CATCH NUMBERS AT RINGING STATIONS IS A REFLECTION OF BIRD MIGRATION INTENSITY, AS EXEMPLIFIED BY AUTUMN MOVEMENTS OF THE GREAT TIT (*Parus major*)*

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ABSTRACT

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Results from six ringing stations located along sea coast (maximally 517 km apart) were used to check if the method of catching birds in traps (mist-nets, heligoland) can be applied in analysing the real pattern of daily migrants migration. On the basis of catch dynamics of nearly 440 000 Great Tits, it was possible to demonstrate that the method of catching can be used successfully in studies of the daily passage of migrants, not only in order to probe the overall intensity of migration, but also to analyse migration routes and the influence of atmospheric conditions on birds' movements. It was found that migrating Great Tits cover the area uniformly, but atmospheric conditions disturb the passage.

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Key words: migration, catching dynamics, daily migrants, Great Tit, *Parus major*

INTRODUCTION

A network of bird ringing stations exists in Europe, with the first having been launched over 100 years ago and several others operating for over 40 years now. Nevertheless, it remains an open question as to what extent numbers of birds caught at these ringing stations reflect their true migration intensities. As has been demonstrated by many authors (*e.g.* Svensson 2000, Nowakowski and Busse 2002), catching is a method capable of providing correct information on multi-year trends to the numbers of migrating passerines. What is not clear is the accuracy of the obtained estimates within a season, as well as whether, or with what limitations, the results obtained at a certain location can be interpreted as indicative of migrants numbers across an entire region.

To analyse this problem, I have chosen a species with a simple migration system – the Great Tit, which moves at a relatively low but stable speed (Nowakowski 2001), along a broad front and with a similar migration angle of *ca* 235° being maintained over the whole of Central and Eastern Europe (Likhachev 1957, Payevsky 1971, Hudec 1983, Alerstam 1993, Hudde 1993, Rezvyi *et al.* 1995). As the migration routes of different populations basically do not cross, the interpretation of results obtained is facilitated.

The region of the south-eastern and southern Baltic coast experiences migration of homogeneous groups of Great Tits, which are recorded at all the region's ringing stations (Nowakowski 2002). In a previous paper (Nowakowski 2002), it was demonstrated that the intensity of passage of these birds is reflected well by daily and seasonal (autumn) catch totals. This finding was in agreement with the earlier results of Ulfstrand (1962) and Cofta (1985). With some caution, the total at a single station can be interpreted as reflecting migration intensity in the region as a whole in a given season (Nowakowski 2002), although it is very likely that results obtained at different stations reflect this intensity to differing degrees. What remains unknown are: the extent of any such discrepancies, the reasons for their occurrence and the influence they may exert on the correct interpretation of data collected at single stations. In the cited paper (Nowakowski 2002), I demonstrated that migration intensity in a whole region is best described by the average of the catch totals from all stations there. However, it was not possible to sufficiently identify the limitations of the method.

The present paper has therefore two aims:

1. to describe and explain differences in the multi-year and seasonal catch dynamics noted between particular ringing stations, with reference to the two working hypotheses that:
   - The discrepancies between stations reflect true differences in migration intensity in various localities and are thus a source of important scientific information;
   - The differences between stations reflect shortcomings in the method (*i.e.* varying efficiency of bird catching dependent on many factors like the arrangement of traps, winds and other weather conditions, food abundance in the area changing over time, *etc.*), and therefore only serve to impede fuller interpretation of the results.
2. to check possible biases of the method estimating migration intensity on the basis of the average from the catch results for many ringing stations.

