Egg size variation in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* in relation to habitat differences in snail abundance

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Abstract. Wild passerines, especially tits, utilize snail shells as the main source of calcium necessary for laying females to construct egg shells. This research found that the two study areas, representing two habitat types — a mature deciduous forest and a human-disturbed parkland — are inhabited by different snail assemblages: both species richness and density are much higher in the parkland than in the forest. This means that less calcium is available to female tits in the forest than in the parkland, which could result in calcium limitation in the former habitat. Egg size traits, i.e. volume, length and breadth, in the Blue Tit show a consistent long-term pattern of variation that reflects the pattern of calcium availability: egg trait values are higher in the parkland than in the woodland. No habitat-related variation in egg size traits was found in the Great Tits. We suggest that the lack of a relation between Great Tit egg characteristics and snail availability results from the higher ecological plasticity of this species in comparison with the Blue Tit, including its ability to exploit alternative sources of calcium.

Key words: birds, tits, egg sizes, habitat contrast, calcium, shelled snails

Received — July 2010, accepted — Dec. 2010

INTRODUCTION

Egg sizes in birds are shaped as part of the allocation of resources to different components of parental effort (Smith & Fretwell 1974, Stearns 1992, Charnov et al. 1995). The stage of egg formation is very nutritionally demanding for females, which must have consequences for allocation decisions (Perrins 1996, Nager 2006). A recent meta-analysis of an often suggested positive influence of egg size on nestling quality and performance has definitely found a lot of data conforming it (Krist 2010). Thus egg sizes have an impact on offspring fitness, which together with clear patterns of low intra-female and high inter-female variation (Bańbura & Zieliński 1998, Christians 2002) supports an inference that they constitute an important life-history trait (Stearns 1992). The expression of this trait is obviously dependent on habitat-related resources, such as food in general as well as some special nutrients. This is especially important because the eggs of small passerines are produced on the basis of current intake of resources and not on resources deposited in the body in advance (Perrins 1996, Ward & Bryant 2006, Reynolds & Perrins 2010).

As a consequence, it would be expected from life-history theory that egg quality and sizes should differ between habitats representing varying availability of principal resources (Horak et al. 1995, Chabi et al. 2000, Bourgault et al. 2007). Yet clear environmental patterns of variation in egg size and shell traits reported in the literature are rather scarce, except some cases of habitats characterized by poor, acidic soil, especially under the influence of acid rains (Graveland & van der Val 1996, Graveland & Drent 1997, Mand et al. 2000). Characteristically, in these cases the influence on birds takes place through the influence on shelled snails. In the case of tits, snail shells are the
Variation in autumn migration strategy in the first-year Wood Sandpipers *Tringa glareola*

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DOI 10.3161/000164510X551273

Abstract. Wood Sandpipers are generally known to follow a time-minimization migration strategy on their autumn passage. We investigated whether the migration strategy adopted by first-year Wood Sandpipers is susceptible to temporal variations. Wood Sandpipers were trapped during the July–September period from 1997 to 2007 at the Jeziorsko reservoir, central Poland. Intra- and inter-seasonal variation in stopover length, refuelling rates, departure fat loads and flight range were investigated. There was a constant decline in the refuelling rates over the course of the migratory season, reaching 0.55 g/day at the end of August. Such low refuelling rates are considered typical of energy-minimizers. Despite showing high refuelling rates at the beginning of the season, first-year Wood Sandpipers left the stopover site with relatively low fuel reserves, resulting in a low potential flight range of about 1200 km, which suggested travelling in small hops — a trait characteristic of energy-minimizers. There was also considerable inter-seasonal variation in the adopted migration strategy. The results suggest that sandpipers caught at the beginning and at the end of the migratory season behaved as energy-minimizers, at least in some aspects of the migration strategy, unlike the intermediate migrants, which adopted a typical time-minimization schedule. These observations indicate that the migration strategies of waders may depend on the environmental conditions encountered en route and are thus likely to exhibit high intra- and inter-seasonal variation.

