights from this analysis to evaluate prospects of the birds' ability to cope with forecasted climate warming.

2. METHODS

2.1. Study area

The Białowieża Forest complex is situated at the Polish–Belarusian border. Its western part (613 km², ~45% of the area) belongs to Poland. The forest is a remnant of the vast lowland forests that once covered large parts of temperate Europe. Its current unique features result from its considerable size and an exceptionally good state of preservation (Tomiałojć & Wesołowski 1990, 2005). The majority of the tree stands in the Polish part are now under management, but a 47.5 km² section of the best-preserved primeval old-growth stands has been strictly protected within BNP. The primeval stands preserved in the BNP are distinguishable by an array of features: they are multi-storey, have mixed species, are uneven-aged, contain many oversized trees (the tallest Norway spruce *Picea abies* can reach 55 m, and several other species reach 42 to 45 m), have a large amount of decaying timber and uprooted trees and have a high frequency of tree holes (Wesołowski 2007b). Detailed descriptions and photographs are available in Tomiałojć & Wesołowski (1990, 2005). Field data were collected in the strictly protected part, mostly in upland oak–lime–hornbeam stands composed mostly of hornbeam *Carpinus betulus*, lime *Tilia cordata*, pedunculate oak *Quercus robur*, spruce *Picea* spp. and Norway maple *Acer platanoides*. Data were also collected in a swampy riverine area of the forest, made up mainly of alder *Alnus glutinosa*, ash *Fraxinus excelsior* and spruce *Picea* spp.

2.2. Weather data

Meteorological data were obtained from the local weather station at Białowieża village, which is situated in the centre of the Białowieża Forest, <1 km from the

southern edge of BNP (Wesołowski et al. 2009, T. Wesołowski unpubl. data). To describe long-term changes in yearly and monthly temperatures, we used averages of mean daily temperatures for respective time intervals.

2.3. Bird breeding dates

Following Matthysen (1989), we used fledging dates to characterise variations in breeding season across years. Data on the appearance of families were gathered during the bird mapping census work (Tomiałojć 1980, Wesołowski et al. 2002) carried out between 10 April and 25 June in the springs of 1975–2007 (33 yr). Observers mapped birds in fairly large (24 to 33 ha) permanent census plots situated in old-growth forests in BNP. Throughout the season, all plots were visited every 8 to 10 d on a rotational basis. Thus, each day (with a few exceptions due to inclement weather), observations were gathered within at least one of these plots. The field work was not focused on recording the freshly fledged families; instead, the observers mapped their occurrence as one of the signs of bird-breeding activity (Tomiałojć 1980). As the species considered in our analyses breed in coniferous habitats only irregularly and in low numbers (Wesołowski et al. 2003), we restricted our searches to census plots in deciduous habitats (7 plots, totalling 185.5 ha in 1975–1979; 4 plots, 112.5 ha thereafter) (see Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990, Wesołowski et al. 2002, Wesołowski 2007b for detailed descriptions). For every plot, the first date of family observation (i.e. fledging date) of a species was extracted, if available. Next, we compared these dates and used the earliest family observation date of a species for a given season in BNP for further analyses.

We also ensured that variation in the first family observation records (extreme family observation dates) adequately described variation in the timing of breeding of local populations across years. We compared dates recorded for the start of egg laying, which was back calculated from the first family observation records using mean dates of first egg laying recorded in the same years during the intensive population studies in BNP (Wesołowski & Stawarczyk 1991, Wesołowski 1998, 2000, Rowiński 2001, T. Wesołowski & P. Rowiński unpubl. data).

