Habitat and Annual Variation in Arthropod Abundance Affects Blue Tit Cyanistes caeruleus Reproduction

Authors: Marciniak, Barbara, Nadolski, Jerzy, Nowakowska, Magdalena, Loga, Barbara, and Bańbura, Jerzy

Habitat and annual variation in arthropod abundance affects Blue Tit *Cyanistes caeruleus* reproduction

Barbara Marciniak[1], Jerzy Nadolski[2], Magdalena Nowakowska[1], Barbara Loga[2] & Jerzy Bańbura[1]*

[1]Department of Experimental Zoology and Evolutionary Biology, University of Łódź, Banacha 12/16, 90–237 Łódź, POLAND
[2]Museum of Natural History, University of Łódź, Kilińskiego 101, 90–011 Łódź, POLAND
*Corresponding author, e-mail: jbanb@biol.uni.lodz.pl

Abstract. Arthropod assemblages living in tree canopies in two habitat types — a rich woodland and poor parkland — were studied in 2003–2005 as a background for describing the dynamics of caterpillars; the study system was located in central Poland. Caterpillars, the optimal food of breeding tits, varied in abundance between both habitats and years. The peak abundance of caterpillars was at least 3 times higher in the woodland than in the parkland habitat. There were also pronounced differences in caterpillar production between years, with every consecutive year during 2003–2005 being trophically worse than the previous one. The Blue Tits' timing of breeding coincided roughly with the timing of caterpillar abundance in particular years. Mean clutch size corresponded strictly to the inter-habitat and inter-year pattern of variation in caterpillar availability, suggesting adaptive responses in Blue Tit reproduction to food resources.

Key words: Blue Tit, *Cyanistes caeruleus*, habitat variation, annual variation, arthropods, caterpillars, food, clutch size, timing of breeding

Received — March 2007, accepted — May 2007

INTRODUCTION

Caterpillars are especially important as food resources for insectivorous birds during the breeding period (Morse 1971). Tits, especially the Great Tit *Parus major* and the Blue Tit specialise in exploiting caterpillars as the most profitable food for their nestlings (Blondel et al. 1991, Perrins 1991, Bańbura et al. 1999). Caterpillars contain a balanced proportion of essential nutrients and water necessary for tit nestling development and, in addition, their sizes and physical form are suitable for easy swallowing by nestlings (Perrins 1991, Zandt 1997, Bańbura et al. 1999). Most caterpillar species feeding on fresh foliage of deciduous trees possess these properties and are very numerous. As assessed by Perrins (1979), the foliage of just one big oak tree may be occupied even by a hundred thousand caterpillars. Although it is well known that tit nestlings require also some additional components of their diet, for instance spiders (Perrins 1979, 1991, Tinbergen 1981, Graveland & Drent 1997, Zandt 1997, Bańbura et al. 1999, Naef-Daenzer et al. 2000), yet the timing of Blue and Great Tit breeding is usually adjusted to the period of the rich availability of caterpillars (van Balen 1973, Cramp & Perrins 1993, Dias & Blondel 1996, Bańbura 1997, Lambrechts et al. 1997, Blondel et al. 1999, 2006). Because of time constraints on this food resource, the key condition for tits to efficiently utilise it is to be able to synchronise the most food-demanding life-stage with it. Tits have been known to more or less precisely synchronise their breeding with caterpillar production in tree canopies even in caterpillar-poor habitats where caterpillar proportion in tit nestling diet is relatively low (Perrins 1979, 1991). In areas where habitats differ in the abundance and timing of caterpillars, tits may or may not make a correct adaptive decision on reproduction with respect to the timing and clutch size, depending on evolutionary and ecological circumstances (Perrins 1965, Pettifor et al. 1988, Dhondt et al. 1990, van Noordwijk et al.

1995, Blondel et al. 1999, Postma & van Noordwijk 2005).

The foliage of tree canopies is a very special habitat for herbivorous insects, including caterpillars, as well as for other arthropods (Clark et al. 1967, Verley 1970, Lowman & Whitman 1996, Murakami 2002). Developing leaves of deciduous trees produce enormous biomass in a very short time, providing herbivores with very rich food resources. Herbivory generates strong pressures on leaves, which can dramatically reduce tree production and survival (Southwood 1984). An adaptive response of trees is a chemical war with herbivores — maturing leaves become unpalatable because of great amounts of secondary metabolites synthesised by the tree and because of the hardening of leaf tissues (Feeny 1970, Southwood 1984, Buse et al. 1998, 1999, Forkner et al. 2004). As a consequence, most herbivorous insects synchronise their life-cycle stages demanding rich food resources with a relatively short time when leaves develop from buds. It is also possible that bud consumption may provide adult tits with some cues when to start laying eggs (Bourgault et al. 2006). Different trees show different chemistry and phenologies, especially at the inter-species level but also, to some extent, at the intra-population level (Lawrence et al. 1997, Martel & Kause 2002, Cizek et al. 2006).

The herbivore assemblage is shaped by interactions with plants as well as under the influence of natural enemies, predatory and parasitoid arthropods and insectivorous birds (Schoenly 1990, Murakami & Nakano 2000). Caterpillars or the larvae of Lepidoptera and in some habitats caterpillar-like larvae of sawflies (Symphyta, Hymenoptera) (hereafter both called caterpillars) constitute a very important component of the tree foliage insect assemblage (Veistola et al. 1995, Martel & Kause 2002). They can reach enormous numbers and biomass, yet they have only occasionally been analysed at the background of the whole tree canopy arthropod community (Clark et al. 1967, Lowman & Whitman 1996).

The aim of this study was to show habitat- and year-related variation in the abundance of caterpillars at the background of the entire arthropod assemblage living in tree foliage. With great differences in the availability of caterpillars resulting from contrasting differences between habitats and years, we expected and analysed corresponding variation in two basic breeding characteristics of the Blue Tit: the timing of egg laying and clutch size.

