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Blackcap *Sylvia atricapilla* numbers, phenology and reproduction in a primeval forest – a 33-year study

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Abstract. Data on Blackcaps gathered in 1975–2007 in an old-growth primeval forest (Białowieża National Park, Poland) are analysed to see whether the species numbers, breeding phenology or reproduction showed any long-term trends. Neither the clutch size (mean 4.8) nor the nesting success (c. 38%) changed but a number of directional changes during 33 years were observed. In comparison with the 1970s, in the 21st century Blackcaps arrived over two weeks earlier, but advanced egg-laying only by eight days. The breeding numbers increased threefold; they had been increasing slowly before 2000, but almost exponentially from 2001 onwards. The densities raised to c. 10 pairs/10ha in luxuriant riverine habitats. Due to structural changes in the oak-hornbeam habitat, in the 21st century Blackcaps situated nests lower, less frequently in conifers. The numerical increases were only partially accountable by structural changes in local habitats, but they were concordant with large-scale increases of Blackcaps across W Europe. It is hypothesised that the forest has recently been invaded by Blackcaps from strongly increasing, SW migrating, populations.

Keywords: timing of breeding, clutch size, nesting success, nest site, arrival date

Zusammenfassung

Anzahl, Phänologie und Fortpflanzung der Mönchsgrasmücke *Sylvia atricapilla* in einem polnischen Urwald – eine 33-jährige Studie

Daten über Mönchsgrasmücken, die zwischen 1975 und 2007 in einem ursprünglich gewachsenen Urwald (Białowieża Nationalpark, Polen) gesammelt wurden, wurden analysiert, um herauszufinden, ob Anzahl, Brutphänologie oder Fortpflanzung dieser Art irgendwelche Langzeit-Trends zeigen. Weder Gelegegröße (im Mittel 4,8) noch Bruterfolg (ca. 38%) änderten sich, doch eine Reihe gerichteter Veränderungen wurde während der 33 Jahre beobachtet. Im Vergleich zu den 1970er Jahren trafen die Grasmücken im 21. Jahrhundert mehr als zwei Wochen früher ein, begannen mit der Eiablage jedoch lediglich acht Tage eher. Die Anzahl brütender Tiere stieg um das Dreifache; vor dem Jahr 2000 war die Zunahme langsam gewesen, seit 2001 ist sie jedoch nahezu exponentiell. In üppigen Flusshabitaten stieg die Dichte auf ca. 10 Paare/10 ha an. Aufgrund von Strukturveränderungen im Eichen-Hainbuchen-Habitat legten Mönchsgrasmücken im 21. Jahrhundert ihre Nester niedriger und weniger häufig in Nadelbäumen an. Die zahlenmäßige Zunahme war nur zum Teil durch Strukturveränderungen in lokalen Habitaten zu erklären, stand jedoch im Einklang mit großräumigen Zunahmen von Mönchsgrasmücken in Westeuropa. Es wird die Hypothese aufgestellt, dass in letzter Zeit Mönchsgrasmücken aus stark zunehmenden, nach Südwesten wandernden Populationen in den Wald eingedrungen sind.

Introduction

Birds in temperate Europe have always had to cope with strongly seasonal and spatially diversified environments. However, during the last three decades or so, both the spatial scale and rate of transformations have been well over the historical background. Climate warming and its effects on birds have been attracting most attention (e.g. reviews in Bairlein and Winkel 2000; Winkler et al. 2002; Pulido and Berthold 2004; Crick and Sparks 2006), but there are more widespread problems to be tackled recently: large-scale changes in habitats (review in Wesołowski and Fuller in press), changes of trophic relationships (e.g. Durant et al. 2005; Wanless et al. 2007) or increased nest predation (review in Langgemach and Bellebaum 2005). This plethora of problems raise a question whether the birds would manage to cope if they were flexible enough to face the challenge (e.g. Stenseth and Mysterud 2002; Visser et al. 2004; Gienapp et al. 2007; Pulido 2007).

As birds have to respond at the same time to numerous – frequently conflicting – types of pressure (see reviews above), finding out which set of factors is responsible for the observed patterns in any individual case can be extremely difficult. It is especially troublesome to differentiate between effects of *in situ* human activities on local populations and factors acting at much larger spatial scales (e.g. climate change or landscape transformations) or – in the case of migratory Blackcaps – events happening thousands kilometres away (Fretwell 1972; Newton 2004, 2008). The correct answer to this question, though, is fundamental to the understanding of the population processes.

To disentangle this causal network, one would have to study birds in places free of direct human impact. Fortunately, this is still possible at few sites in Europe. One of them is the Białowieża Forest, situated on the Polish/Belarussian border, where fragments of primeval forests – which once covered temperate European lowlands – have been strictly protected within the Białowieża National Park (BNP hereafter; Tomiałojć et al. 1984; Tomiałojć and Wesołowski 2005; Wesołowski 2007). The organisms in the BNP live in conditions comparable with those prevailing in European forests before their transformation by humans, which makes this forest an invaluable reference site for all studies in forest ecology (Wesołowski 1983, 2005, 2007; Tomiałojć et al. 1984), including ones on indirect human impact. In contrast to the vehement changes in the man-managed habitats (see references above), the primeval forest appears as an oasis of relative

stability (Wesołowski et al. 2006, in press). Some signs of climate warming are detectable, but the rate and amplitude of these changes are still far below those observed in many other places (Wesołowski and Cholewa 2009; Wesołowski and Maziarz 2009).

