Changes in breeding phenology and performance of Wood Warblers *Phylloscopus sibilatrix* in a primeval forest: a thirty-year perspective

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Abstract. The reproductive behaviour of Wood Warblers was studied in a primeval forest area in the Białowieża National Park (E Poland). Observations carried out during twelve seasons (1976–1979, 1985–1988, 2002–2005) in deciduous and coniferous old-growth habitats spanned a 30-year period. The present paper examines whether the birds advanced their breeding dates during that time and whether any long-term shifts in fecundity or productivity were detectable. Though temperatures in the settlement period (the second half of April) rose, neither males nor females significantly advanced their dates of arrival. Wood Warblers bred earlier in 2002–2005 than in the two previous periods — the combined effect of earlier female arrival and shortening of post settlement breaks. Clutch size declined with season, was smaller in the coniferous habitat and in rodent outbreak years, but no long-term trend was perceptible. Apart from two exceptionally successful years (2003 and 2004) breeding losses remained high during the whole study. Predation was responsible for 80–95% of them and was concentrated on the nestling stage. Overall Wood Warbler phenology and breeding performance in BNP have changed relatively little during the last 30 years. These findings support the results of other studies demonstrating the remarkable resilience of this primeval forest biota to environmental change.

Key words: Białowieża National Park, timing of breeding, climate change, clutch size, nest loss, nestlings’ ageing

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INTRODUCTION

Organisms inhabiting Europe are usually well prepared to live in spatially and temporally varying environments. However, during the last decades the rates of environmental transformation have exceeded enormously the background level: intensification of agriculture (reviews in Schifferli 2001, Newton 2004); trophic changes in marine habitats (e.g. Durant et al. 2005, Wannless 2007); increased nest predation (review in Langgemach & Bellebaum 2005); intensification of forestry (review in Hanski & Walsh 2004); climate change (e.g. reviews in Walther et al. 2002, Parmesan & Yohe 2003). The extent and rates of these changes raise a question whether the birds would be able to cope with them, if they were flexible enough to face the challenge (e.g. Stenseth & Mysterud 2002, Visser et al. 2004, Gienapp et al. 2007, Pulido 2007). Widespread declines observed in many species — 43% of European birds reached the “unfavourable conservation status” by the beginning of this century (Burfield & van Bommel 2004) — indicate that these concerns are well justified.

As birds have to respond simultaneously to numerous, frequently conflicting pressures, finding out which set of factors is responsible for the observed changes in any individual case can be extremely difficult, especially differentiation between effects of in situ human activities on local populations and of factors acting at much larger spatial scales (e.g. climate change) or — in the case of migratory birds — events happening thousands kilometres away (e.g. Webster et al. 2002, Pain et al. 2004, Szép et al. 2007). The correct answer to this question, though, is fundamental to any successful conservation action.

Therefore, studying birds in habitats with no direct human impact could be very helpful. Fortunately this is still possible in a few places in Europe, e.g. in the Białowieża Forest, situated on the Polish/Belarusian border. There, fragments of primeval forests, which once covered temperate European lowlands (Tomiałojć & Wesolowski 2005, Wesolowski 2007b), have been strictly
protected within the Białowieża National Park (BNP hereafter). The organisms at BNP live in conditions which prevailed in European forests before their transformation by humans, what makes this forest an invaluable reference site for all studies in forest ecology (Wesołowski 1983, 2005, 2007a, Tomiałojć et al. 1984), including studies of indirect human impact (e.g. Mitrus et al. 2005, Wesołowski & Cholewa 2009). In contrast to the vehement changes in the man-managed habitats (see references above), the primeval forest appears as an oasis of relative stability. Despite directional changes in numbers of some birds, species composition and structure of the breeding bird community at BNP remained stable during 30 years (Wesołowski et al. 2006). Similarly, though some signs of climate warming are detectable (Mitrus et al. 2005, Wesołowski & Cholewa 2009), the rate and amplitude of these changes are still far below those observed in many other places.

Wood Warblers are long-distance migrants breeding in Europe and wintering in equatorial Africa (Fouarge 1968). Conditions that they are exposed to in those areas, as well as, along the migration routes could have long-lasting, carry over effects (body condition, timing of arrival) on them. Therefore, Wood Warbler breeding performance could be to a large extent determined by events on the wintering grounds, or along migration route (Piotrowska & Wesołowski 1989, Sillett et al. 2000, Webster et al. 2002, Drent et al. 2007, Szép et al. 2007) and not by conditions within the breeding area itself. Within the European breeding area this ground nesting species showed a steady numerical decline in 1980–2006 (its numbers halved between 1990 and 2006, V migrant. So far, the declines are limited to the northern and western parts of the continent (Burfield & van Bommel 2004), whereas in Central (including Poland, Chylarecki & Jawińska 2007) and Eastern Europe their numbers fluctuate without any trend (Burfield & van Bommel 2004). It is completely unknown whether this pattern is due to some change in the breeding areas or outside them.