MATERIALS AND METHODS

Study sites

This study was part of a long-term research into the breeding biology of tits around Łódź, central Poland. The study was carried out in two contrasting types of habitat: parkland and woodland habitats. The two types of habitat were chosen deliberately on the basis of the premise that the quantity and quality of insects, and especially caterpillars in the parkland habitat is lower than in the woodland habitat as a result of the influence of human-related and urban-related factors.

The description of the parkland part of the study area is based on Krzemińska-Freda (1996). The parkland area consists of two units, the Łódź Botanic Garden (65 ha) and the neighbouring Łódź Zoological Garden (17 ha). Both gardens belong to a south-west part of a large parkland area (ca. 500 ha) in the western part of the city of Łódź; the whole area is a remnant of an ancient deciduous forest dominated by hornbeam *Carpinus betulus* and oaks *Quercus robur* and *Q. petraea*. The vegetation of the Zoological Garden comes from the forest but it has been heavily fragmented by paths, buildings and fenced deforested exposition spaces for animals. There are some small patches artificially wooded with Scots Pines *Pinus silvestris*, birches *Betula* sp. and some exotic tree species. Only a very limited fragments of the Botanic Garden consist of the forest. The vegetation of the most part of this garden was formed artificially for the purpose of plant exposition, so that the tree cover is patchy with a large area of tree-free spaces. Tree patches are a mosaic of different stands of deciduous and coniferous trees, in some part exotic species, usually dispersed among native species. Among native deciduous trees, the most numerous are birches *Betula* sp., poplars *Populus* sp., oaks *Quercus* sp., willows *Salix* sp., limes *Tilia* sp., maples *Acer* sp., alders *Alnus* sp. and many others, usually more dispersed. In the studied nestbox-supplied part of the parkland habitat, the first four tree genera are dominant and approximately equal in numbers. The south and south-east sides of the Botanic Garden border on a highly urbanised area of the town with numerous blocks of flats.

The woodland study habitat, Łagiewniki forest, is a rich deciduous forest of considerable size, ca. 1250 ha, located N–E of Łódź (Kurowski 2001). Some fragments of the forest were chopped down in the 1940s and have subsequently been reforested. The most of the forest directly comes from the

ancient woodland typical for the geographical area of central Europe. It represents different plant communities, mostly oak and hornbeam forests. In the study sites that are located in the central part of the forest, covering ca. 200 ha, oaks *Quercus robur* and *Q. petraea* are dominating tree species. The tree age structure is mature with all age-classes represented, and many trees as old as ca. 200 years present. Some dead tree logs are usually maintained at places where they have grown.

Arthropods

In 2003–2004, we carried out a study of arthropods using Moericke traps — round yellow containers, diameter 16.6 cm, with a mixture of water, glycol and detergent (Moericke 1951, Nadolski et al. 2004). The containers, 28 in the woodland and 18 in the parkland, were hanged under tree canopies. Frassfall was collected in 2003–2005 into tissue collectors, 1 x 1 m or 1 m^2 squares on a metal framework, also hanged below tree canopies, 9 in the woodland and 5 in the parkland. Both types of traps were checked and emptied every 5 days. The frassfall collectors in the parkland were placed under birches (2), oak (1), willow (1) and poplar (1) to roughly represent the relative numbers of particular tree genera within the study area. In the forest, the collectors were placed under oaks, with some overlap with hornbeam and birch crowns in two cases; the distribution also being proportional to tree species composition. Moericke traps were also distributed in proportion to tree genera abundance but with the wider spectrum of tree species included.

In the laboratory, the arthropod samples collected in Moericke traps were segregated into orders, and into age stages where applicable, counted and weighed to the nearest 0.1 mg. Samples from frassfall collectors were inspected under the microscope to separate caterpillar frass from other particles. The frass particles were dried (60° C) and weighted to the nearest 0.1 mg. For each study site, the resulting masses and counts were recalculated and are given as mean values per trap per day. As the samples of frassfall for the parkland study site in 2003 got lost, we used counts of caterpillars from the Moericke traps from the same trees where frassfall collectors were placed to estimate values of corresponding frassfall, taking into account the fact that peak amount of frass occurs ca. 10 days before the date of maximum number of caterpillars in Moericke containers (Nowakowska 2007). The peak amount of frass is considered the most important because it direct-ly indicates the production of caterpillar biomass exploited by birds (Zandt 1994, Fischbacher et al. 1998). Moericke traps are known not to be a reliable method for all groups of arthropod but we consider it useful for both the purpose of alternative estimating of caterpillar abundance and, especially, the purpose of obtaining general characteristics of tree canopy arthropod communities.

Blue Tit breeding

This study was conducted in 2003–2005, using wooden nest boxes — 250 located in the woodland site and 200 in the parkland site. In both the sites, distances between neighbouring nest boxes were at least 50 m. To collect basic data on the breeding cycle of Blue Tits, the nest boxes were visited at least every week. Two breeding variables concerning the first brood only were analysed for the purpose of this study, the date of first egg laying (laying date) and clutch size. The number of analysed clutches ranged from 19 to 33 per year in the parkland and from 35 to 79 per year in the woodland.

Most Blue Tits in our study populations laid only the first or repeat clutch. Only a very low fraction of ca. 5% had also the second brood. In comparison with many other populations the level of ectoparasitism was low in our study areas (Słomczyński et al. 2006).

Data analyses

Graphical and statistical analyses were conducted applying STATISTICA 6 (StatSoft, Inc. 2003).