Blackcaps commonly breed in the understory of temperate forests across Europe. They exhibit a whole array of wintering habits, from total sedentariness in SW Europe, through short-distance, European migrations, to long-distance migrations to tropical winter grounds in Africa (summarised in Glutz von Blotzheim and Bauer 1991; Cramp et al. 1992). Additionally, European populations show migratory divide: the ones West of 12^0 E heading chiefly SW, those East of 15^0 E heading chiefly SE (Glutz von Blotzheim Bauer 1991 after Zink 1973, but see Cepák et al. 2008). Although the Western populations have intensively been studied both in the breeding (e.g. Bairlein 1978; Bairlein et al. 1980; Gnielka 1987; Weidinger 2000, 2001; Remeš 2003a; Schaefer 2004) and the non-breeding seasons (e. g. Helbig et al. 1994; Berthold and Pulido 1994; Bearhop et al. 2005; Belda et al. 2007), data on the breeding ecology of the eastern populations are limited to few, mostly decades' old, papers (Steinfatt 1942; Ptušenko and Inozemcev 1968; von Haartman 1969; Malčevski and Pukinski 1983; Bocheński 1985; Payevsky 1999). Thus, data from the BNP (c. 24^0 E), spanning over three decades will substantially contribute to fill the gap.

Here I present data on Blackcap's numbers, breeding phenology and reproduction in the primeval forest collected during 1975–2007 (33 years). I check whether, in comparison with the 1970s, the birds breeding in the BNP have changed their numbers or reproductive performance; if their spring arrival and onset of breeding have advanced; whether their clutch size has increased; if their breeding productivity has changed.

Study area

The study was carried out in the best preserved central part (area of 47.5 km^2, strictly protected since 1921) of the Białowieża National Park in the Białowieża Forest (E Poland). A detailed description of this area can be found in earlier papers (e.g. Tomiałojć et al. 1984; Tomiałojć and Wesołowski 2004; Wesołowski et al. 2006). The Białowieża Forest is a remnant of vast European lowland forests once extending over a greater part of the continent and the BNP stands are distinguished among temperate forests by some specific features characteristic of rich primeval forests. These are: the multi-storey profile of stands, multi-species tree communities, an

impressive age, height and size of trees (the tallest Norway spruce *Picea abies* can reach 55 m, and several other species can be 42–45 m high), large amount of dead timber and uprooted trees, high species richness of other plants and animals inhabiting them (summarised in Wesołowski 2007).

The field work was mostly carried out within seven permanent census plots (total area of 187.5 ha) established in 1975–1976 (Tomiałojć et al. 1984). All the plots are situated in never managed old-growth stands of natural origin. Detailed descriptions of the vegetation composition in individual plots in different periods plus a map of their localisation in the BNP are given in Tomiałojć et al. (1984), Tomiałojć and Wesołowski (1996), Wesołowski et al. (in press). Below, only features of plots potentially relevant to Blackcaps, as well as information on changes in structure of their habitats during the study period, are summarised.

Ash-alder riverine forest *Circaeo-Alnetum* – plot K (33 ha). Open-canopy swampy riverine forest, made up mainly by alder *Alnus glutinosa*, ash *Fraxinus excelsior* and spruce, with c. 6 ha of dry 'islands' of the oak-lime-hornbeam type (see below). The rich understory is composed of hazel *Corylus avellana*, bird cherry *Padus avium*, rowan *Sorbus aucupari*a, and young canopy trees. The ground layer (0.5−1.7 m) is very luxuriant, with numerous currants *Ribes sp*, ferns *Athyrium filis-femina*, nettles *Urtica sp*. and reeds *Phragmites australis*. In comparison with the 1970s, the area is less swampy, its tree stands have become more patchy due to formation of new wind-fall gaps.

Alder-swamp forest *Carici elongatae-Alnetum* – plot L (25 ha). The alder carr gradually turns into an ash-alder association, both types with an admixture of spruces. It is largely an inundated area with a patchwork of almost permanent pools and minute tree-covered dry islands formed by tree-roots. It is characterised by a most luxuriant ground layer, and transparent canopy. During 33 years this patch of forest has hardly changed, becoming only more heterogeneous due to more intensive gap formation, and somewhat drier.

Oak-lime-hornbeam forest *Tilio-Carpinetum*. The most multi-layered forest association and with the highest and most complex canopy. Three, structurally fairly similar plots are situated in this forest type: W (25.5 ha), CM (24 ha) and MS (30 ha). The tree layer is composed mostly of hornbeam *Carpinus betulus*, lime *Tilia cordata*, pedunculate oak *Quercus robur*, spruce and Norway maple *Acer platanoides*. During 33 years tree falling led to creation of some new gaps. The proportion of old spruces was declining, while the share of lime and hornbeam was

increasing. There was no spruce regeneration but saplings of lime, hornbeams and – in the recent years – also Norway maples were plentiful. The shrub layer, mostly hazel and tree saplings, remained underdeveloped under the canopy but – in the last decade – the height of saplings and young trees in gaps was increasing much faster than previously; in several old gaps thickets (1–3 m tall) of young trees appeared. The latter was probably due to reduced pressure of large herbivores: in the last decade the numbers of red deer *Cervus elaphus* in the Białowieża Forest got reduced to a third of their 1990s level (Jędrzejewski et al. 2006).

Coniferous forest *Peucedano-Pinetum* – plots NW (25 ha) and NE (25 ha). The tree layer is composed of spruce and Scots pine *Pinus sylvestris* with an admixture of birches *Betula* sp. and of oaks. Trees are of moderate size, growing very densely. During 33 years the number of old pines and spruces decreased, and numerous new openings due to falling of clumps of dead spruces by wind appeared. The bush layer remained underdeveloped in the close canopy fragments, but the windfall gaps were rapidly colonised by young hornbeams, birches, limes and some spruces. As a consequence, the formerly old-growth, close-canopy, conifer-dominated stands were being progressively replaced by patches of young (up to 25 years), mostly deciduous, trees, a mixture of species characteristic rather of the oak-hornbeam habitat type.

Material and methods

Field data

Data on Blackcap's numbers were gathered during the bird mapping censuses (combined version, Tomiałojć 1980) carried out in 1975–2007 (33 years) within permanent census plots, distributed in all the main types of the old-growth forest in the BNP (see above). In total, they covered 187.5 ha. The observers mapped birds every day (except for few breaks in inclement weather) between c. 10 April and 25 June, shifting the plots on a rotational basis. Throughout the season, each plot was visited every 8–10 days. Detailed descriptions of the plots in different periods, as well as the census results for 1975–2007, are given in Tomiałojć et al. (1984), Tomiałojć and Wesołowski (1994, 1996), Wesołowski et al. (2002, 2006, in press).

