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DOES MIST-NETTING PROVIDE RELIABLE DATA TO DETERMINE THE SEX AND AGE RATIOS OF MIGRATING BIRDS? A CASE STUDY INVOLVING THE GREAT TIT *(Parus major)* AND THE BLUE TIT *(Cyanistes caeruleus)*

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Abstract

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Ringing results of tits caught at two stations on the Polish Baltic coast were used to check if mist-netting could be successfully used to analyse the composition of sex and age classes of migrating birds. Four hypotheses are discussed, describing the distribution of age and sex classes during migration, and the consequences these distributions might have for the catching results. We analysed records of 59 000 Blue Tits and more than 84 000 Great Tits that were caught and we found a similarity in the results of catches at stations 188 km apart, and a higher similarity among catching sites 0.5–16 km apart. These results proved that mist-netting provides reliable data on the sex and age structure of migrating flocks, and that these data can generally be interpreted as representative for at least the area in a radius of more than 10 km. The results also showed a migratory divide through the central part of the Polish Baltic coastline between irruptive Blue Tits in the west and regular partial migrants in the east. Great Tits showed no tendency for irruptions anywhere in the study area. A high correspondence in the age and sex ratio was found for Great Tits and Blue Tits, in particular where both species are regular migrants. We found that the ratios of females and immatures did not differ by more than 1% over many years of study in these areas.

Key words: migration, methodology, sex ratio, age ratio, *Parus major*, *Cyanistes caeruleus*.

Introduction

Many studies have proved that the numbers of birds caught at ringing stations accurately reflect the migration dynamics of a species in the region of a station (Cofta, 1985; Svensson, 2000; Zehnder, Karlsson, 2001; Nowakowski, Busse, 2002; Nowakowski, 2002, 2003). Thus data of this type can be effectively used in the analyses of migration phenology (Peiro, 1997; Fowler, Hounsome, 1998; Schekkerman, 1999; Jenni, Kery, 2003), and for the seasonal or yearly migration intensity of certain species (Busse, 1994; Nowakowski, 1999; Sokolov et al., 2001). Using data from many ringing stations we can try to track a continental pattern of migration intensity and changes in the population size of each species (Woźniak, 1997; Nowakowski, Busse, 2002; Nowakowski, 2003; Nowakowski et al., 2005). Data from catches at ringing stations are also used to analyse the composition of the migrants' sex and age classes (Peiro, 1997; Nowakowski, 1999; Schekkerman, 1999; Scebba, 2001), and these results are considered to be representative of larger areas, or even of a whole country (Peiro, 1997; Nowakowski, 1999; Schekkerman, 1999; Scebba, 2001). But we did not find any evidence in the literature to justify this interpretation, and we formulated three hypotheses that questioned this interpretation:

1. The sex and age groups prefer slightly different habitats or local conditions, such as the catching localities' exposure to strong winds.

The wings of adult and immature birds have different flight properties (Alatalo et al., 1984; Hedenström, Pettersson, 1986; Mulvihll, Chandler, 1990; Arizaga et al., 2006), which affect their ability to counteract unfavourable weather and their need to seek places less exposed to predatory pressure. Birds of different ages and sexes might also prefer different types of food (e.g. Ebenman, 1986; Durell, 2000; Scheiffarth, 2001).

2. Individuals of higher social rank (usually older birds and males) (Saitou, 1979; Sandell, Smith, 1991; Gosler, 1993, 1996) choose more favourable habitats that are safer and provide more abundant food or better protection against unfavourable weather. They displace lower-ranked individuals to worse habitats (Woodrey, 2000; Newton, 2008).

Males might also establish territories during stopovers (Bibby, Green, 1980; Mehlum, 1983; Titov, 1999). Higher-ranked individuals in the flock might also defend resources during short stopovers and movements in short hops, the way tits migrate.

3. Different sex and age classes form groups during migration and tend to migrate together.

Immatures and adults of many passerines migrate separately. In spring males and females might migrate separately (Hussell et al.,1967; Ely, 1970; Gauthreaux, 1982; Francis, Cooke, 1986; Spina et al., 1994; Dierschke et al., 2005; Salewski, Bruderer, 2007). Even when different age and sex classes migrate at the same time, they might form flocks based on their sex and age because of the different flight properties of their wings (Arizaga et al., 2006).