Key words: Wood Sandpiper, *Tringa glareola*, migration strategy, waders

Received — Feb. 2010, accepted — Dec. 2010

INTRODUCTION

Migration is an energetically expensive activity for long-distance migratory birds, often consuming up to a half of their annual energy budget (Drent & Piersma 1990). Various migratory species have adopted different migration strategies to successfully deal with this energetic burden and two main selective forces were suggested to shape their evolution: time and energy (Alerstam & Lindström 1990). According to this view, birds follow two distinctive schedules of migration, which are classified as energy- or time-minimization. Populations of energy-minimizers are usually limited by the capacity of wintering habitats, where they face lower food availability than at breeding sites or staging areas, due to its lower abundance or more intense intraspecific competition (Meltofte 1996). Consequently, they depart from breeding grounds relatively late and travel slowly in order to delay their arrival at the wintering quarters. Their autumn migration is characterized by low refuelling rates and long staging periods, possibly exceeding the time necessary to restore depleted fat reserves (Włodarczyk et al. 2007). Such long staging periods may be partially caused by using stopover sites as moulting areas, since there is often no temporal separation of moult and migration in energy-minimizers. By contrast, time-minimizers are limited by the capacity of breeding grounds and they face more favourable conditions at their wintering quarters. Therefore early arrival at wintering grounds constitutes a fitness advantage for time-minimizers. In consequence, they refuel quickly, exhibit short staging times, and postpone moult until the completion of migration. Time-minimizers may also bypass poorer sites and stop only in areas that ensure efficient refuelling (Gudmundsson et al. 1991). Although this classification of migration strategies...
Nest construction costs affect nestling growth: a field experiment in a cavity-nesting passerine

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Abstract. Nest construction effort is seldom taken into account in avian life history studies, although activity duration and the amount of nest material collected may affect the condition of parent birds and their subsequent capacity to care for dependent offspring. In the present work, we reduced the effort needed to construct the nest in a cavity nester, the Pied Flycatcher Ficedula hypoleuca, where females are the main builders. To this end, we placed stored complete nests in certain nest-boxes as soon as nest building was initiated, whereas stored complete nests were placed in the control nest-boxes as soon as nest building had ceased. Thus, no nest-box contained the original nest. Pairs collected more nest material and for longer periods in the control nest-boxes, although the experimental pairs still added some nest material after the manipulation. Nest-boxes were filmed for 1 to 3 h during incubation and on days 4 and 11 of the nestlings’ life. Female attendance during incubation was negatively affected by nest mass, this parameter explaining almost half the variation in attendance, which suggests an effect of nest mass on incubation efficiency. The female provisioning effort on day 4 was significantly higher in the experimental nests, whereas other parental care variables were affected by date, weather conditions and brood size or brood mass. Mean tarsus length at fledging was significantly longer in the experimental nests. The savings by females in nest construction effort were expressed in higher provisioning at early nestling stages and in improved nestling growth.

Key words: Pied Flycatcher, incubation, nest construction, nestling growth, nest mass, nest building effort, brooding

Received — April 2010, accepted — Nov. 2010

INTRODUCTION

Nest construction is a potential source of life history trade-offs in birds (Collias & Collias 1984). There is evidence that nest building implies marked energetic costs in some species (Withers 1977, Lens et al. 1994, but see Slagsvold & Lifjeld 1990, Stanley 2002) and considerable time allocation (Hotta 1994, Nores & Nores 1994). Nest construction rate may be related to physiological stress as expressed through stress proteins (Morales et al. 2008, Moreno et al. 2008) and nest maintenance may impinge on adult body condition (Fargallo et al. 2001). Health as expressed through blood parasitemia (Tomás et al. 2006) and survival (Gill & Stutchbury 2005) may be associated with the effort spent on nest construction. Nest construction activity may be estimated through its rate (de Neve & Soler 2002, Gill & Stutchbury 2005, Moreno et al. 2008), through its duration (Szentirmai et al. 2005) or through the mass of material collected (Soler et al. 2001, Szentirmai et al. 2005, Tomás et al. 2006) or associated evidence (Borowiec et al. 2006). Collection of specific materials may be costly due to search costs, although very little is known about this possibility.