Records of the timing of Blackcap's arrival to the BNP were usually made during the bird mapping censuses but the observers also noted the species' first appearance, even when outside the plots. Therefore, there was a fair chance to detect arriving Blackcaps (singing males

as a rule) without any substantial delay. Usually some days passed between the first observation (an extreme event) and the beginning of more numerous appearance of consecutive males. So, apart from the arrival date, the male settlement date (= the first day with > 1 singing males recorded in any of the deciduous plots) was extracted from the field maps.

Meteorological data were obtained from the local weather station at the Białowieża village, situated in the centre of the Białowieża Forest (Wesołowski et al. 2009; Wesołowski and Cholewa 2009; and unpubl. data of T. Wesołowski).

Nests were mostly found during standard census work, and checked at consecutive visits to the plots (every 8–10 days). Some nests detected outside the plots were also taken account of. Details of nest localisation were noted on finding, and changes in the nest content were recorded on the consecutive visits.

Data analysis

To analyse the influence of local temperature variation on the settlement dates, the mean temperatures (averages of daily means) for individual periods preceding the respective events were calculated. An assumption was made that the migrating birds were close enough to the BNP to be influenced by the local weather as early as three days before their arrival. Therefore, 6 April (three days before the earliest Blackcap observation in the BNP) was used as the initial date in the analysis. Temperatures were calculated for two periods: the first record temperature – the mean daily temperature between 6 April and the day of the first observation, the settlement temperature – the mean daily temperature between 6 April and the day on which >1 singing males were first recorded in the BNP.

All but few nests were found in the riverine or the oak-hornbeam forest. Therefore, all the breeding data analyses are limited to these two habitat types. Samples of nests from individual seasons were too small to permit year-to-year comparisons. Hence, the data were grouped and divided into three parts of different Blackcaps' densities: two equal-length intervals of low densities (1975–1987, 1988–2000) and a period of high numbers (2001–2007), cf. Fig. 1.

The commencement of egg-laying was directly recorded only for a fraction of nests. In the case of the remaining ones, the first-egg dates were estimated by 'counting-back'. The calculations were based on the following assumptions: females lay one egg a day, clutches contain five eggs (modal clutch size in the BNP, see below), incubation (from laying the last egg to hatching the

last egg) lasts 11 days and the nestling period in undisturbed nests spans 11 days (Glutz von Blotzheim and Bauer 1991; Cramp et al. 1992). Photos available in Berthold et al. (1990) were used to determine the age of nestlings. For the inexactly dated clutches the mid-ranges of possible first egg dates were used in calculations. The number of eggs found in the incubated nests – even if only once controlled – was treated as the clutch size.

As nests were found at different stages of the nesting cycle and their observations were not always continued till the failure or fledging of young, the nesting success was calculated from the nests' exposure. Following Weidinger (2000), the length of observation interval (number of days under control) and fate of the nest on the last visit (success or failure) were extracted from the nest histories. Included were only periods falling between the nest checks done after the onset of laying and those before the nestling age of eight days (potential fledging day, Manolis et al. 2000; Weidinger 2003, 2007). This was so because older nestlings could have left nests when disturbed, and thus beyond the age of 8 days it is impossible to say unequivocally whether the nest was successful or failed (Weidinger 2007). The so calculated exposure intervals were used for estimating the nests' daily survival rates. This was done with the logistic-exposure method (Schaffer 2004) implemented in the SAS statistical package. The nesting success values were arrived at by raising the respective daily survival rates to a power of 24 (= number of days from the onset of laying to nestlings 8 days old).

A nest was considered successful if it contained at least one young at the age of eight days. A nest was treated as lost when it had become inactive prematurely. If no signs of other modes of failure (deserted eggs, dead nestlings) were found, such nests were treated as depredated.

If not stated otherwise, the statistical procedures follow the formulae given in the STATISTICA for Windows (1996). All the probability values shown in the text are two-tailed.

Results

Breeding numbers. The numbers of Blackcaps in the BNP substantially increased with time – initially rather slowly, but the increase accelerated very strongly after 2000 (Fig. 1). Recently Blackcaps in the BNP have become became over three times more abundant than in the 1970s (Fig. 1). The increases occurred synchronously in all study areas (r = 0.65–0.90, P < 0.0005 for any pair-wise comparison of plots). As a result, within each area, mean densities were higher in 2001–2007 than in the two earlier periods (Table 1). The ratios of increase, though, were related

to the initial densities (r = -0.77, *P* = 0.024), the strongest increases (700–900%) were observed in coniferous areas with the lowest densities in 1975–1987. Despite these unequal increases, the breeding densities remained the highest in the riverine forest (max. 12.1 territories/10 ha, plot K, 2006), lower in the oak-hornbeam habitat and the lowest in the coniferous stands (Friedman ANOVA = 7.33, chi^2 ‘ 173.5, *P* << 0.001, Table 1).

Spring arrival. The first birds (usually singing males) were observed in the BNP between 9 April (2005) and 10 May (1987), mean 22 April (n = 31 years). The arrival dates strongly advanced with time, the first Blackcaps arrived recently over two weeks earlier than in the 1970s (Fig. 2). The recorded arrival dates were negatively correlated with Blackcap’s breeding numbers (cf. Fig. 1 and Fig. 2, *r* = -0.70, *P* << 0.001, n = 31), which could suggest that the detectability was enhanced by higher abundance. This was not the case, though. After removal of the long-term advancing trend (Fig. 2), the residual values showed only a weak negative correlation (*r* = -0.33, *P* = 0.07, *n* = 31) with the numbers of birds.