If hypothesis 1 or 2 is true, the age and sex ratios of birds caught at ringing stations represent not only the general composition of the migrating population, but also reflect the habitat preferences of each group. Thus, the observed sex and age ratios would depend on the location of the mist nets, so catching birds in specific locations would increase the probability of ringing a bird of a particular sex or age. This would introduce a regular bias into the results, with an over-representation of some groups.

If hypothesis 3 is true, we cannot draw precise conclusions about the composition of age and sex classes among migrants by catching only a portion of the migrating birds, because we randomly catch only some flocks, each of which has a different composition to the mean of all the flocks moving through the area. But with highly intensive studies, conducted over a long period and at many sites that include most of the local micro-habitats at the same time, we can correctly estimate the age and sex ratios in populations, because the composition of age and sex classes of the captured birds would not differ from those of the migrating population in a regular manner.

We also formulated a fourth hypothesis as an alternative to the three earlier ones, which assumes the following:

4. The distribution of sex and age classes is uniform in a population migrating over large areas, and variable catching conditions do not affect the proportions of age and sex classes among the individuals that are caught. All individuals of the species share habitat preferences, and the conditions outside the stopover sites during migration do not favour the retention of a hierarchical structure in the flocks (as suggested by Surmacki, Nowakowski, 2007).

If the fourth hypothesis is true, the data on the sex and age ratios of the migrating population obtained at the ringing stations are reliable and would be representative of the migration over the larger area.

This study is aimed at verifying these four hypotheses.

When birds from different geographical populations migrate through a study area they might prefer different foraging and resting habitats, or they might use the different localities within the area at different intensities. In such a case the sex and age ratios of birds caught at a locality most closely reflect the composition of the most abundant population that uses this site. We would likely obtain different results by moving the catching site a few kilometres or to another habitat, even if the catches accurately reflect the composition of migrating populations at each locality.

So to verify which of the proposed hypotheses is true, we must select a species in which populations arriving from different directions at the study site do not mix. The Blue Tit (*Cyanistes caeruleus*) and the Great Tit (*Parus major*) fulfil this condition. They migrate on a broad front and on the same heading through the whole of Central and Eastern Europe. The migration routes of different populations in both these species do not cross (Winkler,1974; Frelin, 1974; Thielemans, Eyckerman, 1975; Hudec, 1983; Alerstam, 1993; Glutz von Blotzheim, Bauer, 1993; Latja, 1995; Nowakowski, 2003). Both species migrate relatively slowly (Dhondt, 1966; Frelin, 1979; Payevsky, 1971; Nowakowski, 2001, Nowakowski, Chruściel, 2004; Nilsson et al., 2008), "from one bush to the next" (Ulfstrand, 1962). This allows us to sample the whole population of migrants relatively accurately, not only the groups that use the ringing sites for longer stopovers.

Study site, materials and methods

Data were compared from nearby ringing localities that sampled the same migratory population, and between more distant areas where birds caught may come from different populations. These conditions are fulfilled by two ringing stations located on the Polish Baltic coast: Mierzeja Wiślana (MW) and Bukowo-Kopań (BK), located 188 kilometres apart (for a description of both stations see Nowakowski (2001)). At each of these stations in some years birds were caught simultaneously at two sites (referred to later in the text as the catching localities for each station).

Bukowo-Kopań in 1980 operated at locality BK1 (54°20´51″, 16°15´43″) and 3 kilometres away at locality BK2 (54°19´57″, 16°14´15″), in 1981-1982 at BK1 and 16 kilometres away at BK3 (54°27´11″, 16°24´18″). In 1995–1998, 2001 and 2003, localities BK3 and BK4 (54°27´46″, 16°24´38″) located 1.5 kilometres km apart were in operation. Station Mierzeja Wiślana in 1967-1968, 1971-1974, 1982-1983 operated at locality MW1 (54°21´15″, 19°18´56″) and at locality MW2 (54°21´10″, 19°19´21″) 0.5 km apart. These localities were exposed to different wind conditions. The most exposed localities were at BK3 and at MW2. Their habitats also differed slightly, with a different proportion of reeds, varying ages of trees, etc. Generally, at MW2 the habitat was slightly poorer than at MW1. Small woods of alder occurred at BK1 and BK3, which were absent at BK4. The proportion of low willow thickets with reeds was higher at BK4 than at the station's other localities.