Few studies have addressed the potential impacts of nest construction costs on survival and fecundity (Lens et al. 1994, Soler et al. 2001, de Neve & Soler 2002, Gill & Stutchbury 2005). Effort expended on nest construction may constrain reproductive exertion during subsequent phases of breeding and thereby affect reproductive output. Thus, it has been shown that handicapped parents may assign increases in energy expenditure to nestlings by reducing their food allocation (Moreno et al. 1999). Alternatively, effort in nest construction may impinge on adult post-reproductive survival without necessarily affecting productivity during the current breeding event.
Note types and coding in parid vocalizations: the chick-a-dee call of the Mexican Chickadee Poecile sclateri

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Abstract. To understand the communicative functions of any vocalization it is important to describe and classify the elements of that vocalization. Mexican Chickadees produce a namesake chick-a-dee call. Here, the note types (A, C, D, and Dh) from a sample of Mexican Chickadee chick-a-dee calls are identified, described, and classified. Frequency and temporal features of each note type are measured and compared to determine which features may be useful for note-type discrimination. Frequency measures, particularly peak frequency, appear to be most useful for discriminating among note types. Call syntax is analyzed to determine rules for note-type production. Mexican Chickadees produce the notes within their chick-a-dee calls in a consistent order: A → C → Dh → D with the potential for any note type to be repeated or omitted within this sequence. Similar to species in the brown-headed chickadee clade, B notes were not found in the calls of Mexican chickadees, suggesting this species may belong to the brown-headed clade. This work describes the chick-a-dee call of Mexican Chickadees and provides a foundation for future work aimed at understanding the communicative significance of this call within this species, as well as for comparative work on the chick-a-dee call among chickadee species.

Key words: Mexican Chickadee, bioacoustics, Poecile, communication

Received — June 2010, accepted — Oct. 2010

INTRODUCTION

The use of oscine songbirds as a model for human language learning (Doupe & Kuhl 1999), and vocal communication in general (see Slater 2003 for a review), has become increasingly popular over the last few decades. One genus of songbirds, the North American chickadees Poecile, has received a great deal of attention in this regard. All members of this genus produce a namesake chick-a-dee call. There is reason to believe that the chick-a-dee call contains important species-relevant information, and as such it has been the subject of much research aimed at understanding the production, perception, and function of this vocalization (for reviews see Hailman & Ficken 1996, Lucas & Freeberg 2007, and Sturdy et al. 2007).

Chick-a-dee calls are a common vocalization given by both males and females year round; they are composed of a number of discrete units (notes), thus allowing for many potential note combinations and many potential encoded messages (e.g., Ficken et al. 1994). Syntactic evidence from Black-capped Chickadees Poecile atricapillus (Hailman et al. 1985, Hailman et al. 1987) and Mexican Chickadees Poecile sclateri (Ficken et al. 1994) reveals that the chick-a-dee call is an “open” call system such that one can find an increasing number of call types with increasing call sample sizes. Moreover, the chick-a-dee call is produced in a variety of contexts, such as mobbing (Templeton et al. 2005), contact (Smith 1991), flock identification (Nowicki 1989), and food location (Freeberg & Lucas 2002). Taken together, this evidence suggests that the chick-a-dee call is a vocalization that has the potential to convey a variety of important messages.

Previous research on chickadee calls has revealed that different calls, and in fact different note types within calls, are used in different contexts. Black-capped Chickadees in close proximity to a predator produce calls with relatively more B
Measurement error revisited: its importance for the analysis of size and shape of birds

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Abstract. Measurement error in morphological characters is an important issue for many ornithological studies (e.g. ecomorphology, quantitative studies of heritability, studies of systematic and geographic variation). The variation in external morphological characters, such as wing and tarsus length, is usually evaluated using multivariate statistical methods such as principal component analysis (PCA). These are often considered better than univariate statistical methods for explaining size and shape variation in bird populations because they reduce the ‘dimensionality’ of the data — the size of individual measures (wing etc.) are assumed to contain a component reflecting a general character ‘size’. However, the effect of measurement error on principal components has not been formally assessed with respect to such data. Here we report three examples in order to assess the importance of measurement error for analyses within and between bird populations. The effect of measurement error on PCA is also discussed in relation to the importance of levels of error in shape components.