The onset of birds’ arrival was to a large extent unrelated to plant development in the BNP. Buds of hazel *Coryllus avellana* started to break at about the same time in 1979 and in 2006 (25 vs. 22 April), but the first Blackcaps were observed 15 days later in 1979 than in 2006. In 1990, a year of the earliest spring on record (Wesołowski 1998; Wesołowski and Rowiński 2006), hazel buds began to break about 20 March, but the first birds were observed as late as 18 April (Fig. 1).

Consecutive males followed the first ones with a 0–25 (mean = 6) days’ delay. They settled in both types of deciduous forest at the same time. Variation in their arrival times matched that of the first records (r_s = 0.81, *P* << 0.001). The beginning of regular settlement (mean – 28 April, *SD* = 8.31, *n* = 33) strongly advanced with time (*B* = -0.72, *SE* = 0.09, *P* << 0.001), moving by c. three weeks, from the second week of May in the 1970s to mid-April lately. Neither temperatures preceding the arrival (3.3–12.8^{0}C, mean = 7.3, *SD* = 1.99, n = 31) nor regular settlement (5.1–11.0^{0}C, mean = 7.3, *SD* = 1.47, *n* = 33) showed any long-term trend (*B* = 0.07 and -0.19, respectively). They were unrelated to the arrival and settlement dates (r = -0.19, *P* = 0.31) as well.

Timing of breeding. The earliest clutch was initiated on 30 April (2004), whereas the latest on 18 June (1983). The mean laying dates fell on the last decade of May (Table 2). Blackcaps nested in the riverine and oak-hornbeam forest at approximately the same time (Table 2). The

breeding season tended to advance with time in both habitat types (Table 2), but the difference became significant only after pooling the data (Kruskal-Wallis ANOVA $H_{2,242}$ = 8.9, $P < 0.02$). The advancing of breeding across periods was better pronounced when only the initiation dates of the earliest clutches were taken into account. The clutches were initiated c. 8 days earlier after 2000 than in the 1970s (Fig. 3). The advancement of breeding, though, lagged behind the males' accelerated settlement (c. 18 days, cf. Fig. 2 and 3).

Nest sites. Blackcaps placed their nests in a variety of supporting structures, from dry twigs on the ground to low-lying branches of trees (Table 3). In the riverine forest the majority of nests were in currants, while in the oak-hornbeam forest nests in hornbeam predominated (Table 3). In general, the nest substrates showed little overlap (Re = 29.8%) between the habitats. The frequency of nests in spruce dropped from 32.9% (n = 79) in 1975–1987 to 6.0% (n = 201) in later years (chi^2 = 36.3, $P << 0.001$), whereas the usage of hornbeams in the oak-hornbeam habitat – initially low (20%, 1975–2000, n = 70) – increased to 78.6% after 2000 (n = 117, chi^2 = 61.3, $P << 0.001$). The frequency of nesting in trees (low branches, offshoots on trunks) indicated the opposite tendency: 29.0% of nests built in trees within the oak-hornbeam habitat in 1975–2000, compared with only 3.5% recently (chi^2 = 24.7, $P << 0.001$).

Nests were situated from the ground level (2 cases) to a height of 6.5 m. They were placed much higher (mean 1.7 m) in the oak-hornbeam forest in 1975–1987 than in any other habitat or period (mean 54–93 cm, Table 4).

Clutch size. The clutch size ranged from two to six, five- (64.6%) and four-egg (19.6%, n = 189) clutches prevailing. Very small (2–3 eggs, n = 8) values were recorded mostly on single checks of incubated clutches, so they could have included some clutches after a partial nest loss. The mean size of clutches fell within the range of 4.5–5.0 eggs, without any clear differences between habitats or across periods (Table 5).

Nesting success & breeding loss. The overall nesting success in the BNP amounted to 38% (CI 28–48). In 1975–2000 Blackcaps reproduced equally well in the sparsely occupied oak-hornbeam habitat and in densely populated riverine forest (Table 6), but in 2001–2007 the nesting success in the former (26%) was apparently lower than in the latter (72%). However, on account of small samples and wide confidence intervals, neither these, nor any other differences, approached significance.

Nests (*n* = 73) were most frequently lost due to predation – 70%. In three quarters of depredation instances, the contents of nests disappeared traceless, without any damage to the nest structure. The remaining nests were slightly to completely damaged. Other causes of the total nest failure involved desertion (15%, only clutches) and mechanical damage (15%). The latter category included cases in which eggs/nestlings were spilled out from tilted or thrown down the nests. The brood size was on average lower than the clutch size by 0.3 eggs (*n* = 74), and the family size (= nestlings 8 days old) was smaller than the number of hatched eggs by 0.25 (*n* = 20). Overall, the number of fledglings was on average 0.5 young lower than the clutch size.

Discussion

Blackcaps breeding in the BNP displayed a number of directional changes during 33 years of observations. In comparison with the 1970s, currently (i.e. after 2000) they have been arriving substantially earlier, breeding at much higher densities, and using different nest sites (in oak-hornbeam forest). The possible reasons behind these trends will be discussed below, after checking how the BNP observations correspond with the results from other areas.

Similarly as in the BNP (Table 1), lush riverine forests have been the densest inhabited type of natural forest everywhere in Central/Eastern Europe (Ptušenko and Inozemcev 1968; Malčevski and Pukinski 1983; Gnielka 1987; Berthold et al. 1990). Dry deciduous forests, equivalent to the oak-hornbeam habitat in the BNP, have been less densely populated and coniferous forests with a deciduous undergrowth have harboured the lowest densities (review in Glutz von Blotzheim and Bauer 1991).

The onset of breeding in the BNP (the first decade of May, Fig. 3) occurred at the time predicted based on the area's geographic position, i.e. later than in S Germany and Bohemia (second half of April; Bairlein et al. 1980; Remeš 2003a; Weidinger 2008), at the same time as in England – Baillie et al. (2009), but earlier than in the SE Baltic (mid-May, Malčevski and Pukinski 1983; Payevsky 1999). It is unknown for how long Blackcaps in the BNP continued breeding, as observations were usually ceased at the end of June.