Here we present data on Wood Warbler spring arrival, breeding time, clutch size and nesting success in the primeval BNP forest spanning 30 years (1976–2005). The Wood Warbler numbers varied violently there, but without any long-term tendency (Wesołowski et al. 2009). We check if, in comparison with the seventies (1976–1979, Wesołowski 1980, 1985), the birds breeding at BNP 1) have changed their reproductive performance? 2) their arrival to the breeding area and onset of breeding has become earlier? 3) their clutch size has increased? 4) their broods became more secure?

**STUDY AREA**

The Białowieża Forest complex is situated at the Polish-Belarusian border. Its western part (613 km², about 45% of the area) lies inside Poland. The forest represents a remnant of the vast lowland forests that once covered large parts of temperate Europe. It presents a 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 47.7 km² block of the best preserved primeval old-growth stands has been retained within the strictly protected part of the Białowieża National Park (BNP). The primeval stands preserved in BNP are distinguishable by an array of features: they are multi-storey, mixed-species, uneven-aged, contain many oversized trees (the tallest Norway Spruce Picea abies reaches 55 m, and several other species reach 42–45 m), a large amount of dead timber and uprooted trees (Wesołowski 2007b). Detailed descriptions and photographs are available in Tomiałojć & Wesołowski (1990, 2005). Field data were gathered in the strictly protected part, chiefly in upland oak-lime-hornbeam stands composed mostly of Hornbeam Carpinus betulus, Lime Tilia cordata, Pedunculate Oak Quercus robur, Spruce and Continental Maple Acer platanoides. Data were also collected in swampy riverine forest, made up mainly by Alder Alnus glutinosa, Ash Fraxinus excelsior and spruce and in coniferous stands composed of Spruce and Scots Pine Pinus sylvestris with an admixture of birches Betula spp. and some oaks.

**MATERIAL AND METHODS**

**Breeding data**

Data on the timing of Wood Warbler arrival to BNP were gathered during the bird mapping censuses (Tomiałojć 1980, Wesołowski et al. 2006) carried out in 1976–2005 within permanent census plots, distributed in all main types of old-growth forest in BNP (Tomiałojć et al. 1984, Wesołowski et al. 2002, 2006). The observers mapped birds every day (except few breaks due to inclement weather).
between ca. 10 April and 25 June, shifting plots on a rotational basis. They also noted the first species’ appearance, even when found outside the plots. Therefore, there was a fair chance to detect the species’ appearance without any substantial delay.

Other phenological data could be reliably recorded only during three periods of intensive study: 1976–1979 (Wesołowski 1980, 1985), 1985–1988, and 2002–2005 (Maziarz 2006), covering jointly 12 years, stretching across a 30 year period. Then, to gather unbiased data on timing of breeding, clutch size, nesting success and nest loss rates, apart from the standard census work, additional detailed observations of singing males and nest building females (aimed at finding all nests) were carried out. Birds in some plots were additionally colour-ringed in 1976–1979 (Wesołowski 1980, 1985). The data were collected within fairly large (24–33 ha) permanent plots distributed in all main types of old-growth forest in BNP. Totally they covered up to 358 ha in the 1970s, and 187.5 ha thereafter (see Tomiałojć et al. 1984, Wesołowski 1985, Wesołowski et al. 2002, 2006, Wesołowski et al. 2007a, Tomiałojć & Wesołowski 1990, 2005 for detailed descriptions). Up to 90–100% of nests were found during the intensive study seasons. However, due to differences in the size of areas covered in individual seasons and strong fluctuations in numbers of breeding birds (Wesołowski et al. 2009), the number of nests actually found differed among seasons (27–133 nests/year).

Usually some days passed between the first observation (an extreme event) and the beginning of more numerous appearance of the consecutive males, so apart the arrival date, the males’ settlement date (= the first day with > 1 singing males recorded) was extracted from the field maps. Similarly the date of females’ arrival (= the first observation of a paired male in a season) was extracted from the field maps. The appearance of females was easily deduced from changes in the males’ behaviour — males accompanying females sung at lower rates and uttered shorter songs (Fouarge 1968, Wesołowski 1980, Temrin 1986).