Numerous movements of tits between the pairs of ringing localities up to 2 km apart were observed, often on the same day. This fact and also the short distance between the catching localities allow us to assume that tits from the same migratory populations were being caught at these stations. Only about a dozen movements were observed in any year from one locality to another 16 km away at the same station. Stations Mierzeja Wiślana and Bukowo-Kopań lie 188 km apart and very few direct movements of birds ringed at the one and recovered at the other were observed (one every few years). So we assume that the birds caught at these stations do not come from the same stream of migrants, though they probably are from migratory populations moving along nearby routes (Nowakowski, 2003). Busse (1973) presumed that the catches at Mierzeja Wiślana and Bukowo-Kopań stations comprised birds of different migratory populations (in different proportions in different years).

The material we analysed came from the autumn migrations between 1967 and 2003. The records included 28 047 Blue Tits and 50 041 Great Tits caught at Mierzeja Wiślana, and 30 945 Blue Tits and 34 639 Great Tits from Bukowo-Kopań. Each station operated for the whole migration season from mid-August until the end of October, and in some years longer, but not all of their ringing localities were operated throughout the season. To compare data between the stations we therefore analysed only material collected during the tits' migration, i.e. between 15 September and 31 October, and only from the main catching locality, which operated over the whole season and used the greatest number of mist nets. For comparisons between two nearby catching localities operating at a station, only data from identical periods were used. We omitted birds in juvenile plumage, which are seldom migrants, and individuals that had not been aged or sexed. No comparisons were made of catching localities for years when fewer than 20 individuals of a species were caught. For the Blue Tit that was locality MW2 in 1982, for the Great Tit it was MW2 in 1974.

In this paper we consider the differences and the similarities in the composition of age and sex classes among the studied groups of migrants. Questions about similarities are not answered by conventional statistical methods. Conventional statistical methods of analysing the frequency that a given phenomenon occurs are based only on the most probable value, and are thus imprecise (MacKay, 2003). In this paper we applied a direct approach, based on the beta distribution of the probability of the studied phenomenon, using the so-called Bayesian approach to statistical data analysis (Spiegelhalter, 1999).

If in a large population the proportion of females equals 'p' and detectability (the probability of being caught) does not depend on the sex, in any sample of N caught birds we would expect $k \approx p*N$ of females. More precisely, the number of females has the binomial distribution, which we symbolically express as: $k \sim \text{Binomial}(p, N)$. The opposite approach, if based on a sample of N caught birds among which there are k females we want to draw conclusions about the possible values (distribution) of the proportion 'p' in a population we have to apply the beta distribution: $p \sim \text{Beta}(k+1, N-k+1)$. To compare proportions of females in two samples (N_1,k_1) and (N_2,k_2), two hypotheses were formulated:

H1: each sample comes from a different population with different ratios of females: k1 ~ Binomial(p1, N1), and of males k2 ~ Binomial(p2, N2)

H2: both samples come from the same population with a common value for p: k1 ~ Binomial(p, N1), k2 ~ Binomial(p, N2)

Applying the Bayesian approach we can precisely calculate which of these hypotheses is more probable, and how many times more likely one hypothesis is than the other in the light of the available data:

$$\frac{P(H_1 \mid Data)}{P(H_2 \mid Data)} = \frac{Beta(k_1+1, N_1 k_1+1) \cdot Beta(k_2+1, N_2 k_2+1)}{Beta(k_1+k_2+1, N_1+N_2 k_1 k_2+1)} \quad (1)$$

An identical procedure was used in the analysis of the age structure. Two age classes were distinguished in these tits: birds in their first year of life (imm.) and birds in their second or later years of life (ad) (see Busse (1984) and Svensson (1992) for ageing and sexing methods for these tits).

Following Jeffreys (1961), we applied a comparative ranking of the probabilities based on the evidence (Table 1) and used a threshold value of 1 to indicate a significant difference or similarity. Positive evidence implies that hypothesis 1, where the samples originate from different populations, is more probable; negative evidence means that hypothesis 2, where the samples originate from the same population, is more probable.

T a b l e 1. The evidence and its interpretation based on probability calculated for H1.
P_{H1} – probability H1; S_{H1} – odds for H1, $S_{H1} = P_{H1}/P_{H2}$; E_{H1} – evidence for H1, $E_{H1} = 2*log10(S_{H1})$.