To calculate the dates when the first eggs were laid (lay date), we subtracted from the first family observation dates the mean number of days known to be required from the onset of egg laying to fledging in local populations of individual species; *Sitta europaea*: 45 d, *Poecile palustris*: 40 d, *Cyanistes caeruleus*: 44 d, and *Parus major*: 41 d (extracted from Wesołowski 1998, 2000, Rowiński 2001, P. Rowiński & T. Wesołowski unpubl.

data). For all 4 species, these extrapolated lay dates were strongly positively correlated with directly recorded mean first egg dates: *S. europaea* ($n = 10$ yr, $r = 0.83$, $p = 0.003$), *P. palustris* ($n = 21$ yr, $r = 0.75$, $p < 0.0001$), *C. caeruleus* ($n = 12$ yr, $r = 0.68$, $p = 0.016$), *P. major* ($n = 12$ yr, $r = 0.67$, $p = 0.018$). Thus, we conclude that observations of these first families fledging their nests were representative of the course of breeding, and could therefore be used to characterise variation in the timing of breeding across years and between species.

2.4. Temperature variation in sensitive periods

To investigate the influence of temperature variation during the pre-laying period on the onset of egg laying, we calculated mean temperatures over intervals starting at different dates (March 1, March 16, April 1) and ending at the determinant date of a species in a given year. The determinant date (Kluyver 1952) is the day on which a bird has to make its final decision about egg laying, and temperatures after that date consequently cannot affect the timing of egg laying. In *Parus major*, the determinant date precedes the laying date by 4 d (Kluyver 1952). The length of this interval is unknown for the other studied species, but as all of them are small passerines, we assumed they required an equivalent amount of time to develop eggs. We therefore calculated the respective determinant dates for all of these species by subtracting 4 d from the back-calculated mean first egg dates (see above). While the setting of endpoint of temperature influence was straightforward on biological grounds, the exact time when birds start to become sensitive to temperature variation (or its correlate) was not easy to establish objectively. Silverin et al. (1989) experimentally showed that *P. major* are already photosensitive in January (Silverin et al. 1989), and Lambrechts et al. (1996) reported that one can manipulate *Cyanistes caeruleus* to breed in January by simulating very long days. Thus, great and blue tits may be physiologically capable of responding to environmental cues even at such an early time. However, the Białowieża region has a continental climate, and relatively harsh winter conditions (subzero temperatures, snow cover) prevail in January and February (Table 1), which may thus limit the extent to which birds use the physiological mechanisms mentioned above. Hence, it seems that the beginning of March could be the earliest date at which the rising temperatures could affect the birds' decisions on commencement of breeding. Following earlier authors (e.g. Kluyver 1952, Slagsvold 1976, Schmidt 1984), we used temperatures scored from different starting dates and correlated the mean temperatures of these periods with the mean egg laying dates of individual species.

For the final analyses, we used the periods that produced the highest correlation coefficients with the onset of egg laying of individual species.

2.5. Statistics

All statistical procedures follow the formulae given in Statistica for Windows 1996. All probability values shown in the text are 2 *F*-tailed.

3. RESULTS

Mean yearly temperatures in the Białowieża Forest varied widely from 5.9 to 9.7°C (Fig. 1a), with a slight warming tendency ($0.04^{\circ}\text{C yr}^{-1}$; Table 1), which totals $\sim 1^{\circ}\text{C}$ over 30 yr. Except for the month of April (Fig. 1b), the late winter and early spring months did not become significantly warmer (Table 1). The warming of April was entirely due to strong temperature increases in the second half of the month ($B = 0.14$, $p = 0.005$, SE 0.05, increase of 4°C in 30 yr). In contrast, temperatures in the first half of April did not change with time ($B = 0$, $p = 0.999$). Snow disappearance was highly variable among years (February 19 to April 28; Fig. 1c). A tendency toward earlier melting with time (Table 1) is misleading, as the trend was clearly nonlinear, with snow cover disappearing earliest in 1989–1993 and lasting longer thereafter (Fig. 1).