With few exceptions (see below) nests were found at early stages of the nesting cycle (building, egg laying) and were followed from the onset of laying till their destruction or fledging of young. To avoid disturbance to surrounding vegetation the nests were checked mostly from a distance. They were closely approached only to count eggs and nestlings, as well as, to ring nestlings and adults (in 1977–1988). In nests found at later stages, the advancement of incubation was assessed by egg “candling” (Ojanen & Orell 1978, in 2002–2005) and nestlings’ age was assessed from their stage of development (see Appendix I). In order to avoid premature fledging, nestlings were counted at the age of nine days. Nests from which at least one young fledged were treated as successful, while nest from which whole clutches or broods with nestlings ≤9 days old disappeared were counted as depredated.

The start of egg-laying was directly recorded only in a fraction of nests. For the remaining ones, we estimated the first egg dates by “counting-back”. The calculations were based on the following assumptions: females lay one egg a day, clutches contain 6 eggs, and incubation starts after the laying of the last egg and lasts 13 days, while the nestling period is 13 days (Fouarge 1968, Wesołowski 1985, Glutz von Blotzheim & Bauer 1991, Cramp 1992). As in most seasons observations were truncated before the end of Wood Warbler breeding season (which could last till July 25 at BNP, Wesołowski 1985), to enhance comparability, in the current analysis we used only the first brood data, defined as all nests, which relative laying dates (= difference between the absolute date and the median egg-laying date of a season) fell within 20 days after the median (Fig. 1). Such defined first breeding attempts included inevitably a small proportion of replacement clutches (Wesołowski 1985) but without individual marking there was no way to eliminate them. Similarly, to allow for inter habitat comparisons of clutch size variation across years we used the relative clutch sizes (= difference between the absolute clutch size and the median clutch size of a season).
As complete nest histories were available, no need to apply the Mayfield’s estimates existed, and the nest success was expressed as a percentage of nests from which at least one young had fledged. For years in which > 30% of nests were found at the nestling stage (1985, 1988, 2002) different subsets of nests were used to calculate nest survival at the egg and nestling stages. Following Wesolowski (1985), only nests found during building, laying, and the first few days of incubation were used in calculating the pre-hatching losses. For calculation of the post-hatching losses only those nests which were found before hatching were used. The overall rate of nest loss was estimated using the following formula:

\[(1 - a \times b) \times 100\%\]

where \(a\) = fraction of nests with clutches from which at least one egg hatched, and \(b\) = fraction of nests with nestlings from which at least one young fledged. The amount of losses in different years was calculated for two stages of the nesting cycle separately: pre-hatching (egg laying and incubation) and post-hatching (nestling). Following Wesolowski (1985), failures at hatching were treated as the post-hatching losses.

Weather data

Meteorological data were derived from the local weather station at Białowieża village, situated in the centre of the Białowieża Forest, less than 1 km from southern edge of BNP. To describe patterns of temperature change across years and periods of the year we used means of mean daily temperatures for the respective time intervals.

To analyse an influence of variation in the local temperatures on the settlement dates and egg-laying commencement we calculated mean temperatures for individual periods preceding the respective events. The intervals were defined as follows: males’ settlement: between April 7 (the earliest record of Wood Warbler in BNP) and the day on which > 1 singing males were first recorded in a season; females’ arrival: between April 18 (mean date of males’ arrival) and the first observation of female in a given year; earliest clutch initiation: between three days preceding the first record of female in a season to the determinant date of the first laying female during this season; mean clutch initiation: from three days preceding the first record of female in a season to the determinant date of egg-laying commencement in the average clutch of this season.

We assumed that, already three days before arrival, the migrating females would be close enough to BNP, to be influenced by the local weather. On the other hand, the determinant date (Kluyver 1952) is the last day which the female has to make a decision on laying; temperatures after this date cannot influence the timing of laying. The length of the interval between the determinant date and the onset of laying is unknown in Wood Warbler, but we assumed that, similarly as in another small passerine — Great Tit *Parus major* (Kluyver 1952), it amounted to four days. This interval corresponds well with 3–4 days required for nest construction in Wood Warbler (Aschenbrenner 1966).

Defoliating caterpillars

The abundance of caterpillars was estimated once a year, in May, after leaves had fully developed. Each year standard twigs (ca. 0.25 m²) from 50–120 hornbeams in the lower parts of the under-canopy were searched and the caterpillars counted. The mean number of caterpillars/twig in a season served as the yearly index of abundance (extracted from Wesolowski et al. 2009).