MATERIAL AND METHODS

The database for the analysis of multi-year and seasonal dynamics related to 436 239 Great Tits ringed in 1979-1993 at six stations located in Estonia (Kabli), Latvia (Pape), Lithuania (Ventes Ragas and Neringa), the Russian Federation's Kaliningrad District (Rybachy) and Poland (Mierzeja Wiślana) (Fig. 1; for description

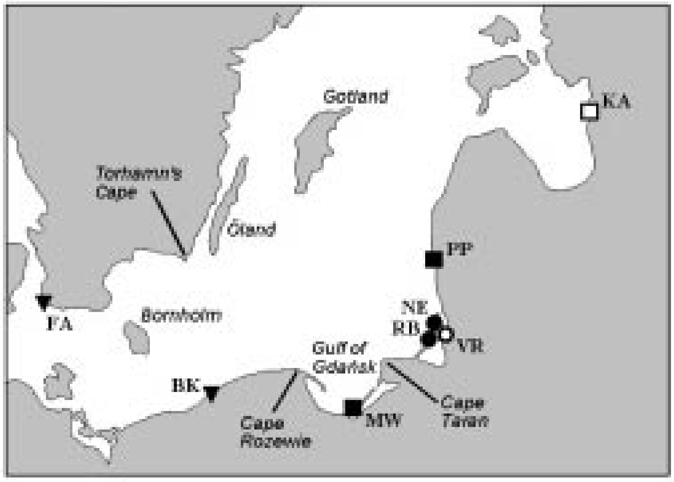

Fig. 1. Location of the bird ringing stations from which the material used in the paper originates: KA – Kabli (58°01'N, 24°27'E), PP – Pape (56°11'N, 21°03'E), NE – Neringa (55°27'N, 21°04'E), VR – Ventes Ragas (55°21'N, 21°12'E), RB – Rybachy (55°09'N, 20°52'E), MW – Mierzeja Wiślana (54°21'N, 19°19'E), BK – Bukowo-Kopań (54°28'N, 16°25'E), FA – Falsterbo (55°22'N, 12°52'E). Squares – stations from which data were used only in comparisons of migration dynamics; circles – stations from which data were used in comparisons of migration dynamics and ringing recoveries; open signs – data were used only in comparisons of multi-year migration dynamics; black signs – data were used in comparisons of multi-year and seasonal migration dynamics; triangles – remaining stations.

of stations and field methods see Busse 2000 and Nowakowski 2001). I also referred to 218 recoveries of birds ringed at the Ventes Ragas and Neringa stations (published in Patapavičius 1982, 1983, 1986a, 1986b, 1986c, 1987, 1988, 1989, Skuodis and Kurpyté 1989) and in Rybachy (in Bolshakov *et al*. 1999, 2001). The numbers of birds caught each autumn (used for the multi-year dynamics) and each day (for the seasonal dynamics) were normalised in relation to the mean number of birds caught in autumn at a given station during the whole study period. To compare the course of seasonal migration dynamics at different stations, mean daily catch totals for 1979-1993 were correlated among the stations (Spearman rank correlation – r_S). To compare multi-year dynamics, I used autumn totals for the stations (Pearson correlation – r). The types of statistics used were adjusted to the distribution of the data.

The same groups of birds arrive at the various areas at different times. The speed of movement of Great Tits in the described region is relatively stable, at 33.2 km/day on average (Nowakowski 2001). It is thus possible to standardise seasonal migration dynamics at different stations (by presenting them in standardised days of passage). For that reason, daily catch totals were shifted to compensate for the number of days Great Tits needed to cover the distance between compared stations (for details see Nowakowski 2002). For this reason, the first standardised day of passage at each station has a different date: 10 September at Pape, 12 September at Neringa, 13 September at Rybachy and 17 September at Mierzeja Wiślana.

The χ^2-test was applied with Yeates' correction.

RESULTS

Comparison of catch dynamics among stations

The autumn catch results from different stations correlated to varying extents (Table 1). Numbers of Great Tits ringed at the Neringa station, located in the middle of the studied region, correlated significantly with catch results at all other stations except Mierzeja Wiślana. In contrast, numbers of birds caught at Mierzeja Wiślana were only correlated significantly with those caught at the station most distant from it, *i.e.* Kabli (Table 1). The between-stations correspondence of the multi-year number dynamics (explained by the value of the correlation coefficient r) was not associated with the distance between them ($N = 15$, $r = 0.15$, $p = 0.592$).

Table 1
Results of Pearson correlations for autumn catch totals among different stations (number of correlated years – $N = 15$). For station symbols see Fig. 1.