RESULTS

The structure of the tree canopy arthropod assemblage differed markedly between the parkland and woodland habitats studied (Fig. 1). Dipterans dominate in both types of habitat but their proportion in the woodland was much higher than in the parkland (Fig. 1). The habitats differed also with respect to seasonal dynamics of the abundance of this order. In the woodland, the peak abundance of dipterans occurred in spring in both years (2003 and 2004), while in the parkland the peak occurred in spring 2003 but in late summer 2004. Additionally, the numbers of dipteran individuals, and, actually, other orders as well, were distinctly higher in the woodland than in parkland. During the peak period, the number of Diptera individuals per one Moericke trap per
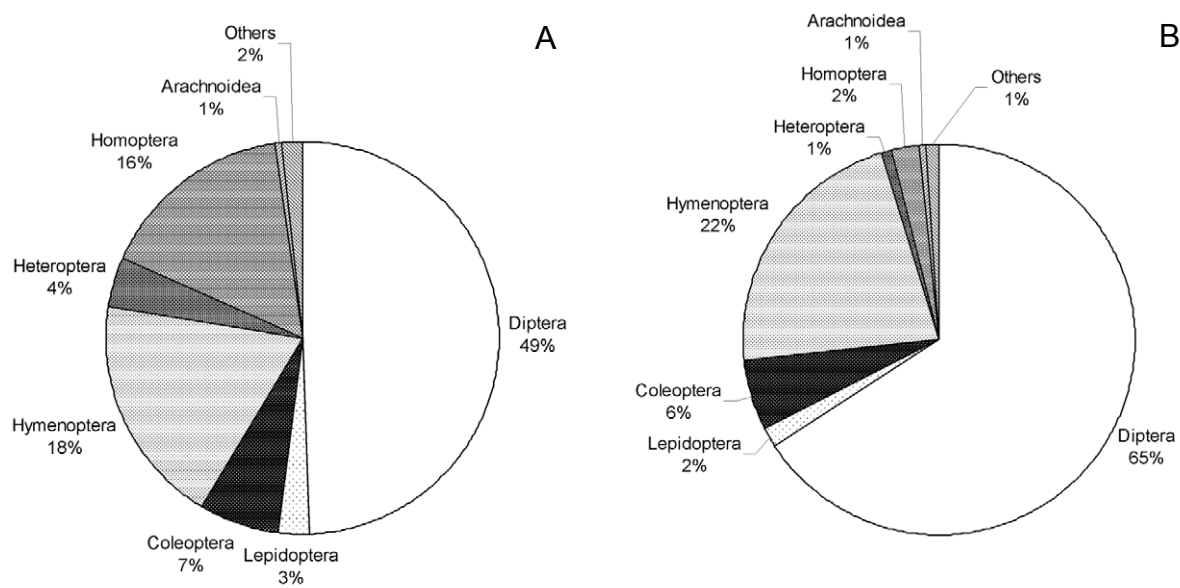
Fig. 1. Composition of arthropod assemblages living in tree foliage in two study habitats, parkland (A) and woodland (B).

24 hours was 60–140, whereas it was only 20–25 in the parkland. A similar pattern was also recorded for Arachnoidea. In general, the woodland habitat was more productive in terms of trophic conditions for insectivorous birds.

At this background, we studied in detail the abundance and seasonal dynamics of caterpillars as the most important component of the diet of nestling Blue Tits. In 2003–2004, using the numbers of descending caterpillars trapped into Moericke traps as a measure of caterpillar abundance, we found distinct differences between habitats and years in the peak abundance (Table 1). Year and habitat effects were significant in a two-way ANOVA ($F_{1,62} = 4.08$, p = 0.048 and $F_{1,62} = 7.38$, p = 0.009, respectively), with the interaction effect being non-significant ($F_{1,62} = 3.59$, p = 0.063). Thus, caterpillars were more abundant in 2003 than 2004, and in woodland than in parkland.

A similar pattern of peak caterpillar abundance was suggested by the results of the frassfall analysis for 2003–2005 (Fig. 2), but in this case all three effects, year, habitat and their interaction are significant ($F_{2,33} = 16.68$, p = 0.00001; $F_{1,33} = 26.47$, p = 0.00001; $F_{2,33} = 9.26$, p = 0.001, respectively) in a two-way ANOVA. The interaction effect resulted from caterpillar abundance in 2003 being very low in the parkland in comparison with the woodland. Thus, a clear pattern of inter-habitat and inter-year differences in peak caterpillar abundance in the study system appeared (Fig. 2). In both habitats, there was a decreasing trend in the abundance of caterpillars in the subsequent years 2003–2005. In all years, the peak abundance of caterpillars in the woodland was at least 3 times higher than in the parkland (Fig. 2). The dates of peaks were not exactly synchronised between the habitats within years and showed some variation among years (Fig. 2). The peak abundance of caterpillars occurred in the earliest time in 2003, then in 2004, and in the latest time in 2005.

In contrast to this inter-year pattern of caterpillar abundance, the mean laying date in 2003

Table 1. Mean mass of caterpillars at peak abundance trapped with Moericke traps in studied habitats (g/trap/day). N — sample size.

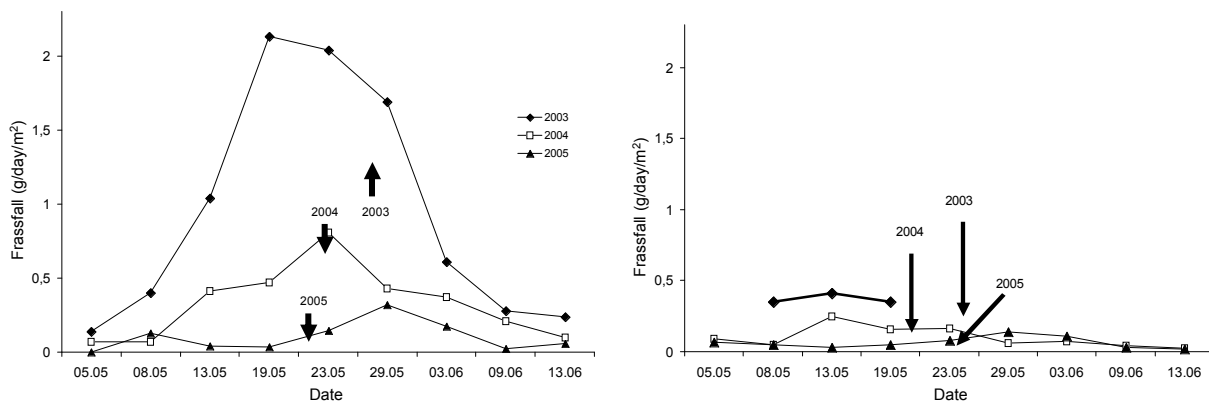| Year	Mean habitat-specific mass of caterpillars (g/trap/day) ± SE	
	Parkland	Woodland
2003	0.00104 ± 0.004 (N = 13)	0.01678 ± 0.003 (N = 21)
2004	0.00061 ± 0.004 (N = 12)	0.00341 ± 0.003 (N = 20)