There was a large variation in the appearance of first families across years (Fig. 2). The difference between the earliest and latest seasons was 19 d in *Sitta europaea*, 26 d in *Poecile palustris*, and 30 d in both *Cyanistes caeruleus* and *Parus major*. *S. europaea* and *P. palustris* fledged at the same time (ca. May 28), which

Table 1. Climatic changes in Białowieża Forest in the period 1975–2007 (33 yr). Variation in temperature (means of yearly means \pm SD) for different intervals are presented, as well as the date of snow cover disappearance (day of the year, d.o.y.). Regression coefficients (B , \pm SE) represent changes ($^{\circ}\text{C}$ or d.o.y. for snow melt) per year

Variable	Temperature ($^{\circ}\text{C}$)	Date (d.o.y.) ^a	Slope of regression	
			B	p
January	-3.2 ± 3.81		0.05 ± 0.070	0.464
February	-2.9 ± 3.72		0.09 ± 0.067	0.212
March	1.5 ± 2.46		0.04 ± 0.045	0.412
April	8.0 ± 1.56		0.07 ± 0.026	0.013
May	14.5 ± 1.70		0.01 ± 0.032	0.700
Whole year	7.7 ± 1.01		0.04 ± 0.017	0.031
Snow melt ^b		88.2 ± 16.3	-0.55 ± 0.286	0.063

^aDay from January 1
^bThe first day on which snow cover was <1 cm deep

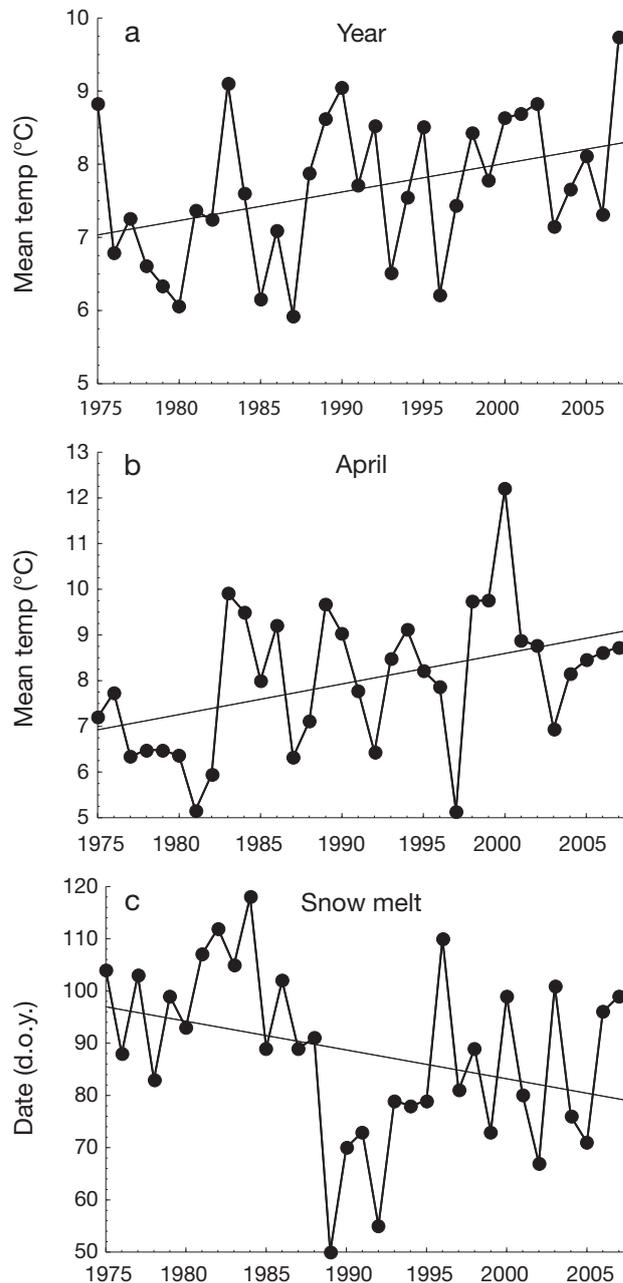


Fig. 1. Variation in (a) yearly and (b) mean April temperatures, and (c) dates of snow disappearance (first day of the year [d.o.y.] when snow cover was <1 cm deep) in the years 1975–2007 (33 yr). Regression lines are shown; regression coefficients (B) are given in Table 1

is on average ~ 10 d earlier than in *C. caeruleus* and *P. major* (ca. June 9) (Table 2). However, as the length of breeding cycles in *S. europaea* was longer than in *P. palustris* (45 vs. 40 d), the former species had to start egg laying earlier (on average 4 d) than the latter for the 2 species to fledge young at the same time. Similarly, *C. caeruleus* had to commence egg laying ~ 2 d

