STOPOVER OF ROBINS (*Erithacus rubecula*) ON AUTUMN MIGRATION THROUGH THE POLISH BALTIC COAST

Łukasz Meina, Małgorzata Ginter and Katarzyna Rosińska

ABSTRACT

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Data were collected during autumn migration at three ringing stations of the Operation Baltic: Bukowo-Kopań, Mierzeja Wiślana and Hel. Apart from different localization at the Polish Baltic coast, these places differ also in topography and habitat. Only data from years with the highest number of caught birds were used in the analyses, thus altogether the data on more than 25 500 ringed Robins and 1700 retraps were included. Based on migration dynamics graphs and number of retraps, a stopover index was calculated. Next, the index values were compared between days with a high and low number of caught birds and also between different fat categories. Differences between birds caught once and retraps were shown in relation to daily activity, age structure and fat level. Additionally changes in weight and fat level between first and last control in retraps were considered. At Mierzeja Wiślana and Hel the stopover index decreased in the course of autumn season in contrast to Bukowo-Kopań where an increasing trend was observed. At Bukowo-Kopań more birds decided to stopover than at Mierzeja Wiślana and Hel but at Mierzeja Wiślana Robins stayed longer than at other stations. Moreover, at Mierzeja Wiślana a half of departing retraps increased in fat level while at the other stations only *ca* 20% of retraps. Our results showed that in Robins the weak body condition is a decisive factor to stopover after crossing the sea. Differentiation in food resources and competition between individuals had an effect on the stopover index. Stopover duration at different ringing stations can depend on distance which birds cover before landing at the coast.

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Key words: Robin, autumn migration, Baltic coast, stopover

INTRODUCTION

The Robin is one of the most numerous species caught during migration at the Operation Baltic stations. Ringing recoveries analysis showed that birds caught in Poland migrated from Finland, Estonia, Sweden, south-western Norway and northwestern Russia (Remisiewicz *et al.* 1997). This species is a medium-distance migrant as its winter quarters are localized in the southern part of Europe and in northern Africa. Autumn migration through the Polish Baltic coast starts approximately in the beginning of September and lasts till the end of October. Like in most *Turdidae* species the passage starts at dusk and usually interrupts at dawn. In Robins the recapture rate is relatively high: 7-20% of birds stopover at the Baltic coast (Szumiło 1987), whereas in the Redstart (*Phoenicurus phoenicurus*) and Song Trush (*Turdus philomelos*) it is 1.3-9.5% and 1.9-8.9%, respectively (Busse 1972, Maksalon 1983). Higher values were observed in southern Portugal for the long distance migrants, like the Bluethroat (*Luscinia svecica*) or Reed Warbler (*Acrocephalus scirpaceus*) (Catry *et al.* 2004).

Not all individuals of the same species of passerines migrating through the same area stopover at the same places. It depends on migration strategy (a population specific migration flyway, distance covered last night), food availability, predatory risk and competition between individuals. Young birds after crossing the sea usually land at the coast, while more experienced adults stay in inland habitats rich in food. Consequently, the proportion of young birds caught at coastal sites is higher than at inland sites. This phenomenon, described as a "coastal effect", is well known in all nocturnal migrants (Ehnbom *et al.* 1993, Payevsky 1998).

Studies on stopover refer to different aspects of this phenomenon: stopover duration, ecology and behaviour or time of arrival and departure from stopover place. Some studies concern also crossing small/large geographical barriers like mountains, deserts or vast open water by long distance migrants or factors influencing stopover (*e.g.* Moore and Yong 1991, Weber *et al.* 1999, Dierschke and Bindrich 2001, Catry *et al.* 2004, Khoury 2004, Keşaplı Can and Bilgin 2005). In Robins some authors described migration strategies of birds caught at different stopover sites localized in south Sweden (Karlsson *et al.* 1988, Åkesson *et al.* 1992, Ehnbom *et al.* 1993). "Short-stage" migrants flew over land and required small fat reserves in contrast to "long-stage" ones that required large fat reserves to complete flight across the Baltic Sea. The first group of migrants dominated at coastal Falsterbo while the second one – at Ottenby. At inland Urasa station Robins probably change migration strategy in the course of migration season and the "long-stage" birds dominated in October. At the Polish Baltic coast probably both Robin groups flying over the land (from eastern Europe) and crossing the sea (from Fennoscandia) are caught. Similarly to south Sweden these groups of birds may differ in migration strategy. Szulc-Olech (1965) based on analysis of retraps proved that there were two groups of birds migrating along the Polish Baltic coast that differed in activity. The first of them was composed of birds with a low recapture rate and in weak condition. These individuals stayed at the stopover site for about two days and their weight all this time was constant or decreased. Birds of the second group usually stayed longer, even more than ten days, they recaptured several times and both fat and weight increased. This could be explained by occupation of feeding territories by birds that stopover for a longer period of time (Szulc-Olech 1965, Mehlum 1983, Titov 1999a). As a result of high competition only the most adapted birds or these in the high social rank are able to defend these territories. Fat reserves are restored after several days of stopover in the occupied territory. Migrants that stop their flight when the number of competitors is high, rebuild fat reserves more slowly than stopover birds under low density conditions (Moore and Yong 1991).