Fig. 2. Comparison of frassfall production between the woodland and parkland habitat in 2003-2005. Average dates of peak nestling demand (10 day-old nestlings) are indicated by labeled arrows. Peak caterpillar abundance in terms of frassfall in 2003 was estimated from the peak number of caterpillars in the Moericke traps.

was several days later than in 2004–2005 (two-way ANOVA: $F_{2,261} = 19.53$, $p < 0.00001$, Fig. 3). A consistent difference in the timing of breeding was recorded between the parkland and woodland habitats, with mean laying date being earlier in the parkland than in the woodland (two-way ANOVA: $F_{1,261} = 12.91$, $p = 0.0004$, Fig. 3). The interaction between the year and habitat effects was non-significant (two-way ANOVA: $F_{2,261} = 1.29$, $p = 0.28$).

Mean clutch size corresponded very well to inter-year and inter-habitat differences in the abundance of caterpillars rather than to analogous differences in the timing of breeding (Fig. 4). The effects of year and habitat were evident (two-way ANOVA: $F_{2,229} = 12.88$, $p < 0.00001$ and $F_{1,229} = 9.58$, $p = 0.002$, respectively), while the interaction between these effects was non-significant (two-way ANOVA: $F_{2,229} = 2.24$, $p = 0.11$).

DISCUSSION

Although we are aware of different dimensions of the ecological variation between different types of habitats, including those connected with abiotic factors as well as predatory animals and parasites, we focus in this paper on the potential prey base of Blue Tits during the breeding period. The differences in habitat quality between the
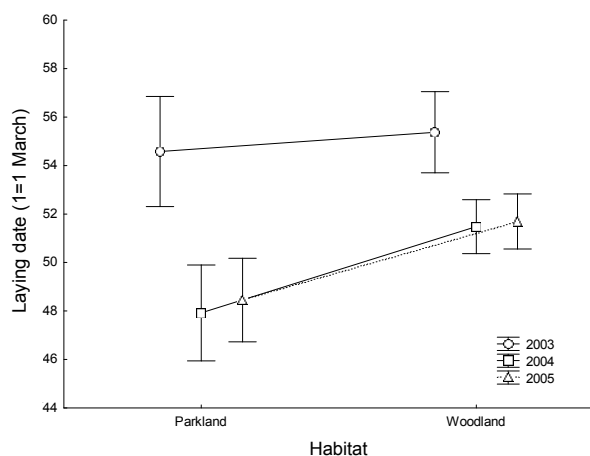

Fig. 3. Habitat and annual differences in mean date of the onset of laying eggs by female Blue Tits. Means and 95% confidence intervals are given.
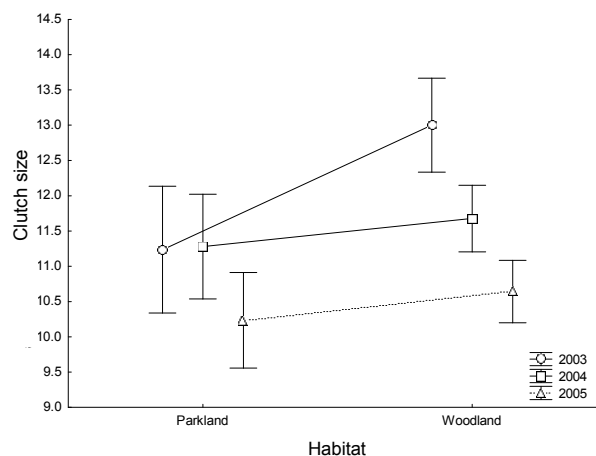

Fig. 4. Habitat and annual differences in mean clutch size Blue Tits. Means and 95% confidence intervals are given.

woodland and parkland habitats are a key feature of our study system. The woodland area is a rich deciduous forest with oaks *Quercus robur* and *Q. petraea* as predominating tree species. The parkland site, including the zoological and botanic gardens, is characterised by highly fragmented tree cover, with extensive lawns and flower beds and other unsuitable areas. As a consequence, the effects deteriorating the parkland habitat structure as compared with the woodland seem to be analogous but more pronounced than in the case of managed vs. natural forests (e.g. Wesołowski et al. 2005, Kosiński et al. 2006). Hence, we initially assumed that the differences in the structure of the two habitats studied would influence trophic conditions for breeding birds (cf. Burke & Nol 1998, Zanette et al. 2000). This assumption was confirmed by our results on arboreal arthropod assemblages. Although qualitative variation is comparable in both types of the habitat studied, the densities of particular groups are clearly higher in the woodland than the parkland. This suggests that the productivity of arthropod populations is much higher in the habitat with the less disturbed structure. This is a case of a more general rule concerning forest ecosystems that undisturbed, less fragmented woodlands are inhabited by richer and relatively stable insect communities (Shure & Phillips 1991, Didham et al. 1996, Jokimäki et al. 1998, Nour et al. 1998, Wesołowski & Rowiński 2006).