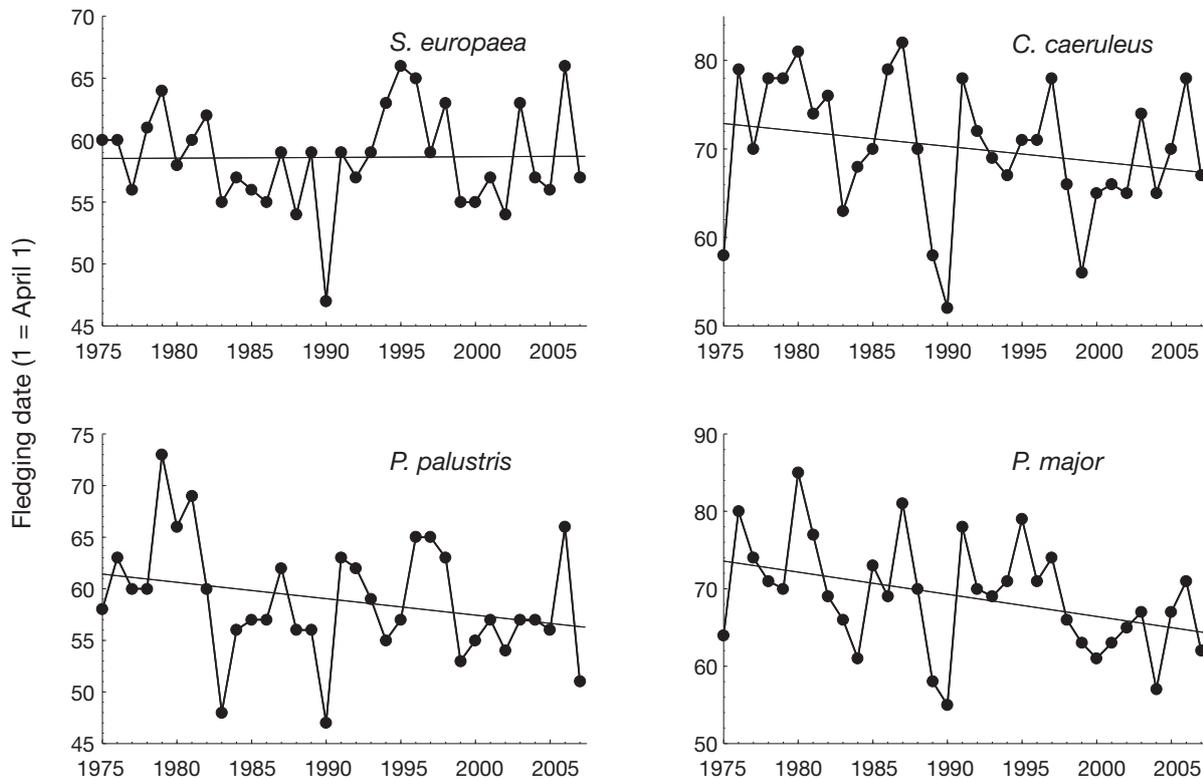


Fig. 2. *Sitta europaea*, *Poecile palustris*, *Cyanistes caeruleus*, and *Parus major*. Variation in fledging time (appearance of first families) in relation to year in Białowieża National Park (1975–2007, 33 yr). Regression lines are shown, regression coefficients (B) are given in Table 2

earlier than *P. major* (respective breeding cycles of 44 vs. 41 d).