In accordance with findings in other areas (review in Glutz von Blotzheim and Bauer 1991; Payevsky 1999; Weidinger 2008), Blackcaps in the BNP used a wide spectrum of nest sites, and

hardly overlapping sets of nest supporting plants in different habitats (Table 3).The high frequency of nests in spruces (mostly small ones) in the BNP is characteristic of birds breeding in NE parts of the species range (Ptušenko and Inozemcev 1968; Malčevski and Pukinski 1983; Bocheński 1985; von Haartman 1969). Young spruces were used in the BNP as long as they were available. Their recent retreat, combined with the increasing availability of hornbeam thickets (see Study area section), could account for the observed shifts in the array of plants chosen for nesting in the oak-hornbeam habitat. Similarly, the availability of nest substrates close to the ground, increased after 2000, could be responsible for the recorded tendency to lower nest placement in the oak-hornbeam forest: after 2000, nests in trees – frequent in the 1970s – were hardly found there.

Breeding numbers. After the recent increases, the highest Blackcap densities in the BNP – 10 (12) territories/10 ha – have approached the highest values ever recorded (review in Glutz von Blotzheim and Bauer 1991). Still higher densities, reaching or exceeding 20 territories/10 ha have only exceptionally been found, usually in small patches (Bairlein 1978; Storch 1998; Remeš 2003b).

The very strong numerical increases observed in the BNP after 2000 (Fig. 1, Table 1) are to some extent explainable by favourable habitat changes – the increasing availability of a dense deciduous undergrowth in the oak-hornbeam and coniferous habitats. Die back of spruces has resulted in appearance of large new windfalls, especially in the coniferous forest. Simultaneously, tree regeneration in the old-canopy gaps has accelerated, in several places thickest of young trees, 1–2 m high, developing (see Study area section). This factor, however, could not account for the concurrent increases in the riverine forests, the habitat structure of which has not changed. Despite this structural stability, the Blackcap numbers (expressed as absolute values) have increased strongest there (Table 1).

In the 33 years of study, the growth of the species' breeding population in the BNP paralleled the increases of Blackcaps over large expanses of (mostly western) Europe, where their numbers nearly doubled in 1980–2005 and have been almost steadily increasing since 1995 (Voříšek and Škorpilová 2010). The increases in the BNP were also congruent with the numerical increases observed in the rest of Poland over the last decade (Chylarecki and Jaźwińska 2007). This suggests that the increases in the BNP, apart from being facilitated by local habitat changes,

were strongly influenced by wide-scale regional processes. The number of would-be settlers arriving at the BNP in spring was apparently much greater than in the 1970s. The increased pressure has resulted in more birds packing into available space, i.e. at higher breeding densities.

Spring arrival. In the 1970s the first Blackcaps were observed in the BNP from the last days of April till early May (Fig. 1). These observations correspond well with earlier findings from the Białowieża Forest (30 April–15 May; 1950–1977; Borowski and Okołów 1988), as well as those from the Romincka Forest, situated c. 200 km NNW from the BNP (3–10 May, 1935–1939; Steinfatt 1942) or Lublin, 200 km SSW of the study area (mean May 4, 1951–1958; Riabinin 1961). These figures taken together indicate a long, lasting for at least several decades, period of relative stability in the species arrival dates in this part of Europe. In the period mentioned Blackcaps arrived in E Poland, c. three weeks later than in Wrocław, a town situated 500 km SW (mean – April 10, Dyrcz et al. 1991). Recently Blackcaps arrive at the BNP and Lublin (Biaduń et al. 2009) over two weeks earlier than before, only about a week later than it is the case in SW Poland (Tomiałojć and Stawarczyk 2003). The mean temperature of the second half of April, the settlement/pre-laying periods of Blackcaps, has increased in the BNP during the last 30 years (but neither have the temperatures in the first half of April nor in May, Wesołowski and Cholewa 2009). It can be argued that Blackcaps have accelerated their arrival in reaction to the warming. This has only partially been confirmed by the evidence, though.

Two other long-distance migrants, coming to the BNP from the E/SE directions at the end of April/beginning of May have advanced their arrival at the BNP only slightly (Red-breasted Flycatcher *Ficedula parva*, c. 8 days, Mitrus et al. 2005) or not at all (Wood Warbler *Phylloscopus sibilatrix*, Wesołowski and Maziarz 2009). The contrast between the latter species and Blackcap is especially striking, as the two species apparently have to fly over the same parts of Europe (E Mediterranean, Balkans) at about the same time, i.e. they may have to face roughly the same weather conditions en route along the European section of their migration. Moreover, the mean April temperatures in SE Europe have not increased. If any change might be the case, some cooling has been observed here (Hüppop and Winkel 2006). Therefore, the advancing Blackcaps would have to fly against a ‘climatic barrier’ (Ahola et al. 2004) S of the breeding grounds. Or perhaps the earliest arriving birds are not coming from SE, as assumed herein, but from a quite different direction (see below).

The advancement of breeding (c. 8 days, Fig. 3) is far less conspicuous than the acceleration of males' arrival. This could be due to the increasing asynchrony between timing of sexes' arrival or, as suggested by data from the S Baltic (Rainio et al. 2007), both sexes could have accelerated their arrival to the same extent, but the earlier coming females spend more time on the breeding grounds before commencing breeding. However, the data at hand do not allow to differentiate between these two possibilities.