Rodent abundance

Indices of spring numbers of rodents were taken from Wesolowski et al. (2009). They show combined numbers of Bank Vole *Myodes glareolus* and Yellow-necked Mouse *Apodemus flavicollis* caught per 100 trapnights in permanent plots in oak-hornbeam forest in spring (April/June).

Statistics

All statistical procedures follow the formulae given in Statistica for Windows (Statsoft 1996). All probability values shown in the text are two tailed. Except regression analyses, non-parametric tests are used throughout.

Presentation conventions

To extend the analysed time period we use the data gathered at BNP in 1976–1979, presented in Wesolowski (1985). We do not reiterate documentation provided there, so in most cases we present only data for the eight later seasons (1985–2005). However, to make a twelve year data set we incorporate the data from 1970s in all analyses of the long-term trends. Wesolowski (1985) has recognised three different habitats but, as Wood Warbler’s nests in swampy, ash-alder habitat were mostly found within drier “oak-hornbeam” patches, in the current analysis we combine these two habitat types into a single “deciduous” forest type.
RESULTS

Spring arrival and timing of breeding
First Wood Warblers were recorded at BNP on April 7–27 (mean = April 18) in different years. Their arrival dates did not change significantly over 30 years (regression’s B = -0.15, F = 1.7, p = 0.21, n = 28; Fig. 2) and were unrelated to changes in numbers (r_s = 0.11, p = 0.74). Consecutive males followed the first ones with a 2–12 (mean = 6) days delay, variation in their arrival dates matched that of the first records (r_s = 0.60, p = 0.040). The beginning of regular settlement did not show a significant long-term trend (Table 1) and was only weakly related to the temperatures in the preceding period (r_s = -0.43, p = 0.168). It was not influenced by varying numbers (r_s = 0.06, p = 0.86). First females appeared April 26–May 10 (mean = May 3), 7–14 (mean = 10) days after the onset of males’ settlement (Table 1). Their arrival dates did not change significantly over 30 years (Table 1) and were not related to the breeding numbers (r_s = 0.26, p = 0.44). The females, though, arrived earlier when the local temperatures were higher (r_s = -0.58, p = 0.064).

Egg-laying commenced between April 30 (2002) and May 17 (1976, 1987) in different seasons. In the majority of years the females had not even begun to settle, by the time the first females were already laying in the earliest spring (see above). The onset of egg-laying in the earliest clutches (Table 1), as well as, the mean laying dates (Fig. 3) advanced over 30 years (regression’s B = -0.20, F = 5.7, p = 0.038, n = 12). These changes, however, did not follow a continuous linear trend; the birds commenced breeding at similar dates in 1976–1988 but bred much earlier in 2002–2005 (Fig. 3). Mean egg-laying dates were strongly dependent on the local temperatures in the pre-laying period (r_s = -0.63, p = 0.039; Fig. 4). Usually, immediately after arrival, females began nest building and laid first eggs after about four days. However, due to bad weather spells, females postponed the nest construction or nests remained empty for up to eight days after completion (Wesołowski 1985). As a consequence, 7–11 days passed in some years between the female appearance and commencement of laying in the earliest clutch. The later first female appeared in a given season, the more days passed between her arrival and commencement of laying in the earliest nest (r_s = 0.62, p = 0.04). There was a tendency towards more synchronised laying in the later seasons (r_s = -0.68, p = 0.015, n = 12); it took 10–11 days from the onset of laying in the first nest to the yearly mean in the earliest springs, but only 4–6 days in the latest ones. Every year the egg-laying took place earlier (on average six days) in the deciduous than in the coniferous habitat (Wilcoxon Matched Pairs test, Z = 2.52, p = 0.012, n = 8; Table 2).