		Correlation coefficient (r)					
		KA	PP	NE	VR	RB	MW
	KA		0.43	**0.72**	**0.52**	0.43	**0.58**
	PP	*ns*		**0.66**	0.35	**0.56**	0.30
	NE	**0.003**	**0.008**		**0.63**	**0.71**	0.18
Significance (p)	VR	**0.045**	*ns*	**0.013**		0.22	0.17
	RB	*ns*	**0.031**	**0.003**	*ns*		0.00
	MW	**0.024**	*ns*	*ns*	*ns*	*ns*	

The material for analyses of the seasonal number dynamics was available for the Pape, Neringa, Ventes Ragas and Mierzeja Wiślana stations. After correcting for the time needed to cover the distances between stations (see *Methods*), seasonal dynamics at all stations were found to be highly correspondent and significantly correlated (Table 2).

Table 2
Results of the Spearman correlations of mean daily catch totals in years 1979-1993 among different stations (number of correlated days in a season – $N = 45$). For station symbols see Fig. 1.

		Correlation coefficient (r_s)			
		PP	NE	RB	MW
	PP		**0.66**	**0.78**	**0.64**
Significance (p)	NE	**< 0.001**		**0.69**	**0.73**
	RB	**< 0.001**	**< 0.001**		**0.69**
	MW	**< 0.001**	**< 0.001**	**0.001**	

Comparison of the catch dynamics for each station and the mean dynamics in the region as a whole

Numbers of Great Tits caught in autumn at the northernmost station Kabli (multi-year dynamics) did not correlate with catch results at Pape – the next station along the migration route (Table 1), but did correlate significantly with the mean migration dynamics pooled for Pape and the next station on route – Neringa ($r = 0.62$, $p = 0.012$). In turn, when the results from the closely adjacent stations at Ventes Ragas and Rybachy were included into the analysis, the correlation coefficient increased to $r = 0.66$ ($p = 0.007$). If we also consider Mierzeja Wiślana, located 517 km from Kabli, in the calculations of the mean migration dynamics, the correlation coefficient reaches $r = 0.79$ ($p < 0.001$). This value is much higher than for the comparison with any single station (see Table 1).

A similar analysis can be done for the Neringa station located at the centre of the studied region. While results from this station correlate significantly with those from Ventes Ragas only 15 km away (Table 1), the correlation is weaker than with the mean migration dynamics pooled for Ventes Ragas and the closely situated Rybachy ($r = 0.84$, $p < 0.001$). The relationship becomes ever stronger with pooling into the mean of the results of more and more distant stations, *i.e.* Pape ($r = 0.87$, $p < 0.001$), and then Kabli ($r = 0.90$, $p < 0.001$). Only when the results from Mierzeja Wiślana are also included, does the correlation again weaken ($r = 0.76$, $p = 0.001$), but the relationship with the mean for the whole region is still much stronger than that with any single station in the region. In the case of the southernmost station Mierzeja Wiślana, the resemblance of the multi-year dynamics both with single stations (other than Kabli – Table 1) and with the mean dynamics pooled for the whole studied region is weak and not statistically significant ($r = 0.31$, $p = 0.094$).

The numbers of Great Tits caught daily at each station (seasonal dynamics) are correlated well among all stations (see first section of *Results*), but it is most often the case that the correlation coefficient goes even higher when results are compared with mean daily catches pooled for all remaining stations (in the whole region). Thus, correlations of daily totals at the Neringa, Rybachy and Mierzeja Wiślana stations with mean daily catches for the region (for NE: $r = 0.77$, $p < 0.001$; for RB: $r = 0.83$, $p < 0.001$; for MW: $r = 0.75$, $p < 0.001$) are in every case higher than those with any other single station (see Table 2). Only the daily totals at Pape are less correlated with the mean for the remaining stations ($r = 0.75$, $p < 0.001$) than with results for Rybachy, although more strongly than with results for Neringa and Mierzeja Wiślana (Table 2).