The order of fledging of the different species was repeatable across years. In reaction to the change in environmental conditions, all the species shifted their breeding time in a similar way ($r = 0.42$ to 0.77 , p at least <0.016 for each pair-wise comparison; cf. Fig. 2). Even in 1990, when February and March were exceptionally warm (mean temperatures 4.0 and 6.2°C , respectively; cf. Table 1), and all species bred unusually early (Fig. 2), the first families of *Sitta europaea*

and *Poecile palustris* still appeared at the same time, several days before those of *Cyanistes caeruleus* and *Parus major*.

Sitta europaea showed no long-term trend towards earlier breeding. Furthermore, only a slight and non-significant tendency to advance egg laying in the season was visible in *Poecile palustris* and *Cyanistes caeruleus* (Table 2). Only *Parus major* showed a significant acceleration (~ 9 d) of its breeding season (Table 2). All the species responded strongly to the fluctuating temperatures across years, as they bred earlier in warmer springs (Table 3, Fig. 3). However, the species differed in terms of the length of periods preceding the onset of breeding to which they were found to be most responsive. *S. europaea* and *P. palustris* were most sensitive to the mean temperatures from March 16 onwards, whereas *C. caeruleus* and *P. major* reacted strongest to temperatures of the longer period (from March 1; Table 3). With the exception of *P. palustris*, all other species exhibited a poor relationship between their timing of breeding and April temperatures: *S. europaea* hardly reacted to the warming in the second half of April, as its determinant dates occurred within this period only in 3 of 33 yr. Similarly, *P. palustris* might have been affected by this change only to a limited extent (in 14 of 33 yr). On the

Table 2. *Sitta europaea*, *Poecile palustris*, *Cyanistes caeruleus*, and *Parus major*. Variation in the date of the appearance of first families in the period 1975–2007 (33 yr [mean \pm SD]). Regression coefficients (B \pm SE) represent changes in fledging time (d yr^{-1})

Species	First family date (1 = April 1)	Slope of regression	
		B	p
<i>S. europaea</i>	58.6 ± 4.05	0.01 ± 0.075	0.944
<i>P. palustris</i>	58.9 ± 5.64	-0.16 ± 0.101	0.125
<i>C. caeruleus</i>	70.1 ± 7.52	-0.18 ± 0.139	0.205
<i>P. major</i>	69.0 ± 7.13	-0.29 ± 0.122	0.026

Table 3. *Sitta europaea*, *Poecile palustris*, *Cyanistes caeruleus*, and *Parus major*. Mean determinant dates and relationships between the determinant dates and mean temperatures of the preceding days in the period 1975–2007 (33 yr). Mean temperatures were calculated for periods beginning at the dates shown, and ending at the determinant dates of respective years. Regression coefficients (B ± SE) represent changes in determinant dates ($d\ ^\circ C^{-1}$)

Species (determinant date)	March 1		March 16		April 1 ^a	
	B	p	B	p	B	p
<i>S. europaea</i> (April 11)	-0.56 ± 0.37	0.135	-0.87 ± 0.37	0.027	-0.44 ± 0.30	0.154
<i>P. palustris</i> (April 15)	-1.53 ± 0.57	0.012	-1.86 ± 0.55	0.002	-0.90 ± 0.38	0.025
<i>C. caeruleus</i> (April 22)	-3.14 ± 0.97	0.003	-2.30 ± 0.96	0.023	-1.25 ± 0.77	0.114
<i>P. major</i> (April 24)	-2.50 ± 0.99	0.017	-2.27 ± 1.03	0.035	-0.34 ± 0.92	0.717