Nest success & habitat quality

The overall nest success of Blackcaps – 38% – remained within the range of values) found for other ground nesters in the BNP (27–40%, Wesołowski and Tomiałojć 2005). It was lower than in numerous other areas (45–60%, Mason 1976; Bairlein et al. 1980; Gnielka 1987; Payevsky 1999; Remeš 2003a; Baláž et al. 2007) but, as the latter figures – calculated with traditional methods – were probably overestimated, the difference could be more apparent than actual. The values recently recorded from Central Europe with the application of the 'nest-exposure' method (15–25%, Weidinger 2000, 2007; Remeš 2003b) are much lower than those found in the BNP. The relatively small samples and large confidence intervals (Table 6) allow only for tentative conclusions. Yet, it seems that there were no consistent differences between the densely populated riverine habitats and the sparsely inhabited oak-hornbeam forest. It appears as well, that the long-term increase in numbers (with a possible exception of the oak-hornbeam forest) did not result in the nest success lowering. As these two habitats did not differ in settlement dates, the timing of breeding (Table 2) or the clutch size (Table 5), either, they constituted equally suitable habitats for breeding Blackcaps, albeit at different densities. This agrees well with Weidinger (2000) but remains in the sharp contrast with the findings by Remeš (2003b). He observed that the nesting success of Blackcaps breeding in a black locust *Robinia pseudoacacia* plantation, occupied early and at a very high density, was only 15%, while in a less densely inhabited and more natural riverine forest nearby it amounted to 59%. This was, however, a case of birds being lured to an attractively looking but dangerous man-made habitat.

Expansion of 'western' Blackcaps?

The European Blackcaps show migratory divide, the 'western' birds heading chiefly SW, the 'eastern' ones heading chiefly SE, through the Eastern part of the Mediterranean (Glutz von Blotzheim and Bauer 1991 after Zink 1973, Cepák et al. 2008). The BNP is situated far east from

the divide, so the Blackcaps coming to breed there should be 'pure eastern' ones. Observations in the 1970s were consistent with this picture. Then Blackcaps appeared in the BNP about three weeks later than in areas situated c. 500 km SW (see above). The delay was too substantial to be explained by the distance between the sites, so the idea that these areas had been colonised by birds coming from different migratory directions was plausible. As temperatures in SE Europe did not rise in the migration period in the last decades (Hüppop and Winkel 2006), the birds coming from the SE direction would not have had a stimulus to advance their arrival (see above). Still, the Blackcap's arrival dates advanced by more than two weeks. I propose here that this is because Blackcaps from the strongly numerically increasing western populations (see above) have recently spread to the East and colonised the BNP. The very early Blackcaps observed lately in the BNP would thus be of SW origin, and the current breeding population would be composed of a mixture of birds from both sides of the migratory divide. This being true, one should be able to demonstrate that the earliest settling birds share the genetic structure, stable isotopes signatures and morphological features with the SW ones (see below).

The recent spread of 'western' birds east of the former migratory divide could also explain the unsubstantial differentiation in mitochondrial and microsatellite DNA between populations from the opposite sides of the SW/SE divide found by Pérez-Tris et al (2004) and Rolhausen et al. (2009). The authors interpret these results as a sign of the recent origin of differences in the migratory behaviour. Could it not be so that the West/East differences were once much more pronounced, but they have diminished now by an invasion of the 'western' genotypes into the Eastern populations? This could be tested by 1) analysing DNA from skins of European breeders collected before the 1970s, 2) sampling Blackcaps from the Easternmost parts of their range. Such comparisons can yield much stronger contrasts.

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Figures' legend

Fig. 1 Changes in numbers of Blackcaps in the Białowieża National Park (1975-2007). The numbers increased slowly in 1975-2000 (B = 0.93, SE = 0.44, P = 0.046) and very fast from 2000 onwards (B = 26.0, SE = 3.94, P = 0.006).

Fig. 2. Variation in Blackcap's first observations dates in relation to year in the BNP (1975-2007, 31 years). The arrival dates significantly advanced with time (regression slope: B = -0.59, SE = 0.11, P < 0.001).

Fig. 3. Variation in onset of Blackcap's breeding in relation to period in the BNP (n = 11-21 nests/period). Median dates (black squares), 25-75% (boxes) and ranges (whiskers) of clutches initiated in the ten days following the earliest clutch within the period are shown. The laying dates significantly advanced with time (Kruskal-Wallis ANOVA $H_{2,52}$ = 24.6, P < 0.001).

Table 1. Blackcap densities (territories /10 ha) in the BNP in relation to habitat and study period.

Habitat & plot	1975-1987		1988-2000		2001-2007		Kruskal-Wallis ANOVA	
	Mean	SD	Mean	SD	Mean	SD	*H*	*P* <
Riverine								
K	5.3	1.1	5.5	1.0	10.0	1.4	16.4	0.001[a]
L	3.7	0.8	3.7	0.6	6.0	1.0	15.0	0.001[a]
Oak-hornbeam								
W	2.6	0.8	2.9	0.7	4.5	1.3	10.2	0.006[a]
CM	2.2	0.6	2.5	0.7	5.5	1.7	16.3	0.001[a]
MS	1.5	0.4	2.1	0.8	4.9	1.7	17.6	0.001[a]
Coniferous								
NE	0.3	0.3	0.5	0.4	2.2	1.3	16.5	0.001[a]
NW	0.3	0.3	0.6	0.3	2.7	1.0	19.2	0.001[a]

[a] densities were higher in 2001-2007 than in any earlier period (Tukey post hoc test, largest P < 0.002).

Table 2. Timing of clutch initiation by Blackcaps in the BNP in relation to habitat and period. Date expressed as April days (1 = April 1).

Period	Riverine		Oak-hornbeam		Mann-Whitney	
	Mean (SD)	*n*	Mean (SD)	*n*	*Z* adjust.	*P*
1975-1987	59.8 (10.8)	33	56.8 (7.1)	33	1.36	0.17
1988-2000	54.6 (11.2)	25	53.2 (10.6)	28	0.14	0.89
2001-2007	54.5 (12.0)	25	51.2 (9.6)	100	1.84	0.45
Kruskal-Wallis	$H = 3.83$,		$H = 3.81$			
ANOVA	$P = 0.15$		$P = 0.14$			

Table 3. Nest sites of Blackcaps in the BNP in relation to habitat.