Reasons for differences

As was shown in previous chapters, the level of similarity to the multi-year migration dynamics described for consecutive stations varied, although it was usually rather high. An exception concerns the catch results for Mierzeja Wiślana, which correspond with neither the multi-year migration dynamics at other stations nor the mean multi-year migration dynamics in the region as a whole (extrapolated on the basis of results from the remaining stations taken together). On the other hand, the fact that the same groups of Great Tits migrate through Mierzeja Wiślana as through the remaining part of the region is suggested by the general migration angle for the Great Tit in Europe, and demonstrated by the great similarity to seasonal migration dynamics and numerous (more than 1500!) ringing recoveries (see Nowakowski 2001, Bolshakov *et al.* 2001).

So why does this situation arise? In four years (1979, 1987, 1988, 1989), while an intensive migration was noted in the studied region, catch totals at Mierzeja Wiślana were exceptionally low (see Fig. 2). These seasons are hereafter called "outstanding years". In the most exceptional of these – 1987, the large groups of Great Tits occurring at all other stations, were not noted at Mierzeja Wiślana at all (Fig. 3A). In the remaining outstanding years, some of the groups of Great Tits recorded at other stations were also obtained at Mierzeja Wiślana, but others were still lacking. For example, in 1979, only the beginning and end of the Great Tit passage were detected at Mierzeja Wiślana (Fig. 3B). When the four outstanding years were excluded from the data, the correlation of autumn catch results at Mierzeja Wiślana and in the region as a whole was high ($r = 0.77$, $p = 0.006$; Fig. 2), and the courses of the seasonal migration dynamics found to be similar (see Fig. 3C and D). To explain these facts, analyses of some parameters of the migrations in outstanding years were carried out.

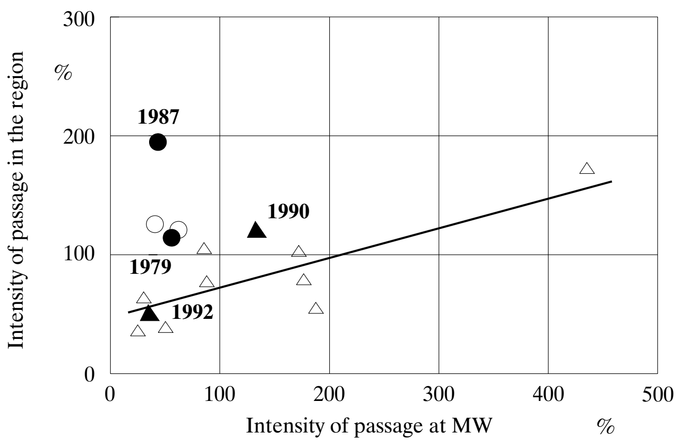

Fig. 2. Correlation of migration intensity (measured by number of birds caught in given year in relation to multi-year mean) at Mierzeja Wiślana and in the region (mean result at remaining stations – KA + PP + NE + VR + RB). Circles – outstanding years; black signs – years for which the seasonal dynamics are presented in Figure 3; the trend line drawn excludes the outstanding years; for station symbols see Fig. 1.

For the stations Neringa, Ventes Ragas and Rybachy, it was possible to determine frequencies with which ringing recoveries (*RR*) were obtained from the area west to Mierzeja Wiślana. Data for the four outstanding years (N = 83 948,