P_{H1}	S_{H1}	E_{H1}	Meaning evidence in favour of hypothesis H1
>0.76	>3.16	≥1	Substancial evidence
>0.91	>10	≥2	Strong evidence
>0.97	>31.6	≥3	Very strong evidence
>0.99	>100	≥4	Decisive evidence in favour of H1 (H2 may be rejected)

In testing the hypotheses for multiyear periods, an equation was applied for the total probability:

$P(H1|1\ to\ N) = P(H1|Y_1)\cdot P(Y_1) + P(H1|Y_2)\cdot P(Y_2) + ... + P(H1|Y_N)\cdot P(Y_N)$ (2)

where $P(H1|Y_N)$ is the probability of the hypothesis H1 in a year N; and $P(Y_N)$ is the probability of the year N. If the probabilities for each year $P(Y_N)$ are equal (as in this case), the equation can be represented in the form:

$P(H1|1\ to\ N) = [P(H1|Y_1) + P(H1|Y_2) + ... + P(H1|Y_N)]/N$ (3)

With the mean probability of H1 we can calculate the corresponding value of the evidence by the equation

$EH1 = 2 * [log10(P(H1)) – log10(1–P(H1))]$ (4)

The figures present 95% credibility intervals for p calculated on the beta distribution. The most probable value (the mode) was marked with the point pMOD = k / N.

Results

A similar composition of age and sex classes was observed in both species at both bird-ringing stations (Mierzeja Wiślana, MW, and Bukowo-Kopań, BK). Over the 37 years that we studied, females constituted 57.5% (±1.5%) of the caught birds and immatures constituted 90% (±2%) as presented in Table 2. An identical proportion of female Blue Tits was recorded at the MW and BK stations, which is strong evidence in favour of hypothesis H2 that both samples come from the same statistical population (Table 2). In the remaining cases differences were highly statistically significant, though relatively small if we consider that in both species the proportion of females and immatures fluctuate by more than 15% year to year.

The ratio of immature Blue Tits at BK varied the most, by as much as 4% from MW (Table 2). This result was caused by two years of irruptions. In 1999 and 2003 station BK caught 36% of all the Blue Tits that have been trapped over the 37 years of studies at this station. In these two years, immatures constituted 95% of all caught Blue Tits, a ratio that was significantly higher than in the non-irruptive years (irruptive years 1999 and 2003: imm. – 95%, N = 9 011; non-irruptive years: imm. – 89%, N = 16 207; $E_{H1} = 117.5$; Fig. 1). No irruptions of the Great Tit were noted at either station, or of the Blue Tit at station MW. The ratios of immature Blue Tits at MW and BK do not differ significantly in non-irruptive years (MW: imm. – 88%, N = 24 724; BK: imm. – 89%, N = 16 207; $E_{H1} = 0.4$).

The age and sex ratios were also similar for both species. The ratios of female Great Tits and Blue Tits at the MW station (where neither species irrupted) differed by only 0.5%, very strong evidence in favour H2 (*Parus major*: imm. – 58.2%, N = 47 446; *Cyanistes caeruleus*: imm. – 58.7%, N = 24 724; $EH_1 = -3.2$). Similarly, the ratio of immatures was significantly similar in both species, with the difference in mean ratios of only 0.6% (*Parus major*: imm. – 88.9%, N = 47 446; *Cyanistes caeruleus*: imm. – 88.3%, N = 24 724; $E_{H1} = -1.7$).

T a b l e 2. Comparison of sex and age ratios between the stations (all years pooled). F – females; Imm. – birds in their first year of life; E_{H1} – evidence in favour of hypothesis H1.

	F % (N)			Imm. % (N)		
	MW	**BK**	**E_{H1}**	**MW**	**BK**	**E_{H1}**
CY CAE	59 (24 724)	59 (25 218)	-3.8	88 (24 724)	92 (25 218)	55.2
PA MAJ	58 (47 446)	56 (31 176)	10.2	89 (47 446)	88 (31 176)	9.7

T a b l e 3. Comparison of sex and age ratios between the stations in different years (irruptive years excluded). Number of years with similar ratios (H2 more probable; $P_{H1} < P_{H2}$; $E < 0$), different ratios (H1 more probable; $P_{H1} > P_{H2}$; $E > 0$) and the evidence of mean probability calculated for all pairs of years (for *C. caeruleus* N = 31 years, for *P. major* N = 33 years) are given. Numbers of statistically significantly similar ($E \leq -1$) and different ($E \geq 1$) years are in brackets.