Table 1. Long-term trends in Wood Warbler arrival times, commencement of breeding, as well as, in spring temperatures, at BNP in 1976–2005 (n = 12 years). Dates expressed as Aprildays (1 = April 1). Definitions of periods see Methods – (Weather data). The regression coefficients (B) show the change (degrees or days) per year. * — 11 years.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>SD</th>
<th>B</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dates of:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>males’ settlement</td>
<td>23.3</td>
<td>3.65</td>
<td>-0.13</td>
<td>0.09</td>
<td>0.203</td>
</tr>
<tr>
<td>females’ arrival</td>
<td>33.2</td>
<td>3.43</td>
<td>-0.15</td>
<td>0.09</td>
<td>0.124</td>
</tr>
<tr>
<td>egg laying commencement</td>
<td>40.2</td>
<td>5.31</td>
<td>-0.30</td>
<td>0.12</td>
<td>0.032</td>
</tr>
<tr>
<td>Mean temp (°C) in periods preceding:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>males’ settlement</td>
<td>7.6</td>
<td>1.64</td>
<td>0.10</td>
<td>0.03</td>
<td>0.014</td>
</tr>
<tr>
<td>females’ arrival*</td>
<td>10.3</td>
<td>2.10</td>
<td>0.04</td>
<td>0.07</td>
<td>0.559</td>
</tr>
<tr>
<td>earliest clutch*</td>
<td>12.1</td>
<td>4.46</td>
<td>-0.02</td>
<td>0.13</td>
<td>0.890</td>
</tr>
<tr>
<td>mean clutch*</td>
<td>13.1</td>
<td>2.62</td>
<td>0.00</td>
<td>0.08</td>
<td>0.988</td>
</tr>
</tbody>
</table>
First clutches usually contained 6–7 eggs (89%, n = 378), eight-egg clutches (n = 4) and clutches with 4–5 eggs (ca. 10%) were infrequent. Mean clutch size differed across years in the deciduous forest (6.0–6.5 eggs, Kruskal-Wallis ANOVA: H = 16.32, p = 0.022; Table 3), though without any long-term trend (regression’s B = 0.00, p = 0.814). The annual variation bore no relationship to the mean breeding dates (rs = -0.14, p = 0.664, n = 12), nor was it significantly related to the availability of leaf-eating caterpillars (rs = 0.39, p = 0.213, n = 12, caterpillar data in Wesołowski et al. 2009). Clutches were smaller, though, during the rodent outbreaks (rs = -0.72, p = 0.009; Fig. 5).

Clutch size in the deciduous forest was on average 0.3 eggs larger than in the coniferous habitat (Wilcoxon Matched Pairs test: Z = 2.20, p = 0.028; Table 3). This was partially due to the strong decline of clutch size within a season (habitats: deciduous — regression’s B = -0.034, F = 21.5, p < 0.0001; coniferous — B = -0.037, F = 30.5, p < 0.0001) and later breeding in the coniferous forest (Fig. 6). However, a comparison of clutch size initiated at the same relative dates (from -2 days before median onwards) in both habitats showed that the clutches in the coniferous forest were still — by 0.2 eggs — smaller (Mann-Whitney’s Z = -2.77, p = 0.006).

Partial breeding losses

In nearly a third of clutches from which eggs hatched, one or more eggs failed to hatch (Table 4), on average 0.5 eggs/nest did not hatch. The partial loss rate in 1985–2005 varied between 0.20 (1986) and 0.80 (1985) eggs/nest, but this difference was not significant (Kruskal-Wallis ANOVA: H = 6.54, df = 7, p = 0.478). Clutch reduction did not significantly differ across clutch sizes (Kruskal-Wallis ANOVA: H = 4.69, p = 0.096; Table 4). There was also no long-term trend in the partial egg loss (regression’s B = -0.00, p = 0.926, n = 12) and it did not differ significantly between the two habitats: 0.53 (n = 248) and 0.32 (n = 62) eggs/nest in the deciduous and coniferous habitat respectively (Mann-Whitney Z_{adj} = 1.65, p = 0.10).

During the nestling period (i.e. from hatching to time when nestlings were 9 days old; see Methods) one or more young disappeared from 38% of 133 nests in 1985–2005. Additionally, at least seven further broods were partially destroyed by predators with nestlings ≥10 days old. The broods lost on average 0.44 nestlings (SD = 0.81, n = 104) in the deciduous habitat, and nearly three times less, i.e. 0.17 young (SD = 0.47, n = 29) in the coniferous stands, but this difference was
not significant (Mann-Whitney: $Z_{\text{adjusted}} = 1.69$, $p = 0.09$).

Partial egg losses were caused mostly by egg infertility and accidental egg eviction from nest. Only in about 30% of cases, in which eggs disappeared, the loss could be due to predation. The brood reduction, on the other hand, was totally due to nestling disappearance, i.e. most probably by partial nest predation. No nest with dead or dying young was found in 1985–2005.

The combined effect of the partial losses in egg and nestling stages resulted in reduction of average family size by 0.7 young below the initial clutch size, to 5.5 (SD = 1.20, $n = 139$) fledglings/nest.

**Total breeding losses**

Percentage of destroyed nests varied from 43.1% to 86.7% (mean = 65.4%, 1976–2005, Wesołowski et al. 2009) in different years. Nest losses in 2003 and 2004 (46.7 and 43.1% respectively) were unusually low, which produced a nearly significant long-term trend (arcsine transformed values, regression’s $B = -0.41$, $p = 0.072$, $n = 12$).