On the other hand, it is conceivable that some disturbed habitats, in spite of being low-productive, may provide favourable opportunities for outbreaks of some herbivorous insect pest, as it regularly happens in planted forest monocultures (Clark et al. 1967). However, it seems not to be the case with most city parks and gardens, even those built on the base of forest remnants. The kind of human-associated disturbance, like high degree of habitat fragmentation and management, typical of city parklands, may negatively influence arthropod communities and their productivity by enhancing edge effects and limiting dispersion (Jokimäki et al. 1998, Gunnarsson & Hake 1999, Bolger et al. 2000, Gibb & Hochuli 2002). Still less trophically productive human-disturbed habitats used by some forest birds, including Blue and Great Tits, are small backyard gardens, as shown by both low breeding results and poor diet supplied to nestlings (Perrins 1965, Schmidt & Einloft-Achenbach 1984, Cowie & Hinsley 1987, 1988).

Effects of habitat-specific variation in the abundance and seasonal dynamics of populations composing tree canopy arthropod community on the energy flow in the corresponding trophic net (Verley 1970, Damman 1993) are enhanced by inter-year variation (Veistola et al. 1995). From the viewpoint of birds feeding on insects in tree foliage, caterpillars are the most important component of the corresponding arthropod community as they constitute high-quality food for nestlings (Perrins 1991, Cramp & Perrins 1993, Bańbura et al. 1999). Actually, the abundance and seasonal changes in availability of caterpillars are a key factor determining the trophic quality of a breeding habitat (Perrins 1991, Cramp & Perrins 1993, Riddington & Gosler 1995).

In our study system, indeed, analogously to the arboreal arthropod community as a whole, also the productivity of caterpillars turned out to markedly differ between the rich woodland and poor parkland habitats. There are probably at least three reasons for this difference, making it a consistent feature of these habitats. First, the changed spatial structure of the parkland, especially the fragmentation of tree stands. Second, the parkland is subject to multi-way management, including the removing of fallen branches and leaves that under natural conditions provide most caterpillars a save place to pupate. Third, the lights of streets and neighbouring big buildings attract moths from the parks outside (own observation), stopping the reproductive cycle of many imagine moths and thus limiting caterpillar production. To our knowledge, this factor has not been considered so far.

The question of a long-term consistency of this inter-habitat difference in caterpillar abundance remains open. Also the question of consequences of such a difference for breeding tits may be more complicated than it seems to be at first glance. If caterpillars were superabundant during the tit breeding season, as it is sometimes suggested (review in Martin 1987, Newton 1998), the effect of inter-habitat and inter-year differences on breeding success would not be significant. It has been shown in many studies that the abundance of caterpillars does influence tit laying time and breeding success (Perrins 1965, van Balen 1973, Blondel et al. 1999, 2006). In general, the abundance of caterpillars in our study habitats is high in comparison with many other areas (Bańbura et al. 1994, Thomas et al. 2001, Bańbura et al. 2004). Blondel et al. (2006) suggested that the abundance of caterpillars has a direct effect on Corsican Blue Tit reproduction up to the threshold value of 0.5 $g/m^2/day$ of frassfall.

The timing of tit breeding has been considered to evolve in response to selection pressures generated by seasonal dynamics of caterpillars (Perrins 1965, van Noordwijk et al. 1995). Most arboreal caterpillars hatch and develop during a relatively short period when the buds of host trees burst. This period of "phenological window" for caterpillar development (Lawrence et al. 1997, Martel & Kause 2002) is also most favourable for tits to rear nestlings. As a consequence, the period when nestlings need the greatest amounts of food is on average synchronised with the seasonal dynamics of caterpillars. Profitability of caterpillars as food for tits depends not only on their numbers but also on their individual body sizes (Blondel et al. 1991, Bańbura et al. 1994, 1999). Because the development of tree leaves and the growth of caterpillars are temperature-dependent processes (Perrins 1991, Nager & van Noordwijk 1995), the optimal time for tits to feed nestlings is about three weeks after the bud-burst, but the date may change even a couple of weeks between years (van Noordwijk et al. 1995, Murakami 2002). However, when a cold weather spell happens after leaves have started to develop, the activity and growth of caterpillars stops and, on the other hand, when it is exceptionally warm, caterpillars develop faster — as a result, both situations may cause mistiming of tit reproduction (van Noordwijk et al. 1995). What is important is not only when to breed but also when to breed in relation to the peak date of food availability; this date being difficult to predict, especially when climate is becoming less stable (Visser et al. 2004). In our study, the spring of 2003 was cold around the normal time of laying but exceptionally warm afterwards, resulting in late breeding and the average time of when the nestlings were 10 days old two weeks after the peak availability of caterpillars. This supports van Noordwijk et al.'s (1995) explanation for such a too late tit nestling stage in the seasons when weather becomes very warm only after the laying of eggs has started. Even if the breeding season 2003 was indeed very late in the study population, the availability of caterpillars at the time of the nestling greatest food demand was much higher than at the caterpillar peak dates in 2004 and 2005. The late breeding season of 2003 was not associated with low clutch size; on the contrary, mean clutch size was the largest then.

The slight difference in the mean laying dates between the two habitats studied results probably from a difference in physical structure of the habitats and from a difference in tree species composition. In the woodland, late-leafing oaks predominate, while in the parkland, earlier-leafing species are much more frequent (Nowakowska 2007). For example, caterpillars appear a week earlier on poplars and birches, very frequent in the parkland site, than on oaks (Nowakowska 2007), analogously to the results reported by Eeva et al (2000) and Nilsson and Källander (2006). Again, even if the average laying dates were later in our woodland site than in the parkland, mean clutch size was higher in the former. Actually, the pattern of clutch size variation recorded in this study seems to be closely corresponding to the pattern of the abundance of caterpillars in particular years and habitats. Whether a season is phenologically early or late is less important. Our study habitats represent two different stages of a gradient from wild non-disturbed to completely human-dependent urban environments, with all the physical (temperature) and biological consequences (insect richness) described in the literature (e.g. Luniak 2004, Adams et al. 2005).