	CY CAE		PA MAJ	
	Sex	**Age**	**Sex**	**Age**
N similar years (significantly)	21 (14)	23 (15)	30 (28)	27 (25)
N different years (significantly)	16 (11)	14 (13)	7 (2)	10 (7)
E_{H1} for mean P_{H1}	>0.0	-0.1	-1.0	-0.6

The age and sex ratios for Great Tits and Blue Tits were similar for most years at both stations, implying H2 – that birds caught at MW and BK originate from the same statistical population – is more probable than H1, but in a few years both species showed a significantly different ratio of immatures or females (Table 3, Fig. 1). In both species the total similarity (Equation 3) calculated for the ratio of immatures or the ratio of females was always higher for H2 (MW and BK represent the same statistical population) than for H1 (MW and BK represent different statistical populations). However, the probability of H2 was significantly higher than of H1 (Table 3) only in the case of sex ratios in the Great Tit.

For the few years in which hypothesis H1 (different age ratios at each ringing station) was more probable we checked if the differences between the stations showed any regular character, i.e. if the ratio of females or of immatures was regularly higher at one of the stations. For each of these years the probability of hypothesis $H1_{BK}$ was calculated (higher ratio of females or of immatures at BK) and total probability of this hypothesis (Equation 3). The evidence of the total probability within the range $-1 < E_{H1BK} < 1$ means that in years when the sex and age ratios differed between the stations these differences did not have a regular character; $E_{H1BK} < -1$ means that in certain years at BK there were regularly more females or immatures than at MW; $E_{H1BK} > 1$ means that in certain years at BK there were regularly fewer females or immatures than at MW.

We found that the sex ratio for both species never showed a regular character: in some years the ratio of females was higher at BK, in others at MW (*Parus major* – $E_{H1BK} = 0.8$; *Cyanistes caeruleus* – $E_{H1BK} = -0.7$). But it was different with the age ratios. For both species in years when the ratio of immatures differed at BK and MW the differences showed a regular character. It was particularly clear in the case of the Blue Tit, where in each of 14 years with a