^a*S. europaea*, n = 32 only, as one of the determinant dates was in March

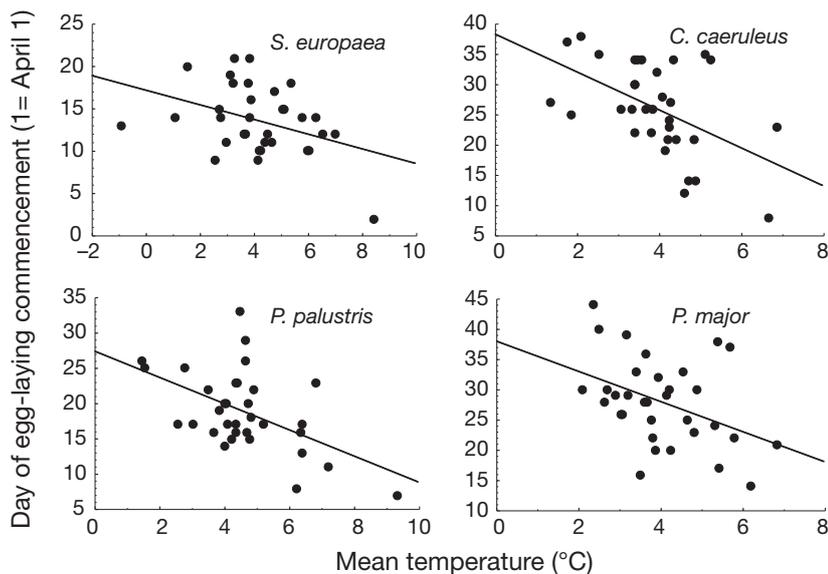


Fig. 3. *Sitta europaea*, *Poecile palustris*, *Cyanistes caeruleus*, and *Parus major*. Timing of the start of egg laying in relation to spring temperatures in Białowieża National Park (1975–2007, 33 seasons). Mean temperatures were calculated over the periods that best predicted the egg laying dates of individual species (Table 3): from mid-March to the determinant date in *S. europaea* and *P. palustris*, and from the beginning of March to the determinant date in *C. caeruleus* and *P. major*. Regression lines are shown, regression coefficients (B) are given in Table 3

other hand, *C. caeruleus* and *P. major* appeared to have been most affected by the warmer April temperatures, with determinant dates occurring in the second half of April in 28 and 30 out of 33 yr, respectively.

Parus major collects much of its food from the ground. Snow could therefore limit the bird's access to food resources, and consequently delay its breeding time in years with prolonged snow cover. However, no signifi-

cant relationship between the dates of snow disappearance (Fig. 1) and *P. major* breeding time ($r = 0.16$, $p = 0.387$) was found in BNP.

The reaction of individual species to increasing temperatures appeared to differ; *Cyanistes caeruleus* and *Parus major* respectively advanced their breeding by 3.1 and 2.5 d with a $1^\circ C$ increase in mean temperatures, while *Sitta europaea* advanced its breeding by only 0.9 d (Fig. 3, Table 3). However, these differences were not statistically significant.

4. DISCUSSION

This study demonstrates that the local climate in Białowieża Forest followed global trends (IPCC 2007) as the temperatures recorded have increased in recent decades (see also Pierzgalski et al. 2002, Mitrus et al. 2005, Sparks et al. 2009). Thus, even without direct human influences, strictly protected primeval areas such as this are still affected by climate change. However, it must be stressed that the climate in the Białowieża region seems to be fluctuating without a clear warming trend when investigated over a longer time period (Schönwiese et al. 1993, Jędrzejewska et al. 1997). Two warmer than average periods were discernible within a 215 year series (1780–1995), namely years 1820–1870 and the current time period from 1970 onwards (Jędrzejewska et al. 1997). Thus, general conclusions strongly depend on the time-frame used, which is a common and probably unavoidable problem in climate change studies (Sparks & Tryjanowski 2005). However, the biologically important point to emphasise is that the higher temperatures observed recently are within the range that local organisms have experienced before. Long-living trees in BNP nowadays experience what is most likely their second warmer period in life and short-lived organisms are descendants of those individuals that have already successfully coped with the warmer climate earlier on.