Our results indicate that, in relation to size (PC1), principal component scores are affected less by measurement error if the covariance matrix is used rather than the correlation matrix. However, the effects of relative measurement error were substantially greater in subsequent axes, which represent shape variation rather than size, than they were in the size axis (PC1). Measurement error may, therefore, be a more important issue for shape axes than for the size axis and this problem may be exacerbated further if very few characters are used in the PCA. Our results also indicate that PCA is especially sensitive to issues relating to sample size. We recommend that if reducing the measurement error in size and shape measures is not possible, and the sample size is small (≤ 30), principal component scores should be derived using the covariance matrix, as these are more likely to give more robust results.

Key words: measurement error, size, shape, principal component analysis, Common Chaffinch, Fringilla coelebs, methods, museum studies

Received — Febr. 2010, accepted — Oct. 2010

INTRODUCTION

The measurement error associated with various morphological characters has a bearing on many ornithological studies, and although these characters are used in studies of ecological processes and ecomorphology (e.g. Van Valen 1965, Johnson 1966, Gosler 1987, Keast & Saunders 1991, Mulvihill & Chandler 1991, Kaboli et al. 2007), age and sex differences (e.g. Arenas & Senar 2004), quantitative studies of heritability (e.g. Gosler & Harper 2000, Merilä & Sheldon 2000, Akesson et al. 2007), evolutionary studies of fluctuating asymmetry (Merilä & Björklund 1995) and evolutionary ecological studies in birds (Hromada et al. 2003, Tryjanowski & Šimek 2005, Tryjanowski et al. 2007), the importance of the measurement error has generally been ignored. This deficiency may be particularly important in systematic studies of taxonomic relationships using morphology, and in studies of geographic variation in birds (Martin 1991, Slotow & Goodfriend 1996, Telleria & Carbonell 1999, Pons et al. 2004, Soobramoney et al. 2005, Dmitrenok et al. 2007). Since systematic inferences have also been made using morphological characters, these may be wrong if measurement error was not evaluated correctly. For example, the likelihood of a Type II statistical error (failure to detect a real effect) increases as the measurement error associated with a trait increases (Bailey & Byrnes 1990, Lougheed et al. 1991, Yezerinac et al. 1992).
Foraging range and habitat use by Aquatic Warblers *Acrocephalus paludicola* during a fall migration stopover

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Abstract. Stopover sites of migratory songbirds are of great importance in the context of the maintenance of a species migration strategy. Here we studied the spatial needs and habitat selection of the endangered Aquatic Warbler at a major migration stopover site in France, the nature reserve of the Seine estuary. We radio-tracked 15 migrant birds in August 2008 to study habitat use and selection at that stopover site, and analysed faeces and blow trap samples to determine the local diet of the species and to compare food availability among the different available habitats in the reserve. Range size was estimated with fixed kernels and was on average 9 ha (90% isopleths), with daily core ranges (50% isopleths) of just over 1 ha. There was no variation in range size or habitat use during the survey period (August) or during an individual stopover stay. Studying habitat selection within the modelled ranges, we found that the species displayed a preference for wet grassland habitats. Larger daily ranges included more reedbed and fewer grassland areas. This matches the habitat preferences known from breeding and wintering grounds. The main identified prey belonged to a few invertebrate orders, with Odonata, Lepidoptera, Coleoptera and Araneida making the largest contributions to the biomass consumed. There was no significant difference in invertebrate availability between grassland and reedbed habitats in the study area. The availability of grassland habitats close to the reedbeds appears to be a key parameter to ensure the rapid and efficient refuelling of migrant Aquatic Warblers during their autumn migration.