Predation was the most important mortality factor responsible for 80–95% of nest losses in different years. The role of predation did not change with time (regression’s $B = 0.08$, $p = 0.570$). Although, the rate of nest loss did not vary directly in relation to the number of rodents (regression’s $B = 3.76$, $p = 0.273$), the probability of failure was greater in the „rodent outbreak years” (Wesołowski et al. 2009).

In all seasons, nests containing eggs were less frequently destroyed than those with nestlings (Wilcoxon Matched Pairs test: $Z = 2.52$, $p = 0.011$; Table 5). Taking into account the unequal length of the two stages (pre-hatching period ca. 19 days, nestling period 10 days); daily loss rates of nestlings were four times those on eggs (5% d$^{-1}$ vs. 1.4% d$^{-1}$). Clutches and broods were destroyed with similar frequency in the deciduous and coniferous habitats (Fisher exact test, clutches: $p = 0.499$, broods: $p = 0.151$).

**DISCUSSION**

Mean temperature of the second half of April (but not of the first half of this month, neither that of May) have increased at BNP during the last 30 years (Wesołowski & Cholewa 2009). As the second half of April coincides with the settlement/pre-laying period of Wood Warblers at BNP, and Wood Warblers strongly react to the spring temperature variation (Wesołowski 1985, Sokolov et al. 1999a, b, Zalakevicius et al. 2006), this could have resulted in some acceleration of Wood Warbler’s spring phenology. That was only partially corroborated. The first arrival dates of males did not significantly change over 30 years, despite
increasing local temperatures (cf. Fig. 2 and Table 1). The females — as before — coming c. 10 days later than the males, have not substantially advanced their arrival dates to BNP either. This is understandable, as mean temperatures along the European section of their flyway (Italy–Central Europe–Białowieża, Fouarge 1968) during the migration period have not increased, if anything, some cooling was observed (Hüppop & Winkel 2006). Therefore, the birds were apparently arrested by “climatic barrier” (Ahola et al. 2004) S of the breeding grounds and could not speed up their arrival to BNP. In accordance with this explanation, Wood Warblers breeding ca. 200 km SW from Białowieża (1982–2006, Biaduń et al. 2009) and ca. 500 km W (1983–2003, Tryjanowski et al. 2005) did not significantly advance their arrival dates, either. However, the birds flying further North could take advantage of the warming weather, so nowadays they arrive to Lithuania significantly earlier than thirty years ago (1971–2004, Vilnius, mean date April 29, Zalakevicius et al. 2006). They also apparently advanced arrival to Tatarstan (ca. 55°N, 49°E, Askeyev et al. 2007). Red-breasted Flycatchers Ficedula parva, arriving to BNP at the beginning of May, took advantage of the warmer end of April as well, and nowadays they appear a week earlier than in the 1970s (Mitrus et al. 2005).

Table 4. Relation between clutch size and number of eggs hatched in Wood Warbler at BNP in 1985–2005. All seasons’ data lumped.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>≤5</th>
<th>6</th>
<th>7–8</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>% of broods being:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>of the same size as the clutch</td>
<td>56.0</td>
<td>74.3</td>
<td>63.5</td>
<td>68.1</td>
</tr>
<tr>
<td>smaller than clutch by one</td>
<td>28.0</td>
<td>18.9</td>
<td>23.4</td>
<td>21.6</td>
</tr>
<tr>
<td>smaller than clutch by two or more</td>
<td>16.0</td>
<td>6.8</td>
<td>13.1</td>
<td>10.3</td>
</tr>
<tr>
<td>Mean difference between clutch and brood size</td>
<td>0.7</td>
<td>0.4</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Sample size</td>
<td>25.0</td>
<td>148.0</td>
<td>137.0</td>
<td>310.0</td>
</tr>
</tbody>
</table>

Wood Warblers at BNP bred earlier in 2002–2005 than in the two former periods (Fig. 3). That was due to a combined effect of their earlier arrival and of reduction of the time lag between settlement and onset of egg-laying. Independent of local conditions, the early breeding at BNP was in many other seasons precluded by the late arrival of Wood Warblers to this area. Therefore — similarly as in Chiffchaff Phylloscopus collybita at BNP (Piotrowska & Wesolowski 1989), the onset of breeding at BNP was to a large extent dependent on factors acting on birds before their arrival to the breeding grounds. The later arrival, however, was usually coupled with longer post settlement breaks due to bad weather spells. Therefore the onset of breeding in the late seasons was additionally delayed by the local weather conditions. The delayed birds, though, apparently attempted to catch up with time, and in the late seasons they commenced breeding much more synchronously than in the early ones. Warmer spring temperatures, which apparently influenced the arrival of females to BNP, as well as, their pre-laying behaviour, resulted in the earlier breeding commencement of laying (Fig. 4). This strong temperature dependence of breeding seems to be the rule among temperate zone birds (Sokolov & Payevsky 1998, Crick & Sparks 1999, reviews in Sparks & Menzel 2002 and Dunn 2004).