Current research is so focused on climate change, climate warming and its consequences, that we tend to forget about short-term weather fluctuations. For short-lived organisms, such as those species investigated in

this article, the long-term climatic trends may be far less important than the challenges of coping with highly variable and unpredictable spring weather patterns. Within an individual's life span, local conditions can vary so much that in order to deal with them, breeding time has to be shifted as much as almost 4 wk between the 2 consecutive seasons (cf. *Parus major* in 1990/1991; Fig. 2). In BNP, all 4 species bred earlier when spring temperatures were higher (Fig. 3). As these species also advanced their breeding time in warmer springs in other geographical regions (reviewed by Matthysen 1998, Wesołowski 1998, Visser et al. 2003, Dunn 2004), the ability to react to fluctuating spring temperatures is apparently a species specific feature. It is still unclear whether spring temperatures act directly on the onset of egg laying (Kluyver 1952, Stevenson & Bryant 2000) or indirectly (e.g. by influencing food resources; Perrins 1970, Slagsvold 1976, Schmidt 1984, Wesołowski 1998, Nilsson & Källander 2006). However, if temperatures acted directly, their thresholds of acceptance were not constant. Much higher daily temperatures were necessary to induce breeding early than late in the season, and we suggest that temperature needs to be weighted (calibrated) against daylength to trigger the start of the breeding season (Wesołowski 1998, Lambrechts & Perret 2000, Gienapp et al. 2005). Notwithstanding the exact mechanism by which temperature influences the onset of breeding, birds in BNP are already equipped with physiological and behavioural response mechanisms allowing for a very plastic reaction to changing environmental conditions. The spring of 1990, when February and March were extremely warm (mean temperatures +5°C higher than these months' averages, equivalent to the 'worst' IPCC warming scenario), served as a natural experiment, showing what would happen when the late winter/early spring period got substantially warmer. All 4 species were able to react to this challenge by advancing the onset of breeding to unusually early dates (Fig. 2) that are usually found only in the Mediterranean populations (Minelli et al. 1995, Dolenec 2005). As they started breeding at much shorter daylength, their breeding at later dates in other years (in contrast to the Corsican *Cyanistes caeruleus*, Lambrechts et al. 1996) was apparently not caused by proximate limitations in daylength. The ability to react even in these extreme conditions shows that the range of phenotypic plasticity in these birds is far greater than normally observed, and suggests that there is still unexpressed potential in lay date flexibility. Why such apparent excess capacities in shifting breeding times exist is also a question of immense biological importance. However, what is of great importance to the current discussion is the fact that local birds are already prepared to cope with envisaged warming, suggesting that there is no need for new response mechanisms to evolve. The studied birds in BNP

seem to share more similarities with English great tits than with their Dutch counterparts, the former appearing plastic enough to track shifting resources (Charmanier et al. 2008), and the latter being unable to phenotypically adjust to advancing food supplies (Visser et al. 1998).

The second necessary condition for the long-term advancement of breeding times is for warmer periods to coincide with sensitive time intervals in the pre-laying period during which birds make decisions on when to start laying eggs. The mismatch between the 2 periods could explain the failure to advance egg laying in several populations of *Cyanistes caeruleus* and *Parus major* (Visser et al. 1998, 2003). The onset of sensitive periods and their endpoints (determinant dates) differed across species in BNP, so they could be affected differently by the same temperature changes. The only time period in spring that was found to become significantly warmer with time in BNP was the second half of April (Table 1). This was too late in terms of determinant date to affect breeding decisions of *Sitta europaea*, as the start of egg laying for this species was generally made before that period. Thus, *S. europaea* had no stimulus to advance breeding, and this is what was indeed observed (Fig. 2). Similarly, *Poecile palustris* started egg laying before the second half of April in most seasons, and showed only a non-significant tendency to advance breeding (Fig. 2). In contrast, *C. caeruleus* and *P. major* might have been affected by the warmer period, as their determinant dates fell on the second half of April in most years. As expected, *P. major* substantially advanced its breeding time, although *C. caeruleus* failed to do so significantly (Fig. 2). There may be several possible factors contributing to this interspecific difference: on average, *C. caeruleus* in BNP starts breeding 2 d earlier than *P. major*; thus, its determinant dates overlapped with the warming period to a lesser extent. This difference, albeit contributory, was probably too small to account for this interspecific contrast alone. Both species winter outside the forest (see Introduction), and their living environment during this time is unknown. This could in turn differentially affect bird condition and trigger some carry-over effects (Webster et al. 2002) that influence their behaviour in the breeding grounds. Finally, as proposed by Visser et al. (2003), *C. caeruleus* could change the frequency of second broods, instead of advancing egg laying. Further work is required to test the relative importance of these hypotheses.