Key words: *Acrocephalus paludicola*, fixed kernel, habitat selection, diet, tracking, wet grasslands

Received — August 2010, accepted — Dec. 2010

INTRODUCTION

Long-distance migration requires exceptional energetic reserves, and migratory songbirds must rest and deposit fat reserves at stopover sites while travelling between breeding and wintering grounds. In songbirds, most of the migration period is spent at stopover sites. As a consequence, understanding the impact of environmental changes such as habitat loss or fragmentation along the migratory routes is essential for efficient conservation planning (Huutto 1998). The vital importance of migration stopover sites to en route songbirds has come to the forefront of avian conservation (Petit 2000). The Aquatic Warbler *Acrocephalus paludicola* is Europe’s most threatened migratory songbird, as it has declined dramatically over the last century largely because of the drainage of its wetland breeding habitats. Much of its former habitat has been transformed and lost during the last century, especially in the Western part of its range (Birdlife International 2009). Its global population is estimated at 10,500–14,200 singing males. Most birds use a western migration route in autumn, with large numbers visiting French coastal marshes mainly in August (Julliard et al. 2006). During migration, Aquatic Warblers had been reported to strongly favour low stands of sedges and reeds near open water, normally along rivers, estuaries and coastal lagoons (de By 1990). However, these habitat preferences can be challenged when considering the similarity of habitats used by the species on its breeding and wintering areas, where it forages in wet grassland habitat types (Salewski et al. 2009). The identification of high-priority stopover sites and of stopover habitats critical to the long-term persistence of the migratory strategy are necessary to implement comprehensive conservation schemes (Yong et al. 1998, Petit 2000). In France, many
Feeding effort of male Tawny Owls *Strix aluco* follows a fixed schedule: a field experiment in the early nestling period

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Abstract. The ‘fixed schedule hypothesis’ proposes that parental investment is independent of offspring needs in order to maximize adult survival or to prevent reduced future fecundity. We tested this hypothesis on Tawny Owls *Strix aluco* by experimental manipulation of brood size. We measured the call frequency of begging chicks, feeding frequency of males, overnight weight gain of nestlings and parental body condition in reduced or enlarged broods, and in control broods. In reduced or enlarged broods nestling begging calls reflected the respective decrease or increase in demand, but the frequency with which the males fed did not differ between the reduced and enlarged broods. Consequently, chicks gained body weight more rapidly in reduced broods, whereas those in enlarged broods grew more slowly. Male body weight did not change during the early nestling period when they delivered food to reduced or enlarged broods, but the condition of females worsened in the enlarged broods. As the males did not increase the feeding frequency in the enlarged broods, the females were under pressure to pass on more of the prey to nestlings begging in these broods. Male Tawny Owls regulated their feeding effort according to a fixed schedule, independently of the chicks’ needs, to maintain their body condition. Nevertheless, the females whose condition deteriorated during the feeding of enlarged broods did not stop brooding earlier, nor did they suffer mortality in the breeding period.

Key words: brood manipulation, chick demands, parental condition, parental effort, *Strix aluco*, Tawny Owl

Received — Sept. 2009, accepted — Nov. 2010

INTRODUCTION

Life history theory suggests that animals should balance their current investment in offspring against their chances to reproduce in the future (e.g., Roff 1992, Stearns 1992). This life history trade-off is referred to as the cost of reproduction: if reproductive effort one year leads to decreased adult survival or a loss in future reproductive output, then the optimal effort in the current season is less than the effort that would maximize the number of young produced in that season (Williams 1966, Charnov & Krebs 1974).

Studies manipulating the number of offspring show that parents are able to produce more young than they actually raise in a single year, but that any increased investment leads to decreased adult survival or lower future fecundity (e.g., Gustafsson & Sutherland 1988, Lindén & Møller 1989). However, these studies have been carried out on short-lived passerines, where the probability of survival to the future breeding attempts is often so low that an increased effort in current reproduction, at the expense of parent survival, might be expected (Charlesworth 1980).