Tit reproductive decisions on the timing of breeding are made several weeks in advance of the time of caterpillar peak abundance (Perrins 1991), whereas the decision on the number of eggs in a clutch can still be made earlier or later during the time of laying the clutch. This enables females (pairs) to optimise the reproductive investment in clutch size with respect to weather, food abundance and individual physiological condition (Perrins 1965, Pettifor et al. 1988). The inter-habitat and inter-year differences in clutch size that clearly correspond to differences in the abundance of caterpillars suggests that the response of Blue Tits in both habitats of the study system is rather adaptive than non-adaptive (Pettifor et al. 1988, Dhondt et al. 1990, Thomas et al. 2001, Postma & van Noordwijk 2005, Blondel et al. 2006, Ziane et al. 2006). The breeding success response to differences in food abundance may probably be wider in range than suggested by Blondel et al. (2006) for Mediterranean populations of Blue Tits, as shown by the pattern of inter-year and inter-habitat variation in clutch size linked to variation in caterpillar availability in our study system.

In general, mean clutch size of the Blue Tit shows a lot of geographic variation, with the Mediterranean population being characterised by low values and British and continental populations by high values (Cramp & Perrins 1993, Fargallo 2004). Mean clutch sizes found in this study, ranging between years from 10.6 to 13 in

the woodland and from 10.2 to 11.3 in the parkland, belong to relatively large values. The interhabitat difference in clutch size has quite often been reported in tits (Perrins 1965, van Balen 1973, Blondel 1985, Cramp & Perrins 1993), and also specifically in the case of woodland v. parkland/garden contrast (Schmidt & Einloft-Achenbach 1984, Cowie & Hinsley 1987). In studies, where the quantity of caterpillars has been known for different habitats, the relation between clutch size and potential food varied. For example, in a recent study of Algerian Blue Tits, poor and rich habitats showed no difference in mean clutch size (Ziane et al. 2006), whereas such differences existed in other Mediterranean systems (Lambrachts et al. 1997). As our study system clearly shows adaptive differentiation of clutch size in response to the availability of caterpillars we predict that biologically significant consequences for chick condition and survival would be expected.

ACKNOWLEDGEMENTS

REFERENCES

Adams L. W., Van Druff L. W., Luniak M. 2005. Managing urban habitats and wildlife. In: Braun C. E. (ed.). Techniques for Wildlife Investigations and Management. 6th ed. Wildlife Society, Bethesda, pp. 714–739.

Bańbura J. 1997. Variation in blue tit breeding timetables: what factors trigger reproduction. TREE 12: 293–294.

Bańbura J., Blondel J., de Wilde-Lambrechts H., Galan M.-J., Maistre M. 1994. Nestling diet variation in an insular Mediterranean population of Blue Tits Parus caeruleus: effects of years, territories and individuals. Oecologia 100: 413–420.

Bańbura J., Lambrechts M. M., Blondel J., Perret P., Cartan-Son M. 1999. Food handling time of Blue Tit chicks: constraints and adaptation to different prey types. J. Avian Biol. 30: 263–270.

Bańbura J., Perret P., Blondel J., Thomas D. W., Cartan-Son M., Lambrechts M. M. 2004. Effects of Protocalliphora parasites on nestling food composition in Corsican Blue Tits Parus caeruleus: consequences for nestling performance. Acta Ornithol. 39: 93–103.

Blondel J. 1985. Breeding strategies of the Blue Tit and Coal Tit (Parus) in mainland and island Mediterranean habitats: a comparison. J. Anim. Ecol. 54: 531–556.

Blondel J., Dervieux A., Maistre M., Perret P. 1991. Feeding ecology and life history variation of the Blue Tit in Mediterranean deciduous and sclerophyllous habitats. Oecologia 88: 9–14.

Blondel J., Dias P., Perret P., Maistre M., Lambrechts M. M. 1999. Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. Science 285: 1399–1402.

Blondel J., Thomas D. W., Charmantier A. Perret P., Bourgault P., Lambrechts M. M. 2006. A thirty-year study of phenotypic and genetic variation of blue tits in Mediterranean habitat mosaics. BioScience 56: 661–673.

Bolger D. T., Suarez A. V., Crooks K. R., Morrison S. A, Case T. J. 2000. Arthropods in urban habitat fragments in Southern California: Area, age, and edge effects. Ecol. Applicat. 10: 1230–1248.

Bourggault P., Caro S. P., Perret P. 2006. Do Blue Tit time their breeding based on cues obtained by consuming buds? J. Field Ornithol. 77: 399–403.

Burke D. M., Nol E. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. Auk 115: 96–104.

Buse A., Dury S. J., Woodburn R. J. W., Perrins C. M., Good J. E. G. 1999. Effects of elevated temperature on multi-species interactions: the case of pendunculate oak, winter moths and tits. Funct. Ecol. 13: 74–82.

Buse A., Good E. G., Dury S. 1998. Effects of elevated temperature and carbon dioxide on the nutritional quality of leaves of oak (Quercus robur L.) as food for the winter moth (Operophtera brumata L.). Funct. Ecol. 12: 742–749.

Cizek L., Fric Z., Konvicka M. 2006. Host plant defences and voltinism in European butterflies. Ecol. Entom. 31: 337–344.

Clark L. R., Geier P. W., Hughes R. D., Morris R. F. 1967. The ecology of insect populations in theory and practice. Methuen & Co Ltd., London.

Cowie R. J., Hinsley S. A. 1987. Breeding success of Blue Tits (Parus caeruleus) and Great Tits (Parus major) in suburban habitats. Ardea 75: 11–20.

Cowie R. J., Hinsley S. A. 1988. Feeding ecology of Great Tits (Parus major) and Blue Tits (Parus caeruleus), breeding in suburban gardens. J. Anim. Ecol. 57: 611–626.