The early occurrence of breeding with springs getting warmer solves only part of the problem, as it is important for an organism to advance its phenology only enough to remain in pace with other organisms. Too much or insufficient changes in the timing of breeding could result in the disruption of the synchrony between different links in trophic cascades,

and lead to a mismatch between e.g. plants and herbivores or predators and their prey (Visser et al. 1998, Stenseth & Mysterud 2002, Durant et al. 2003). This could in turn negatively affect population dynamics and community functioning. However, as discussed above, the highly variable onset of spring in the north temperate zone is not a recent phenomenon that may have been brought about only by climate change. Thus, varying spring weather is something organisms living in highly seasonal environments have coped with all along. Therefore, we should also expect to find a wide range of flexibility in community level interactions, allowing the maintenance of interspecific synchrony despite large-scale temporal variation. We should observe that community processes remain buffered against weather fluctuations except in the case of extreme events.

This aspect of temporal variation seems to be largely neglected, yet there is ample evidence that different species shift their phenology across years in a similar fashion, such that the absolute dates of achieving the same phenological stage can differ by as much as 1 mo, although the relative timing or order in which individual species achieve this stage remains fixed. This is visible in different areas: the order of the timing of breeding of the 4 species found in BNP remains mostly the same as in other parts of Europe, despite great differences in the absolute laying dates among them (e.g. Dunn 1976, Schmidt 1984, Visser et al. 2003). This phenomenon is also clearly noticeable among different groups of organisms in BNP (e.g. timing of bud burst in trees, Wesołowski & Rowiński 2006, 2008; development of herbs on the forest floor, Faliński 2001, Sparks et al. 2009). The temporal arrangement of spring events in BNP remains largely the same, despite high variation in the onset of spring and in the rate of the phenological change. Thus, birds, trees and herbs in this primeval forest apparently 'read' environmental cues in a similar way and react to them in a comparable fashion. Since these organisms are native to the area (there are no long-term data on birds, but trees and herbs growing at the BNP had naturally colonised this area in the post-glacial period; Faliński 1986, 2001), they have been exposed to the same vagaries of local climate over ages if not millennia, and there was plenty of time to match phenology of interacting species with one another. The long period of species coexistence makes BNP and other primeval areas in the world especially suitable benchmark sites for studies of the impact of climate change on biological communities. It should also be kept in mind that environments may change in many different ways and, in order to survive and reproduce, organisms have to cope with all these challenges simultaneously, not just with the effects of climate change. Therefore, a broader ap-

proach, including other aspects of variation, would be worthwhile. Studies on mechanisms of interspecific temporal matching, carried out in primeval situations could be particularly valuable in elucidating these problems.

In summary, the temperatures in this primeval forest have indeed increased in the last decades, but this warming presumably remained within the range of conditions historically experienced by the local biota. As all the bird species studied in BNP were phenologically plastic and strongly responded to rising spring temperatures by breeding earlier, they were behaviourally and physiologically equipped to adjust phenotypically and are probably able to adjust to much stronger climate warming than observed at present, provided that warming occurred at the appropriate (i.e. pre-laying) period of the year. Highly parallel phenological changes found in different taxa in BNP across years allowed for the maintenance of synchrony within local communities, despite large-scale time shifts between different seasons. Therefore, a small to moderate climate warming, even with temperature increases concentrated in the early spring, would apparently not have a very strong, disruptive effect on the local communities. A broader approach that would allow the study of mechanisms of community resilience to all sources of environmental variation, including climate change, would be worthwhile, primarily when carried out in primeval environments.

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