For long-lived birds, a small reduction in adult survival would have a large influence on the number of subsequent breeding attempts, thereby greatly lowering lifetime reproductive success. Hence, long-lived species are more restricted in the degree to which they exhibit increased effort and, consequently, the current year’s breeding success does not depend on the reproductive cost invested in the previous year (Charlesworth 1980, Curio 1988, Wooler et al. 1992). Ricklefs (1987, 1992) proposed the term ‘fixed schedule’ for long-lived species where parental investment, including the food supply for chicks, is independent of offspring needs. Sæther et al. (1993) suggested that parental effort regulated by a fixed schedule maximizes the chance of survival of adults. Nevertheless, testing of this hypothesis has
Song variability in Pied Flycatchers *Ficedula hypoleuca*: impact of the sympatry with Collared Flycatchers *F. albicollis*

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Abstract. In the sympatry zone many Pied Flycatcher males perform songs that resemble those of a sibling species (Collared Flycatcher): these are so-called mixed songs. The higher abundance of the Collared Flycatcher was once considered a possible cause of mixed singing. To examine this hypothesis we studied the influence of the Collared Flycatcher on the interpopulational song variability in the Pied Flycatcher in four areas with different abundances of Collared Flycatchers. We focused on: 1) the abundance of mixed singers and their distribution; 2) geographical variations of typical Pied Flycatcher songs. We show for the first time that mixed singing in the Pied Flycatcher is common also when its abundance is as high as and higher than that of the Collared Flycatcher. In the old area of sympathy about 40% of all Pied Flycatcher males had Collared-Flycatcher-like syllables in their repertoire. At the same time, the habitat distribution of mixed singers matches that of the Collared Flycatcher. In the context of our data we propose a hypothesis of mixed song-formation. We have also demonstrated interpopulational variability in pure Pied Flycatcher songs, with species-specific differences being more pronounced in sympatric populations than in allopatric ones. This pattern is in agreement with the theory of character displacement and acoustic divergence in a sympatry zone, but the differences discovered in pure vocalizations are evidently not the result of interactions with the sibling species.

Key words: Pied Flycatcher, Collared Flycatcher, interspecies interactions, character displacement, mixed singing, acoustic divergence, acoustic convergence, interpopulation song differences

Received — Nov. 2009, accepted — Dec. 2010

INTRODUCTION

Hybridization between sibling species in the zones of their secondary contact is a widespread phenomenon in birds (Panov 1989, McCarthy 2006). In a number of cases such hybrids have reduced viability or fertility compared to individuals belonging to the parental species due to genetic incompatibility between the two parent species (Mayr 1963, Price & Bouvier 2002, McCarthy 2006). The theory of reinforcement predicts that natural selection against hybridization with reduced fitness will lead to a divergence in traits that are responsible for assortative mating and species identification (Dobzhansky in Grant & Grant 1997).

In birds acoustic signalization plays an essential role in species identification (for references see Slabbekoorn & Smith 2002). However, despite the reinforcement hypothesis, birds’ acoustic divergence as a result of species-species interactions has never been shown sufficiently clearly; in fact, only one proof has been found recently in birds with inherited songs (Seddon 2005).

On the other hand, there is some evidence for vocal convergence in sympatry zones. In a number of cases one of the pair of sibling species performs songs that resemble the song of the other species to a varying degree (Helb et al. 1985, Eriksson 1991, Osiejk & Kuczyński 2000, Gorissen et al. 2006). More rarely both species change their songs to become more similar in sympatric populations (Grabovsky & Panov 1992, Secondi et al. 2003). These unusual songs are characteristic of genetically pure species (Haavie et al. 2004), though hybrids can also have intermediate songs (Gelter 1987). Such changes in the songs of species in a sympathy zone are not random, occasional events, but are observed in a considerable part of the population. This phenomenon was
Ringing procedure can reduce the burden of feather lice in Barn Swallows *Hirundo rustica*