Cramp S., Perrins C. M. (eds). 1993. The Birds of the Western Palearctic. Vol.VII. Oxford Univ. Press.

Damman H. 1993. Patterns and interactions among herbivore species. In: Stamp N. E., Casey T. M. (eds). Caterpillars. Chapman & Hall, New York, pp. 132–169.

Dhondt A. A., Adriaensen F., Matthysen E., Kempenaers B. 1990. Nonadaptive clutch sizes in tits. Nature 348: 723–725.

Dias P. C., Blondel J. 1996. Breeding time, food supply and fitness components of Blue Tits Parus caeruleus in Mediterranean habitats. Ibis 138: 644–649.

Didhan R. K., Ghazoul J., Stork N. E., Davis A. J. 1996. Insects in fragmented forests: a functional approach. TREE 11: 255260.

Eeva T., Veistola S., Lehikoinen E. 2000. Timing of breeding in subarctic passerines in relation to food availability. Can. J. Zool. 78: 67–78.

Fargallo J. A. 2004. Latitudinal trends of reproductive traits in the blue tit Parus caeruleus. Ardeola 51: 177–190.

Feeny P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51: 565–581.

Fischbacher M., Naef-Daenzer B., Naef-Daenzer L. 1998. Estimating caterpillar density on trees by collection of frass droppings. Ardea 86: 121–129.

Forkner R. E, Marquis R. J., Lill J. T. 2004. Feeny revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of *Quercus*. Ecol. Entom. 29: 174–187.

Gibb H., Hochuli D. F. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol. Conserv. 106: 91–100.

Graveland J., Drent R. H. 1997. Calcium availability limits breeding success of passerines on poor soils. J. Anim. Ecol. 66: 279–288.

Gunnarson B., Hake M. 1999. Bird predation affects canopy-living arthropods in city parks. Can. J. Zool. 77: 1419–1428.

Jokimäki J., Huhta E., Itämies J., Rahko P. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Can. J. Forest Res. 28: 1068–1072.

Kosiński Z., Ksit P., Winiecki A. 2006. Nest sites of Great Spotted Woodpeckers *Dendrocopos major* and Middle Spotted Woodpeckers *Dendrocopos medius* in near-natural and managed riverine forests. Acta Ornithol. 41: 21–32.

Krzemińska-Freda J. 1996. [Botanic garden in Łódź. In: Kurzac T. (ed.). [Natural History of the Botanic Garden in Łódź]. OWR Sagalara, Łódź, pp. 7–24.

Kurowski J. K. (ed.). 2001. [Vegetation of the Łagiewniki Forest in Łódź]. OWR Sagalara.

Lambrechts M. M., Blondel J., Hurtrez-Bousses S., Maistre M., Perret P. 1997. Adaptive inter-population differences in Blue Tit life-history traits on Corsica. Evol. Ecol. 11: 599–612.

Lawrence R. K., Mattson W. J., Haack R. A. 1997. White spruce and the spruce budworm: defining the phenological window of susceptibility. Can. Entom. 129: 291–318.

Lowman M. D., Wittman P. K. 1996. Forest canopies: methods, hypotheses and future directions. Ann. Rev. Ecol. Syst. 27: 55–81.

Luniak M. 2004. Synurbization — adaptation of animal wildlife to urban development. In: Shaw W. W., Harris K. L., Van Durff L. (eds). Urban Wildlife Conservation. Univ. Arizona, Tucson, pp. 50–55.

Martel J., Kause A. 2002. The phenological window of opportunity for early-season birch sawflies. Ecol. Entom. 27: 302–307.

Martin T. E. 1987. Food as a limit on breeding birds: a life — history perspective. Ann. Rev. Ecol. Syst. 18: 453–487.

Moericke V. 1951. Eine Farbfalle zur Kontrolle des Fluges von Blättlausen, insbesondere der Pfisichblattlaus *M. persicae* (Sulz). Nachrbl. Dtsch. Pflzschutzd. 3: 23–24.

Morse D. H. 1971. The insectivorous bird as an adaptive strategy. Ann. Rev. Ecol. Syst. 2: 177–200.

Murakami M. 2002. Foraging mode of four insectivorous bird species under temporally varying resource distribution in a Japanese deciduous forest. Ornithol. Sci. 1: 63–69.

Murakami M., Nakano S. 2002. Species-specific bird functions in a forest-canopy food web. Proc. Roy. Soc., London B 267: 1597–1601.

Nadolski J., Marciniak B., Nowakowska M., Szczepko K., Kowalczyk J. K. 2004. [Preliminary results of quantitative investigations of the insect fauna of Łódź]. In: Indykiewicz P., Barczak T. (eds) [City Fauna of Central Europe in 21st Century]. LOGO, Bydgoszcz, pp. 37–48.

Nager R. G., van Noordwijk A. J. 1995. Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. Am. Nat. 146: 454–474.

Newton I. 1998. Population limitation in birds. Academic Press, San Diego.

Nilsson J.-Å., Källander H. 2006. Leafing phenology and timing of egg laying in great tits *Parus major* and blue tits *P. caeruleus*. J. Avian Biol. 37: 357–363.

Nour N., Currie D., Matthysen E., Van Damme R., Dhondt A. A. 1998. Effects of habitat fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and blue tit). Oecologia 114: 522–530.

Nowakowska M. 2007. [Seasonal and habitat variation in potential food base of insectivorous birds: consequences for the breeding of the Great Tit *Parus major* and the Blue Tit *Parus caeruleus*.] Ph. D. Thesis. Univ. Łódź, Łódź.

Perrins C. M. 1965. Population fluctuations and clutch size in the Great Tit *Parus major* L. J. Anim. Ecol. 34: 601–647.

Perrins C. M. 1979. British Tits. Collins, London.

Perrins C. M. 1991. Tits and their caterpillar food supply. Ibis 133, Suppl.: 49–54.