Every year Wood Warblers bred earlier and laid larger clutches in the deciduous than in the coniferous forest (Wesolowski 1985, Table 2, 3), which could suggest that the latter habitat was of poor quality. However, since females chose to breed in the coniferous habitat even in the years, when there were hardly any Wood Warblers breeding in the deciduous habitat (Wesolowski et al. 2009), as nestlings in the two habitats grew at the same rate (Cisakowski 1988) and the breeding success did not differ between them, the coniferous habitat did not appear basically worse. Thus the later onset of breeding was probably due to phenological differences between habitats.

Table 5. Total failures (%) of Wood Warbler nests at BNP in relation to year and stage of the nesting cycle in 1985–2005.

<table>
<thead>
<tr>
<th>Year</th>
<th>Egg stage</th>
<th>Nestling stage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>% lost</td>
</tr>
<tr>
<td>1985</td>
<td>21</td>
<td>15.8</td>
</tr>
<tr>
<td>1986</td>
<td>31</td>
<td>28.6</td>
</tr>
<tr>
<td>1987</td>
<td>49</td>
<td>54.3</td>
</tr>
<tr>
<td>1988</td>
<td>32</td>
<td>36.8</td>
</tr>
<tr>
<td>2002</td>
<td>17</td>
<td>31.3</td>
</tr>
<tr>
<td>2003</td>
<td>86</td>
<td>6.2</td>
</tr>
<tr>
<td>2004</td>
<td>118</td>
<td>18.8</td>
</tr>
<tr>
<td>2005</td>
<td>59</td>
<td>17.9</td>
</tr>
<tr>
<td>Mean year</td>
<td>26.2</td>
<td>49.8</td>
</tr>
</tbody>
</table>
Insects, especially caterpillars, tend to be available earlier in the deciduous than in the evergreen habitats, e.g. Netherlands (oak vs. pine woods, van Balen 1973), S France (deciduous vs. evergreen oak stands, Blondel et al. 1993).

Despite the very strong decline of clutch size with date visible within a season (Fig. 6), Wood Warblers did not lay larger clutches in the early springs. Thus, in contrast to e.g. Pied Flycatcher *Ficedula hypoleuca* (von Haartman 1982, Winkel & Hudde 1997), they showed the relative type of clutch determination (earliest birds — largest clutches, independent of season, von Haartman 1982, Winkler et al. 2002). The same mode of clutch size determination was found also in other long-distance migrants: Reed Warbler *Acrocephalus scirpaceus* (Halupka et al. 2009) and in Great Reed Warbler *Acrocephalus arundinaceus* (Dyrcz & Halupka 2008).

Wood Warbler’s clutches at BNP became smaller in the rodent outbreak years (Fig. 5). Thus, Wood Warblers not only refused to settle at BNP during the outbreaks (Wesołowski et al. 2009) but the few birds which indeed bred then, reacted to the apparently perceived threat by laying fewer eggs.

Despite some variation, the partial nest loss rate remained the same throughout the whole study period and successful Wood Warbler broods contained on average 1.2 fledglings less than the number of eggs laid. Similarly predation stayed the most important mortality factor responsible for 80–95% of nest losses, and nests with young continued to be more frequently destroyed than the ones with eggs. Nesting success, though, appeared to be higher in 2002–2005, than in the earlier periods. However, it remains to be seen, whether the tendency to a more successful breeding would persist, or it was just an effect of the two exceptionally ‘good’ seasons concentrated near the end of our data series. The high nesting success in those years was not due to the lack of potential nest predators, as simultaneously studied Collared Flycatchers *Ficedula albicollis* (Walankiewicz 2007) and Marsh Tits *Poecile palustris* (T. Wesołowski, unpubl. data) did not face unusually low nest predation rates then. Only the pressure of rooting Wild Boars *Sus scrofa*, known to be an important threat of broods in 1970s (Wesołowski 1980), was much weaker in 2003–2005 (Maziarz 2006).