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Abstract. Chewing lice (Insecta: Phthiraptera) are the most widespread obligate ectoparasites living in the plumage of birds. Lice have to cope with unusual mechanical effects during ringing, and they could fall off their hosts. We assumed that trapping birds in nets, taking measurements and estimating condition could reduce their louse burdens. Lousiness affects life expectancy and reproductive success, so if ringing causes remarkable louse loss, the fitness of ringed birds could be altered. Lice are usually collected at ringing sites, and ringing precedes parasite sampling. This may therefore lead to an underestimation of louse prevalence and intensity. Here we tested whether ringing reduces the louse burden. We allocated Barn Swallows *Hirundo rustica* in the breeding season to two experimental groups — the birds were subject to either a standard ringing procedure (recording biometry, fat and other condition scores, feather hole counts), or a reduced one (only feather hole counts). We used feather holes (traces of louse chewing) as a measure of louse loads. Holes were recounted after a month. Significantly more new holes appeared in the reduced ringing procedure group, indicating that the usual ringing procedures effectively reduce louse loads. We believe this is the first evidence that bird ringing affects ectoparasite infestations.

Key words: Barn Swallow, lice, bird ringing, handling of birds, louse collection, louse sampling, fitness alteration, ectoparasites, feather holes, Amblycera, Ischnocera

Received — July 2010, accepted — Nov. 2010

INTRODUCTION

Bird ringing is a more than 100 years old method in ornithology. It was originally developed for studying bird migration; however it can be used — especially if combined with colour-banding — in other ornithological investigations as well. Bird ringing is applied in population biology, behavioural studies, breeding biology, conservation biology, faunistic studies and even in avian parasitology. Thanks to the co-operation of international organisations (e.g. EURING) the procedures including capture methods, handling of birds and the taking of measurements are standardised and used almost in the same way by every ringer (Svensson 1992). Strict rules are implemented to avoid negative effects on birds caused by catching and ringing. Hereafter the term ‘ringing’ means the whole ringing procedure from catching with mist nets until releasing.

Birds act as habitat islands for other animals, such as ectoparasitic lice (Insecta: Phthiraptera: Amblycera, Ischnocera). Lice are the most widespread ectoparasites of birds, and the only parasitic insects that complete their entire life cycle on the body surface of birds (Clayton & Tompkins 1994, 1995). Ischnoceran lice (Phthiraptera: Ischnocera) live and feed on feathers, while Amblyceran lice (Phthiraptera: Amblycera) partly feed on feathers and partly also on living tissues (Johnson & Clayton 2003, Rózsa 2003, Mey et al. 2007). A number of influential papers showed that lice affect both life expectancy and reproductive success of hosts (Clayton 1990, Booth et al. 1993,
Breeding bird dynamics in a primeval temperate forest over thirty-five years: variation and stability in the changing world

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Abstract. The composition and structure of the breeding bird assemblage in the Białowieża National Park (BNP) were documented in 2005–2009 and compared with the data from the previous 30 years. Mapping censuses were carried out in seven plots located in three forest types: ash-alder riverine, oak-hornbeam, and mixed coniferous forest. We checked whether the bird community composition had remained stable over the 35 years and the extent to which the numerical trends in BNP followed the regional trends. The composition of breeding avifauna and species richness was basically unchanged, except for the strongly increasing Sylvia atricapilla, which became a regular dominant in all habitats. The density gradient across habitats — highest in the riverine, lowest in the coniferous stands – was retained. After a maximum in 2001, the numbers of birds declined slightly, but densities were still among the highest in 35 years. Numbers of 18 of the 26 commonest species were higher in 2005–2009 than in 1975–2009; only Anthus trivialis, Phylloscopus sibilatrix, Ficedula parva showed negative trends, and Ficedula hypoleuca almost went extinct recently. Some numerical changes were attributable to local habitat changes (increases in Phylloscopus collybita and Sylvia atricapilla, declines in spruce-dependent species). Numbers of only four of 22 species (Dendrocopos major, Erithacus rubecula, S. atricapilla, Parus major) changed concurrently in BNP and the rest of Poland. The apparent lack of a relationship between changes in bird numbers and the local and regional situation suggests that factors acting on a far larger scale could have been involved. Despite these numerical changes, the breeding bird assemblage of primeval temperate forest stands out as an example of remarkable stability.