Nest site	Riverine		Oak-hornbeam	
	n	%	n	%
Ribes sp. – currant	52	56.5	4	2.1
Picea abies – spruce	11	12.0	21	11.2
Athyrium filis-femina – lady fern	8	8.7	0	0
Coryllus avellana – hazel	5	5.4	11	5.9
Carpinus betulus – hornbeam	4	4.3	106	56.7
Tilia cordata – lime	0	0	16	8.6
Urtica sp. – nettle	3	3.3	15	8.0
Dry branches	2	2.2	11	5.9
Other	7[a]	7.6	3[b]	1.6
Total	92	100	187	100

[a]*Humulus lupulus* – 3, *Padus avium* – 2, *Rhamnus catharticus* – 1, rootpads of fallen tree – 1

[b]*Padus avium* – 1, *Ulmus sp*. – 1, rootpads of fallen tree – 1

Table 4. Height above the ground (cm) of Blackcap nests in the BNP in relation to habitat and period.

Period	Riverine		Oak-hornbeam		Mann-Whitney	
	Mean (SD)	*n*	Mean (SD)	*n*	*Z* adjust.	*P*
1975-1987	93 (83)	29	173 (130)	35	2.78	< 0.006
1988-2000	76 (56)	25	74 (81)	28	-0.90	< 0.37
2001-2007	67 (51)	20	54 (39)	91	-1.15	< 0.25
Kruskal-Wallis ANOVA	*H* = 1.29, *P* = 0.52		*H* = 27.4, *P* << 0.001[a]			

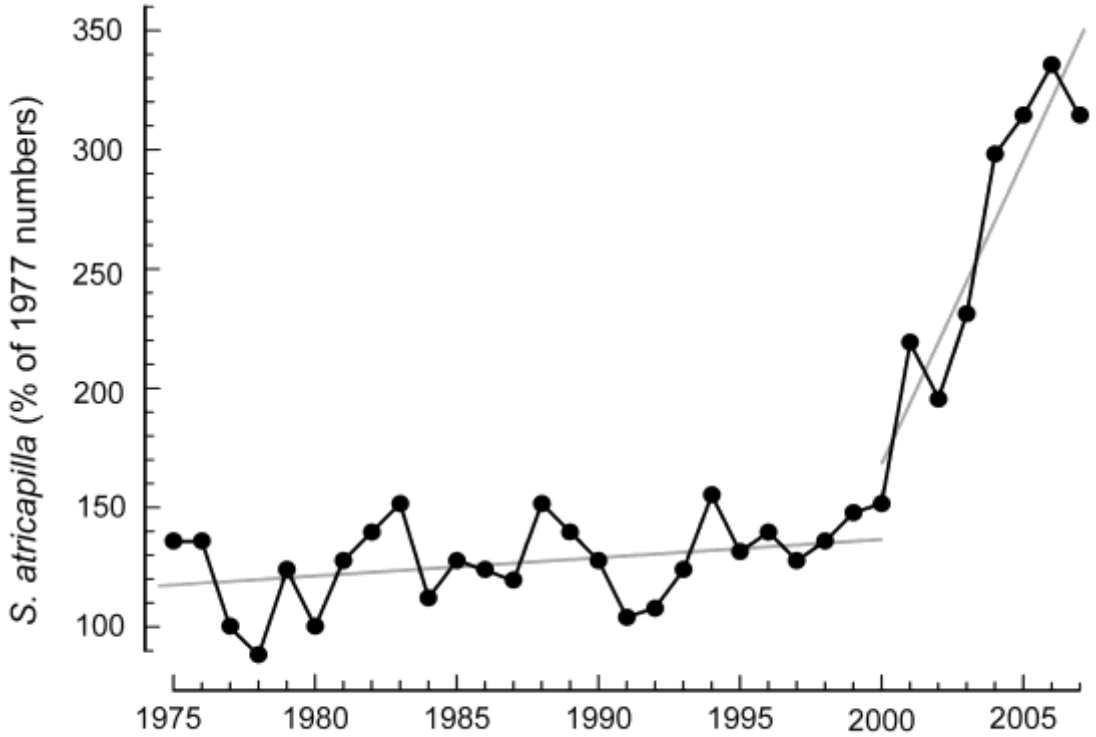
[a]due to difference between the earliest and middle periods (*H* = 19.8, *P* << 0.001).

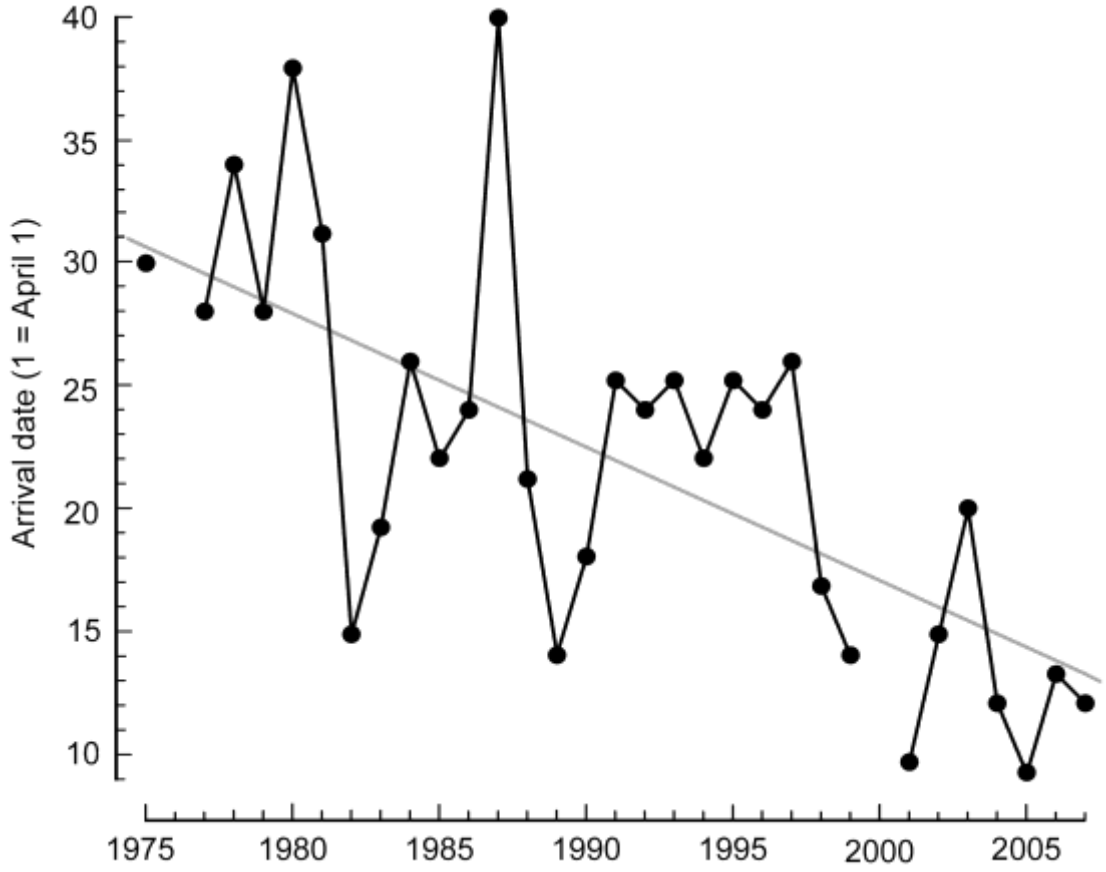
Table 5. Clutch size of Blackcaps in the BNP in relation to habitat and period.