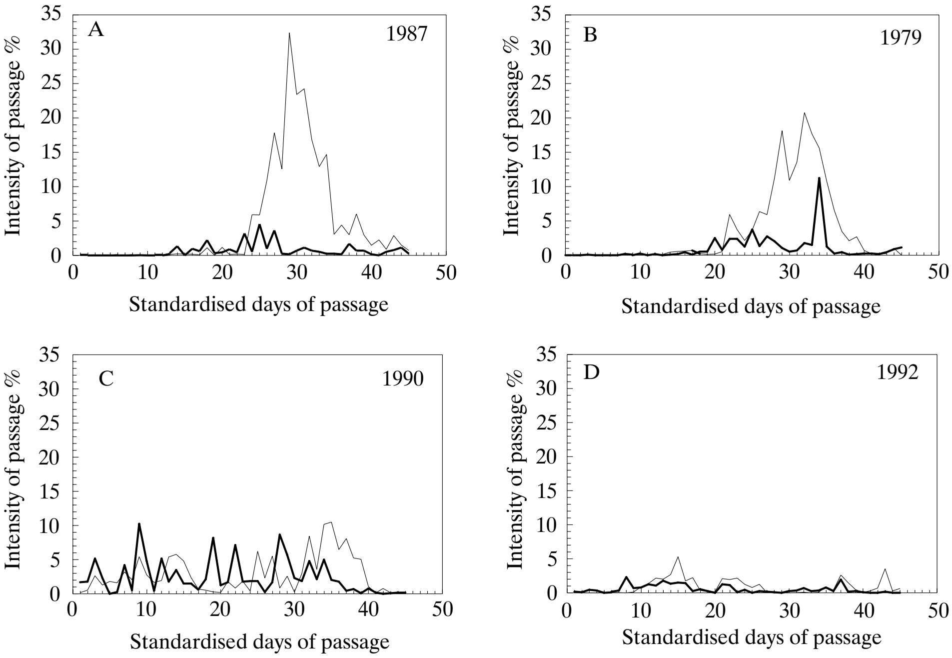

Fig. 3. Comparison of migration dynamics at the Mierzeja Wiślana station – thick line – and in the region (mean result for remaining stations) – thin line; subsequent figures present years with: A – migration that is very intensive in the region but very weak at MW, B – migration that is intensive in the region and weak at MW, C – intensive migration at all stations, D – very weak migration at all stations. The first standardised day of passage at MW = 17 Sep.; migration intensity measured as percentage of birds caught on a given day in relation to the mean number of birds in autumn seasons 1979-1993.

RR = 0.10%) and the remaining period (N = 128 365, RR = 0.11%) were not found to differ significantly ($\chi^2 = 0.26$, $p = 0.609$).

The median of recovery angles for the area west to Mierzeja Wiślana, as calculated for the stations Neringa, Ventes Ragas and Rybachy, was 249.5° (N = 82) in the four described years, while in the remaining period it was 245.5° (N = 136). This difference is at the margin of significance (Wheeler and Watson test: $W = 5.90$, $p = 0.052$). The reason for it was a higher percentage of ringing recoveries from Sweden and Bornholm in the outstanding years than in the remaining ones. However, this higher percentage was reported during autumn migration (before 15 November, respectively: 53%, N = 45 and 27%, N = 51; $\chi^2 = 5.66$, $p = 0.017$) only, while it was not noted in the winter season (15 November – 28 February, respectively: 3%, N = 37 and 2%, N = 85; $\chi^2 = 0.27$, $p = 0.602$).

In the outstanding years, the Ventes Ragas station caught 21% (N = 161 061) of the Great Tits noted in the northern and central part of the region (KA, PP, NE, VR and RB jointly), while in the remaining years – only 18% (N = 258 276) – χ^2 = 614.68, $p < 0.001$.

DISCUSSION

The obtained results can be explained by the following sequence of reasoning:

1. Over the whole described region the same migratory groups of Great Tits move at a certain migration intensity and with given dynamics (as confirmed by numerous ringing recoveries between the described stations – Nowakowski 2001).
2. Catch results at consecutive stations most often offer a good reflection of these general migration dynamics, although smaller or greater deviations are noted at all stations. These are not associated with the distance between stations (see first section of *Results*), and are not synchronised at subsequent stations.
3. For the above reason, mean catching results for the whole region better reflect the general migration dynamics and intensity there than do results obtained at each given station separately. Therefore, greater accuracy to the estimate of migration intensity is obtained when data for a greater number of stations are considered.
4. While comparing results from two stations, a difference that reflects deviations of the results for both the stations from the general parameters of migration in the studied region is revealed.
5. While comparing results from one station with the mean for all remaining stations in the region, nothing more than the difference resulting from the deviation of only one station's results from the general parameters of migration in the studied region is revealed (that is why higher correlation coefficient is generally being found).

As was shown in the second section of *Results*, in the case of the northernmost station Kabli and the centrally-located Neringa, the correlation coefficient grew larger as data for consecutive stations were included (despite the fact that the stations included were ever more distant). In the light of the above reasoning, this should be interpreted as an increase of similarity of mean catch totals to the real migration intensity in the region with the rise of the number of localities regarded in calculations.