Additionally to the relatively high nesting success in 2002–2005, Wood Warblers that bred earlier had more time to initiate replacement clutches, or even to attempt second broods (Fouarge 1968, Wesołowski 1985, Lovaty 1987, Moreau 2001). Similarly as in Reed Warbler (Halupka et al. 2008) this could enhance their productivity even more than indicated by the data on the nesting success alone. So, those seasons were probably the most productive ones during the whole study period, and — at least — there was no indication of any decline in the reproductive output at BNP. Accordingly, the Wood Warbler numbers, though enormously variable, did not show any long-term decline in the Forest (Wesołowski et al. 2009). Therefore, nothing in BNP data indicates problems which could lead to extensive numerical decreases. Studies within the Wood Warbler’s decline areas in NW Europe (Burfield & van Bommel 2004, Vörišek et al. 2008) should be urgently carried out to see whether their current problems stem from worsening conditions on the local breeding grounds, or they are perhaps caused by events far away, e.g. on the tropical African wintering sites.

Summing up, in contrast to numerous studies in other areas, showing profound recent changes in birds’ ecology and behaviour (see Introduction), Wood Warbler’s phenology and breeding performance at BNP has changed relatively little during the last 30 years. Most patterns recorded in the late 1970ties (Wesołowski 1985) were still observable in 2002–2005. The birds kept arriving at much the same time, laid similar number of eggs, and had to cope with similar types of threats to their nests (predators attacking mostly nests with young). They only started to breed a few days earlier and, if that was not due to unusual events (see above), tended to breed more successfully. These results, along with the earlier ones (e.g. Tomiałojć & Wesołowski 2005, Wesołowski et al. 2006, Wesołowski & Cholewa 2009), confirm the remarkable resilience of this primeval forest to environmental change, underline the role of this place as an invaluable benchmark for all studies of forest biology (Lack 1965, Wesołowski 1983, 2007a, b, Tomiałojć & Wesołowski 1990, Stutchbury & Morton 2001, Blondel 2003).

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długoterminowych zmian. Zniesienia zmniejszały się jednak istotnie z upływem sezonu, były mniejsze w borach niż w lasach liściastych, zmniejszały się też w latach gradacji gryzoni (Tab. 3, Fig. 5, 6). W blisko1/3 legów zanotowano częściowe straty lęgowe (Tab. 4). Z wyjątkiem dwóch wyjątkowo korzystnych sezonów (2003 i 2004), straty całkowite były wysokie przez cały okres badań (Tab. 5). Ich główną przyczyną było drapieżnictwo (80–95%); drapieżniki najczęściej niszczyły gniazda z pisklétami. W okresie 30 lat zarówno fenologia, wielkość zniesień jak i efektywność rozrodu świstunek w Białowieskim Parku Narodowym zmieniły się tylko w niewielkim stopniu. Wyniki te są zgodne z rezultatami innych badań pokazujących dużą stabilność biocenoz tego pierwotnego lasu. W pracy (appendix) podano także cechy charakterystyczne w rozwoju piskląt świstunki pozwalające określić wiek młodych.

Appendix I. A key to ageing Wood Warbler’s nestlings. Based on descriptions of changes in nestling appearance in four broods at BNP in 2002.

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Appearance</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>hatching; naked (only down), reddish or orange colored, with bulging bellis</td>
</tr>
<tr>
<td>1</td>
<td>naked, hardly visible dark spots on wings</td>
</tr>
<tr>
<td>2</td>
<td>wings with distinct dark stripes, dark spots on back, head naked</td>
</tr>
<tr>
<td>3</td>
<td>remiges’ quills 1–4 mm, quills puncture skin on back, head with dark spots or stripes</td>
</tr>
<tr>
<td>4</td>
<td>remiges’ quills 4–7 mm, quills puncture skin on back and flanks</td>
</tr>
<tr>
<td>5</td>
<td>remiges’ quills 1 cm, quills break on throat and flanks (yellow feathers appear)</td>
</tr>
<tr>
<td>6</td>
<td>remiges with 1 mm feathers, quills break (green feathers appear) on head and back</td>
</tr>
<tr>
<td>7–8</td>
<td>remiges with 1–2 mm feathers, back feathered but quills’ bases still visible, quills on head</td>
</tr>
<tr>
<td>9</td>
<td>remiges with 4–5 mm feathers, quills on head break</td>
</tr>
<tr>
<td>10</td>
<td>remiges with 1 cm feathers (inner primaries with 1.5 cm feathers), rectrices 2–4 mm long, back completely feathered, quills’ remains still visible on head, young attempt to escape</td>
</tr>
</tbody>
</table>