Key words: bird community structure, long-term study, species richness, density changes, Białowieża National Park, population trends

Received — Jan. 2010, accepted — Oct. 2010

INTRODUCTION

Large-scale anthropogenic changes in environmental conditions (e.g. climate change, deforestation, forest fragmentation) can have profound effects on forest bird communities. Yet in most cases, their impact is difficult to separate from effects of direct human interventions (e.g. habitat management). To be able to do this one has to study birds in areas free of direct human influence, which could provide reference data (Tomiałojć et al. 1984, Wiens 1989, Wesołowski & Tomiałojć 1997, Gatter 2000, Wesołowski & Cholewa 2009). The Białowieża Forest, on the Polish/Belarusian border, is one of few such places left in the temperate Europe. Here, fragments of primeval forests, which once covered European lowlands, have been strictly protected within the Białowieża National Park (BNP hereafter; Tomiałojć & Wesołowski 2005, Wesołowski 2007a). Fauna and flora recorded in the BNP are expected to live in conditions which prevailed in European forests before these were anthropogenically altered. These pristine features have been well documented (Faliński 1986, Tomiałojć 1991, Jędrzejewska & Jędrzejewski 1998, Wesołowski 2007a). The data collected here may, therefore, provide a benchmark for the bird community studies made in

To Ludwik Tomiałojć, the initiator of the ornithological studies program in the Białowieża Primeval Forest, on his 70th birthday
Several Oligocene bird remains of Poland have been found in marine deposits of the Menilite Formation of Outer Carpathians, SE Poland, which is primarily known for its rich marine fauna of fishes (Kotlarczyk et al. 2006). The avian fossils were collected from four various exposures located in small villages of Winnica, Hłudno, Bachów, and Przysietnica in the Podkarpackie Voivodeship. One of the skeletal remains was described as a hummingbird *Eurotrochilus noniewiczii* from the Oligocene (Rupelian) deposits of Winnica (Bocheński & Bocheński 2008). Three other partial specimens were referred to the passeriforms (Bocheński 1989, 1993, 1996). However, their reevaluation revealed that one of them, ZPALWr. A/4003, is not a passeriform.

The fragmentary fossil ZPALWr. A/4003 has been collected at Bachów I, i.e. in one of the four exposures situated in the village of Bachów, about 18 km south of Przemyśl and 47 km south-east of Rzeszów. Geographical coordinates for the village of Bachów are 49°48’ N, 22°30’ E. Bachów I is a small natural outcrop (5 m in maximum extension and 2.5 m thickness) excavated between 1972 and 1986. The specimen was found together with 500 completely articulated fish imprints in the fossil layers consisting mainly of thin-bedded, brown clay-siliceous shales (Kotlarczyk et al. 2006). The fossiliferous horizon of Bachów I has been dated to Chattian, Oligocene (ca. 26 MYA) on the basis of the fish assemblage (Kotlarczyk et al. 2006). The horizon occurs within the calcareous nannoplankton of the NP25 zone (middle part of NP25 zone *sensu* Berggren et al. 1995).

Osteological terminology follows Baumel & Witmer (1993). Dimensions are given in millimeters and refer to the greatest length along the longitudinal axis of the bone (Table 1).

The specimen is housed in the Zoological Institute, University of Wrocław, Poland.

ZPALWr. A/4003 consists of a slab and counter slab with imprints of a right avian foot, which includes a broken along its longitudinal axis tarsometatarsus, well-preserved digits I and II, and hardly distinguishable remains of digits III and possibly IV that superimpose over each other (Fig. 1).

The medial side of a nearly complete but poorly preserved tarsometatarsus is visible on the main slab. A fragment of its distal part is also present on the counter slab. In contrast to many extant taxa with long and thin tarsometatarsus (e.g.