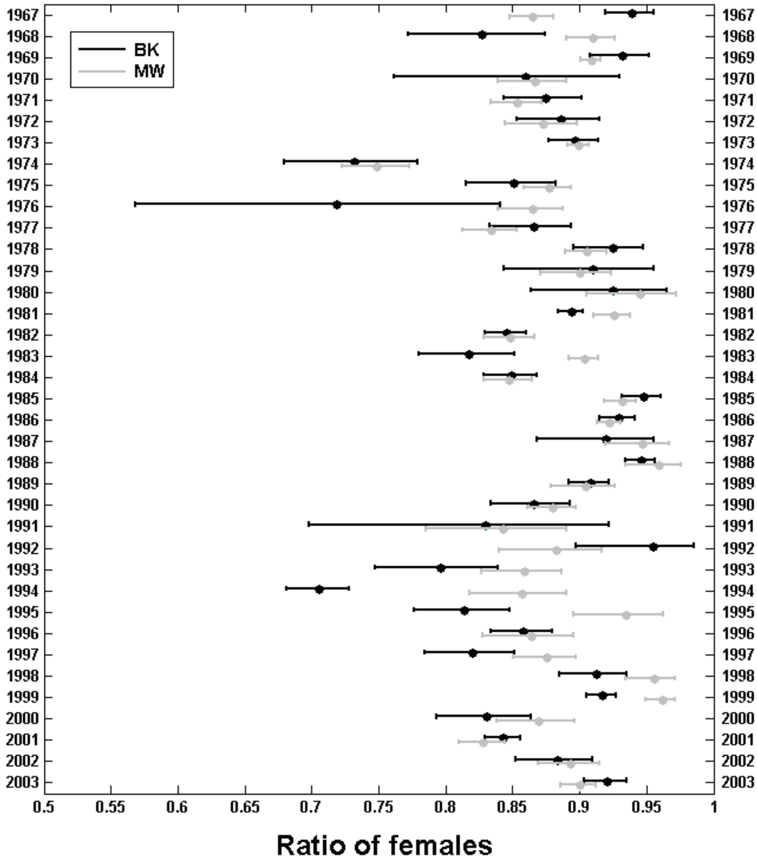

Fig. 1. Comparison of the proportions of immature Great Tits at stations Bukowo-Kopań (BK) and Mierzeja Wiślana (MW). Note that in the abundance of birds in 1977-1990 the ratio of immatures at both stations was usually similar (in 9 of 14 years the difference was less than 2%, which gives strong evidence in favour of H2), but in 1983 the difference was 9% (decisive evidence in favour of H1). The most probable value (mode) and 95% credibility intervals are marked in the figure.

significant difference a higher proportion of immatures was recorded at BK ($E_{H1BK} = -2.8$; in total in these years at BK – 93% imm., at MW – 84% imm.). In the Great Tit for the 10 years in which these differences were observed, immatures were more numerous at MW in 9 years ($E_{H1BK} = 1.7$; respectively BK – 87% imm., MW – 90% imm.).

Stronger similarities were noted among the nearby catching localities within each ringing station than between the stations, regardless of whether the catching localities were 0.5–3 or 16 km apart (Table 4). In these cases the total probability of H2 was also significantly higher than of H1 only when analysing the ratio of female Great Tits. In all 16 years the ratio of females was significantly similar (Table 4, Fig. 2). But even in the sex ratios of the Blue Tit, which showed the smallest similarities between the localities, in 9 years the ratios of females

T a b l e 4. Comparison of the age and sex ratios at pairs of catching localities at one station, located 0.5–3 km (A) and 16 km (B) apart. For other description see Table 3.

		CY CAE		PA MAJ	
		Sex	**Age**	**Sex**	**Age**
A	N similar years (significantly)	10 (8)	12 (9)	14 (14)	10 (9)
	N different years (significantly)	4 (3)	2 (2)	0 (0)	4 (3)
	E_{H1} for mean P_{H1}	-0.4	-0.8	-1.8	-0.5
B	N similar years (significantly)	2 (1)	2 (1)	2 (2)	2 (2)
	N different years (significantly)	0 (0)	0 (0)	0 (0)	0 (0)
	E_{H1} for mean P_{H1}	-1	-0.8	-1.5	-1.9
Together	E_{H1} for mean P_{H1}	-0.5	-0.8	-1.8	-0.6

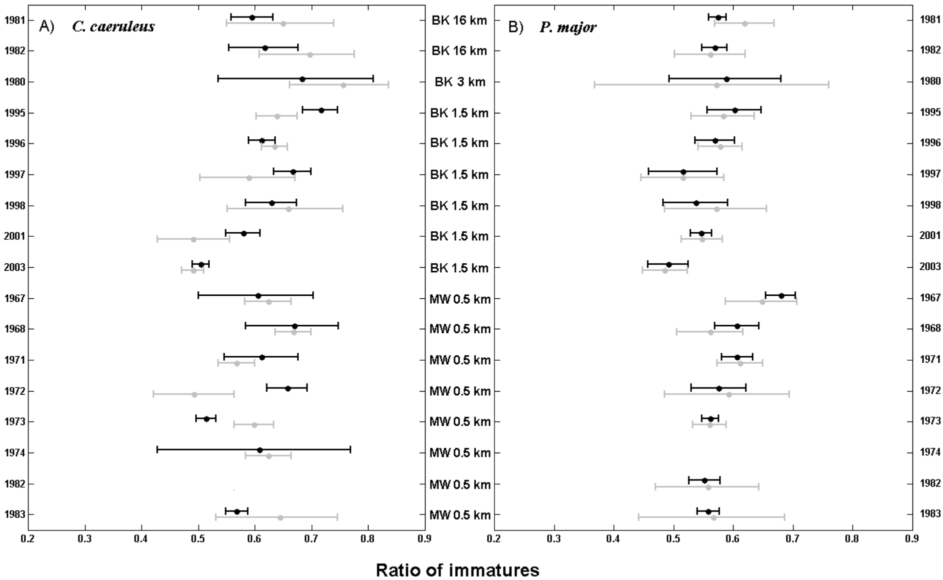

Fig. 2. Comparison of the ratios of female Blue Tits (A) and Great Tits (B) at pairs of catching localities at one station. For each pair of localities at the station, the year and the distance between the catching localities is given below the X axis. The most probable value (mode) and 95% credibility intervals are marked in the figures.