For correct interpretation of the multi-year and seasonal dynamics revealed at ringing stations it is crucial to answer the question: what is the reason for the described differences in catch totals from station to station? This phenomenon was most distinct at Mierzeja Wiślana, where catch results did not correlate significantly with those obtained at other stations. However, more noticeable differences were only found for 4 of the 15 analysed years, during which the intensive movements of Great Tits noted at other stations in the region were not observed at Mierzeja Wiślana. In relation to the two general hypotheses put forward in *Introduction*, it is possible to advance three further, more detailed hypotheses regarding the deviations to be observed at Mierzeja Wiślana:

1. In some years the migration undertaken by Great Tits is shorter, with the majority of birds wintering in the area between the Rybachy and Mierzeja Wiślana stations.

2. In some years, the migration of the Great Tit proceeds in a slightly different direction, such that birds avoid Mierzeja Wiślana.
3. In certain circumstances, the migration dynamics obtained for the Great Tit simply do not reflect the real intensity of migration at Mierzeja Wiślana.

As the percentages of Great Tits migrating towards winter quarters located west from other stations to Mierzeja Wiślana did not differ in outstanding years and remaining years, the first hypothesis may be rejected.

In contrast, the obtained results can sustain the second hypothesis. It is known that, with very strong southern or south-eastern winds, Great Tits can be displaced in masses over the Baltic to Sweden, in a manner inconsistent with their normal migration direction (Lindholm 1978, Alerstam 1993). In the outstanding years, a higher percentage of recoveries from Sweden and Bornholm was indeed noted, indicating that the above situation did arise – probably between Rybachy and Mierzeja Wiślana. Moreover, unfavourable weather conditions might be expected to encourage a majority of the birds to migrate at some distance from the sea coast. This idea can be sustained too, as the migration at the only station located a little more inland (Ventes Ragas) was exceptionally intensive in the outstanding years. In these years, therefore, the passage of Great Tits would have avoided Mierzeja Wiślana to a great extent.

Additional information could be obtained through an analysis of the multi-year migration dynamics for the Bukowo-Kopań station located even further to the west. Unfortunately, Bukowo-Kopań is situated inside the zone of beech forests, such that the crop of beechnuts is partly capable of stopping birds' passage (Ulfstrand 1962). What is not known in this regard is how large proportion of the migrants might break passage in this way, as well as in which area and at what intensity the abundance of beechnuts is necessary. All this naturally impedes any drawing of precise conclusions. Nevertheless, bearing all these reservations in mind, an additional comparison for the outstanding years was done. As has been shown in *Results*, the Mierzeja Wiślana passage of Great Tits in these years was poor (with average catch totals at just 41% of the mean level from the remaining years), even though the migration in the eastern part of the study region was intensive (for Kabli, Pape, Neringa, Ventes Ragas and Rybachy jointly – 143%). At this time, the migration intensity at Bukowo-Kopań was also higher (82%). Alerstam (1993) describes that Great Tits displaced by strong southern winds to the Swedish coast reversed crossing the Baltic and head for continental Europe immediately after the weather had calmed down. However, other flocks continued their migration along the Swedish coast and joined the usual flyway crossing of the Strait of Sund and Denmark. This description can well explain the results obtained in this study. If Great Tits along the coastline between Rybachy and Mierzeja Wiślana were displaced towards Sweden, and a part of them then returned to the southern Baltic coast, these birds should be noted at the Bukowo-Kopań station (see Fig. 1). Also birds migrating further inland on account of very strong winds would, following the end of unfavourable weather conditions, return to the more coastal flyway and be present in at least some of their original strength at Bukowo-Kopań.