Period	Riverine		Oak-hornbeam		Mann-Whitney	
	Mean (SD)	n	Mean (SD)	n	Z adjust.	*P*
1975-1987	4.9 (0.61)	24	4.8 (0.88)	26	-0.22	0.83
1988-2000	4.5 (0.77)	19	5.0 (0.59)	21	-1.79	0.07
2001-2007	4.9 (0.56	22	4.8 (0.75)	74	0.02	0.99
Kruskal-Wallis ANOVA	H = 3.47, *P* = 0.18		H = 0.47, *P* = 0.79			

Table 6. Nesting success of Blackcaps in the BNP in relation to study period and habitat. Nest/days – *n* nests/*n* observation (exposure) days. DSR – daily survival rate, CI – 95% confidence interval. Success – percentage of nests surviving 24 days.

Period	Riverine			Oak-hornbeam		
	Nest/days	DSR (CI)	Success (CI)	Nest/days	DSR (CI)	Success (CI)
1975-1987	21/157	0.965 (0.917-0.985)	42 (12-70)	24/283	0.969 (0.939-0.985)	47 (22-69)
1988-2000	16/169	0.956 (0.905-0.981)	34 (9-62)	16/193	0.966 (0.927-0.985)	44 (16-69)
2001-2007	15/165	0.987 (0.947-0.997)	72 (27-92)	71/616	0.945 (0.922-0.962)	26 (14-40)
1975-2007	52/491	0.970 (0.949-0.983)	48 (28-65)	111/1092	0.958 (0.941-0.969)	35 (23-47)

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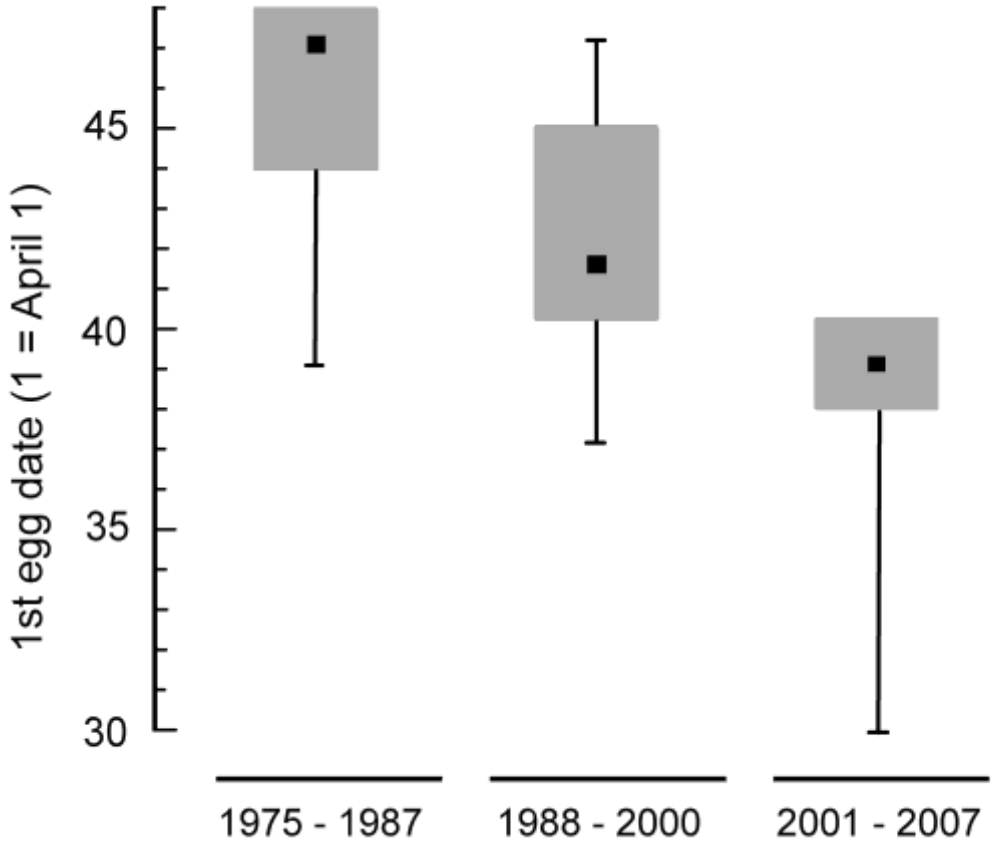
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1975 - 1987
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