Pettifor R. A., Perrins C. M., McCleery R. H. 1988. Individual optimization of clutch size in great tits. Nature 336: 160–162.

Postma E., van Noordwijk A. J. 2005. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. Nature 433: 65–68.

Riddington R., Gosler A. G. 1995. Differences in reproductive success and parental qualities between habitats in the Great Tit *Parus major*. Ibis 137: 371–378.

Schmidt K.-H., Einloft-Achenbach H. 1984. Können isolierte Meisenpopulationen in Städten ihren Bestand erhalten? Vogelwelt 105: 97–104.

Schoenly K. 1990. The predators of insects. Ecol. Entom. 15: 333–345.

Shure D. J., Phillips D. L. 1991. Patch size of forest openings and arthropod populations. Oecologia 86: 325–334.

Słomczyński R., Kaliński A., Wawrzyniak J., Bańbura M., Skwarska J., Zieliński P., Bańbura J. 2006. Effects of experimental reduction in nest microparasite and macroparasite loads on nestling haemoglobin level in blue tits *Parus caeruleus*. Acta Oecol. 30: 223–227.

Southwood T. R. E. 1984. Insect-plant adaptations: on origins and development of adaptation. Ciba Foundation Symposium 102: 138–151.

StatSoft, Inc. 2003. STATISTICA (data analysis software system), version 6. www.statsoft.com.

Thomas D. W., Blondel J., Perret P., Lambrechts M. M., Speakman J. R. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291: 2598–2600.

Tinbergen J. M. 1981. Foraging decisions in starlings (*Sturnus vulgaris* L.). Ardea 69: 1–67.

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

van Noordwijk A. J., McCleery R. H., Perrins C. M. 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. J. Anim. Ecol. 64: 451–458.

Veistola S., Eeva T., Lehikoinen E. 1995. Seasonal occurence of arthropods as a source of food for birds in Finnish Lapland. Entom. Fennica 6: 177–181.

Verley G. C. 1970. The concept of energy flow applied to a woodland community. In: Watson A. (ed.). Animal Populations in Relation to their Food Resources. Blackwell, Oxford, pp. 389–405.

Visser M. E., Both C., Lambrechts M. M. 2004. Global climate change leads to mistimed avian reproduction. Adv. Ecol. Res. 35: 89–110.

Wesołowski T., Czeszczewik D., Rowiński P. 2005. Effects of forest managment on Three-toed Woodpecker *Picoides tridactylus* distribution in the Białowieża Forest (NE Poland): conservation implications. Acta Ornithol. 40: 53–60.

Wesołowski T., Rowiński P. 2006. Tree defoliation by winter moth *Operophtera brumata* L. during an out break affected by structure of forest landscape. Forest Ecol. Manage. 221: 299–305.

Zandt H. S. 1994. A comparison of three sampling techniques to estimate the population size of caterpillars in trees. Oecologia 97: 399–406.

Zandt H. S. 1997. Water content of prey of nestling blue tits in a Corsican habitat. Neth. J. Zool. 47: 125–131.

Zanette L., Doyle P., Tremont S. M. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. Ecology 81: 1654–1666.

Ziane N., Chabi Y., Lambrechts M. M. 2006. Breeding performance of Blue Tits *Cyanistes caeruleus ultramarinus* in relation to habitat richness of oak forest patches in north-eastern Algeria. Acta Ornithol. 41: 163–169.

STRESZCZENIE

[Środowiskowe i czasowe różnice w obfitości stawonogów: wpływ potencjalnej bazy pokarmowej na rozród modraszki]

Celem niniejszych badań było sprawdzenie, czy bogaty las liściasty różni się od środowiska parkowo-ogrodowego bogactwem ugrupowania stawonogów zasiedlających korony drzew. Ważny element tego ugrupowania stanowią gąsienice, które żerują na świeżych liściach drzew i stanowią główny pokarm sikor. W istocie od ich obfitości i dynamiki sezonowej zależy czas lęgów i sukces reprodukcyjny sikor. A zatem potencjalne środowiskowe i czasowe zróżnicowanie obfitości gąsienic powinno wywoływać reakcję charakterystyk rozrodczych ptaków. Dane były zbierane w latach 2003–2005 na obszarze leśnym i parkowo-ogrodowym w Łodzi. Ogólną charakterystykę ugrupowania stawonogów opracowano na podstawie wyników odłowów przy pomocy misek Moericka podwieszonych pod koronami drzew. Obfitość gąsienic szacowano pośrednio, na podstawie ilości odchodów zebranych na płócienne tace rozpięte na metalowym szkielecie o wymiarach 1m x 1m oraz bezpośrednio, na podstawie gąsienic, które schodząc z koron wpadły do misek Moericka. Stwierdzono, że przy stosunkowo zbliżonej strukturze jakościowej ugrupowań stawonogów, produktywność owadów w lesie była znacznie wyższa niż w środowisku parkowym (Fig. 1). W okresie badań, obfitość gąsienic w środowisku leśnym była przynajmniej trzy razy większa niż obfitość w środowisku parkowo-ogrodowym (Fig. 2). Dla obu środowisk w kolejnych latach badań stwierdzono zmniejszającą się liczebność gąsienic. Sezon lęgowy 2003 charakteryzował się najlepszymi warunkami pokarmowymi, ale był sezonem najpóźniejszego rozpoczynania lęgów (Fig. 3). Dwa kolejne sezony były fenologicznie wcześniejsze. Niezależnie od czasu lęgów, ale w wyraźnej relacji do obfitości gąsienic w danym roku i środowisku kształtował się wzorzec zmienności wielkości zniesienia (Fig. 4). To sugeruje, że modraszka, jako gatunek wysoce wyspecjalizowany w użytkowaniu gąsienic w okresie karmienia piskląt, jest zdolna do przystosowawczej modyfikacji wielkości zniesienia do ogólnych warunków troficznych.