were significantly similar and only in 3 years were the ratios significantly different (Fig. 2; the total probability H2 – p = 0.65 was almost two times higher than the total probability H1 – p = 0.35). Year-to-year fluctuations in the ratios of females or the ratios of immatures observed at the stations provided good reference values to analyse the differences between the localities at the stations. Such a comparison was done for both parameters (the ratio of females and the ratio of immatures) in both species. The mean difference between years at the same locality was in all cases higher than the mean difference between the localities in the same year. But only in the case of the ratio of immature Great Tits was this result statistically significant (E_{H1} = 4.0).

It is difficult to determine unambiguously if the differences that were found between catching localities at one station had a regular character. No more than 2 years with a significant difference were noted at any pair of localities at one station at the same time, which impeded any statistical analysis. The data presented in Fig. 2a show that these differences lacked a regular character, even for the sex ratios of Blue Tits, which showed the greatest number of differences between the catching localities. In the 7 years when localities MW1 and MW2 were operating simultaneously, a significant similarity in the sex ratios of Blue Tits was found in 4 years, an unclear indication of the similarity in 1 year, and significantly different ratios in 2 years. In 1971 significantly more females were observed at MW1, and in 1972 at MW2 (Fig. 2a). The total probability of the hypothesis $H1_{MW1}$ – that at MW1 there were more females than at MW2 – equals the probability of the contrary hypothesis $H2_{MW1}$ – that at MW1 there were fewer females than at MW2 (for $H1_{MW1}$ $p = 0.494$, for $H2_{MW1}$ $p = 0.506$).

Discussion

Generally the high concordance of the results obtained at catching localities situated different distances apart at one ringing station, and even between the two stations located 188 km apart, showed that mist-netting provides reliable data on the age and sex ratios of migrating birds, and that these data are representative of a larger area with a radius of more than 10 km. The differences were no greater as the distance between the localities rose to 16 km, which indicated that the passage was relatively uniform for the sex and age ratios across larger areas (as assumed by hypothesis 4). Significant differences in the age and sex ratios of birds caught at nearby catching localities occurred only in a few years, but even then the differences were not regular. Thus no evidence was found that individuals of a different age or sex selected different habitats for their resting and foraging places. At least in these two species of tits, there was no confirmation for hypotheses 1 and 2.

Differences in the composition of age and sex classes occurred in some years even at the closest pairs of catching localities at station MW, where the central points of the mist-netting areas at MW1 and MW2 were only approx. 500 m apart, and some nets of one locality were only 100 m from the border of the other locality. For example, in 1968 at MW1 69% of the Blue Tits were immatures (N = 124), but at MW2 92% were immatures (N = 854) (see also Fig. 2). This local variation indicated that sometimes groups of birds with very different age and sex ratios occurred at a station and were confined to small patches of the stopover areas. This is in accordance with hypothesis 3, and such differences occurred more often in Blue Tits than in Great Tits (Tables 3 and 4). But usually the composition of age and sex classes was similar at both catching localities operating at one station, even when a small sample of birds was caught (see 1980 for the Great Tit, Fig. 2). So we can conclude that the different assemblages of tits that were observed showed no tendency for birds of the same sex or age to form flocks (which was assumed by hypothesis 3). These different concentrations were more probably formed by birds originating exceptionally from different migratory groups, e.g. one of them migrating from a particularly long distance or displaced over the Baltic Sea by strongly unfavourable winds, as described by Lindholm (1978). Whatever the reasons for this phenomenon, the occurrence of different assemblages means that it is necessary (especially in Blue Tits) to catch a great number of individuals and that the mistnets must be set over a relatively large area to obtain precise data representative of the larger area. Population heterogeneity of migrating birds might be more intensely pronounced in species with a complex migration system, in which the migration flyways of different populations cross. It was found that in such species different migratory populations avoid mixing with each other (Busse, 1985; Bensch, 1999; Remisiewicz, 2002).