A question then arises as to why the described mechanism refers only to Mierzeja Wiślana, and not the other stations. Why are outstanding years only detectable in the data for Mierzeja Wiślana? Maps presented by Hudde (1993) imply that Great Tits can be displaced towards Sweden by southeastern winds along other fragments of the Baltic coast, as well. However, considering the course of the southern coast of the Baltic and locations of each station (Fig. 1) it appears that birds coming back from Sweden to the usual migration route have a low chance of landing near Mierzeja Wiślana, located as it is within the Gulf of Gdańsk. Birds displaced from their normal route between the stations of Pape and Kaliningrad's Cape Taran (Russia), would land on Gotland or Öland, or in the region of Cape Torhamn's in Sweden. If they reverse cross the Baltic from these sites, they would either return to the region of Pape (such that the described stations will not even note their crossing of the Baltic), or would arrive in the region of Cape Rozewie or further west. In the second case the described groups of Great Tits will not be noted at Mierzeja Wiślana, but should occur at Bukowo-Kopań. Conversely, if Great Tits migrating along the Estonian and southern Latvian coasts are displaced by the wind to the west or the north-west, they would rather tend to come back to the Latvian coast near Pape or more to the north (Fig. 1). In this way they will still be noted at all stations. In this context, it is interesting that the correlation coefficient between yearly totals at Mierzeja Wiślana and the remaining stations decreases with shorter distance to these stations (it is highest for the comparison with Kabli, and lowest for the comparison with Rybachy – Table 1). In other words, the coefficient decreases in line with the lower chance that birds displaced during the passage are able to return to their usual migration route.

It also seems that Cape Taran (situated between Rybachy and Mierzeja Wiślana) is a kind of trap for Great Tits, at which the chance of displacement by unfavourable winds over the open sea is especially high. In this place, the coast turns rapidly to the south, even to the southeast, forming an obstacle for Great Tits seeking to continue movement in the normal direction of migration (*ca* 235°). Cape Falsterbo is another such trap, as described in detail by Ulfstrand (1962).

Concluding, it seems that the analysis of geographical conditions can offer a good account of the observed differences in migration intensity in subsequent years among the ringing stations. A large part of the observed variation can be explained by reference to weather conditions (strong winds in particular). Nevertheless, one cannot entirely exclude the possibility that the third of the above hypotheses holds true. However, it does indicate that the level of bias to the results caused by shortcomings in the method of bird catching in mist-nets or heligoland traps is relatively low, and that the way in which results vary between stations reflects to a large extent real differences in the intensity of the migration stream at each locality. These differences can be an important source of information about the large-scale structure of passage in changeable weather conditions.

The above conclusions cannot be applied automatically to nocturnal migrants (which move in long ”jumps” and then rest at stop-over sites), or to species with more complex migration systems (passage in several directions). However, the intensity of nocturnal migrants' movements is also quite well reflected by catching totals, as is shown by studies using radar (Zehnder and Karlsson 2001). Interpretation of the results is more difficult if we analyse data on species in which the migration routes of different populations cross, like the Robin *Erithacus rubecula* (Remisiewicz *et al.* 1997, Remisiewicz 2002), or the Song Thrush *Turdus philomelos* (Busse and Maksalon 1986). In such a situation, the obtained seasonal migration dynamics are a combination of the various periods and intensities of passage of the different populations, while the multi-year dynamics are a result of long-term trends (often opposing one another) in these populations (Woźniak 1997, Nowakowski and Busse 2002). Because representation of each group differs from locality to locality, the result from one station cannot in this case be interpreted as reflecting migration intensity in the region. However, in such species also, the analysis of materials obtained at many ringing stations can give a satisfactory approximation of the general migration pattern (Busse and Trocińska 1999, Nowakowski and Busse 2002).

Summing up, the following methodological conclusions can be drawn:

1. The catching of birds during migration provides reliable data on migration intensity at a given locality. In species with a simple migration system, these results can with some caution be interpreted as reflecting the general migration intensity in the region.
2. Data from some stations (*e.g.* those more exposed to weather conditions) can be more biased than those from other localities.
3. Accurate data on migration intensity in a whole region can only be obtained through analyses of the material coming from many ringing stations working in this area. The accuracy of the method increases, the higher the number of stations considered.
4. Even if temporarily large biases of results at some stations (caused by different factors like the weather) can be suspected, a greater accuracy of the estimated migration intensity in the region is still obtained if all stations are considered, as opposed to a radical limitation of the number of stations in an analysis.
5. For species of more complicated migration systems (with passage in several directions), accurate information on migration intensity can only be obtained through analyses of material from a large number of stations.
6. The assessment of the accuracy of the catching method in relation to particular bird species (especially nocturnal migrants) needs further investigation.

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