Very few direct ringing recoveries have been noted between stations MW and BK for both species of tits. Despite that, the observed age and sex ratios, especially for the Great Tit, were significantly similar at these stations for most years. This would confirm the assumption that the passage of Great Tits along the south-eastern Baltic coast is similar over large areas and that in each year its character is shaped by the same population and environmental factors (Nowakowski, 2002, 2003). That means data obtained for this species at one ringing station can be interpreted in a wide geographical scale as representative for the whole region. The few years when significant differences were detected in the age and sex ratios of Great Tits at the BK and MW stations can be linked to the unusual weather conditions mentioned earlier. Strong winds can displace large groups of Great Tits and Blue Tits over the Baltic Sea, or force some groups of the birds to choose an unusual migration route further inland (Lindholm, 1978; Alerstam, 1993; Nowakowski, 2003).

More differences between stations were recorded for the Blue Tit than for the Great Tit. Significant similarities between MW and BK occurred in about 30% of the years, but there were significant differences for almost the same number of years. So many years with different age and sex ratios cannot be explained only by atypical weather conditions, especially because more immatures were observed at BK for all the years in which the proportion of Blue Tits' age classes differed between these ringing stations. Moreover, an irruptive passage was observed at station BK in 2 years. In both these years the number of Blue Tits was more than 10 times higher than the mean yearly number of this species caught at this station. A high ratio (95%) of immatures was noted, which is typical of irruptive movements. For example Markovets, Sokolov (2002) stated that in the Coal Tit *Parus ater*, a typical irruptive species, the ratio of immatures among birds migrating during irruptions was between 94 and 99.9%. But at MW, as at stations further east in Lithuania, Estonia and Finland, the Blue Tit is a typical regular partial migrant (Nowakowski, Vähätalo, 2003, for MW also the present paper). In Western Europe the Blue Tit is known as an irruptive species (Winkler, 1974; van Balen, Speek, 1976; Lensink, 1990). Busse (1973) assumed that stations BK and MW catch, at least partially, different streams of tits moving through them, or the same streams but in different proportions. We think that station BK is in the border area for the Blue Tit. In some years its passage of migrants is affected by the same factors as on the south-eastern Baltic coast and the same migratory groups pass through it. In other years at this station populations of less regular migrants occur, influenced by conditions that cause irruptions. The presence of beech forests might be one of these conditions. Irruptions of tits are most often associated with the cycle of beech mast abundance (Alerstam, 1993). BK is the first ringing station in the zone of beech forests (Nowakowski, Vähätalo, 2003) that the tits encounter when moving from the north-east to the south-west (Hudec, 1983; Glutz von Blotzheim, Bauer, 1993). Perhaps irruptive populations are of local origin and their occurrence is connected to the cycles of beech mast at their breeding area. Such populations could have high breeding success (high proportion of young Blue Tits at BK not only in years of irruptions), which in some years leads to a high population density and hence to irruptive migrations.

The greatest variation between the catching localities of a station over a year was observed in the sex ratio of Blue Tits (Tables 3 and 4), though the sex ratio in this species at stations MW and BK was identical when many years of data were combined (Table 2). Sexing of Blue Tits is difficult and even highly experienced ringers sex some birds incorrectly (Busse, 1984; Svensson, 1992). These difficulties do not occur in sexing the Great Tit and in determining the age of both species. If at least some of the differences were an effect of mistakes in sexing and the varying experience of the ringers, the sex ratios in Blue Tits caught at the different localities might be even more similar than shown by this study. This seems probable because, in contrast to Blue Tits, the sex ratios of Great Tits showed an exceptionally low variation between stations and localities in the same year.

The differences in the composition of age and sex classes between migrating Great Tits and Blue Tits revealed in this paper did not exceed 3%. This result was, however, affected by results of the BK station, where Blue Tits, as opposed to Great Tits, tend to irrupt. In the area where both species are regular partial migrants, such as around the station MW (Nowakowski, Vähätalo, 2003), differences in the composition of age and sex classes did not exceed 1%. The Great Tit and the Blue Tit co-habit over most of Europe and occupy similar ecological niches, have a similar breeding biology (Cramp, Perrins, 1993) and their wings have similar flight properties (see figures in Jenni, Winkler (1994)) and thus their similar pattern of migration (see Ulfstrand (1962); Berhtold (1993) and Nowakowski, Chruściel (2004)) is not surprising.

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