Geographical location, habitat conditions at recapture sites and migratory strategy of species probably play an important role in frequency of birds stopover, time that birds spend at certain area and fat-weight relationship (Karlsson *et al.* 1988, Ehnbom *et al*. 1993, Kędzior 2002). The aim of our study is to compare stopover duration, body condition (fat reserves, body weight) and age structure of Robins caught at different stopover sites.

MATERIAL AND FIELD METHODS

The data were collected during autumn migration at three ringing stations of the Operation Baltic: Mierzeja Wiślana (54°21'N, 18°19'E), Hel (54°46'N, 18°28'E) and Bukowo-Kopań (54°21'N, 16°17'E) (Fig. 1). Years, in which both relatively high number of caught birds and consequently high number of retraps were observed, were included into this analysis. Therefore, five years at each station were selected. Standard period comparable for all stations was established in the term 7 Sep. – 16 Oct. Juvenile Robins were excluded from analyses because they probably did not start autumn migration before post-juvenile moult was completed. Number of birds and analysed years are given in Table 1.

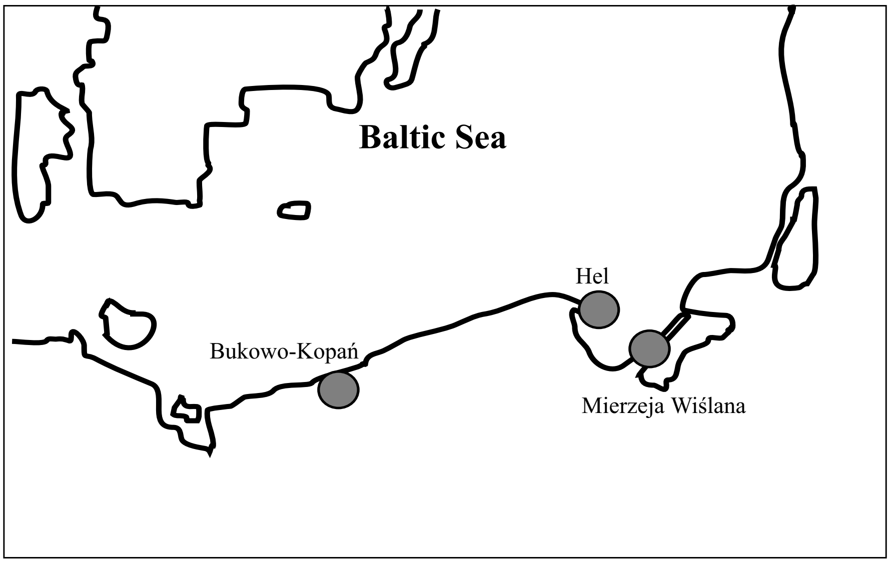


Fig. 1. Localization of Polish ringing stations the data were from

Table 1
Studied years and number of birds caught at particular ringing stations

Station	Years	Number of birds		Stopover (%)
		Ringed	Retraps	
Mierzeja Wiślana	1993, 1995, 1996, 1998, 1999	7901	358	4.43
Hel	1968, 1973, 1979-1981	6483	584	9.01
Bukowo-Kopań	1995-1999	10829	810	7.48

Study area comprised three Polish ringing stations differing in topography and habitat conditions. The advantage is that mechanisms remaining hidden or not clear enough at one ringing site may be obvious at another one. Mierzeja Wiślana ringing station is located on the spit that separates the Vistula Lagoon from the Baltic Sea. The land is 2 km wide at the ringing site. Most birds migrate along the spit. Nets are situated in young pine stand, alder wood, mixed forest with dominating pine and bushes. In all forest types the Rowan (*Sorbus aucuparia*), Alder Buckthorn (*Frangula alnus*), Common Lilac (*Syringa vulgaris*), Elder *(Sambucus nigra)* and rose (*Rosa sp*.) shrubs as well as willows (*Salix sp*.) also occur. Hel station is located at the Hel Peninsula and is a coastal station (Gross 1984) as birds that land in this place cross the sea beforehand. The main habitat is pine forest with poor undergrowth and alder wood. Some forest Rowans, Elders and Bird Cherries *(Padus avium)* also occur in this area. Hel station represents the least diverse habitat among all analysed stations. Bukowo-Kopań is located at the western edge of the Lake Kopań spit in the middle part of the Polish Baltic coast. Birds caught at this station either cross the sea or migrate along the coastline (Gross 1984). Nets are situated in young pine forest with blackberry undergrowth. The rest of the area is covered by alder carr and alder forest. Forest line in this place is half kilometre wide. At the southern edge of the area willow shrubs can be found.

Birds were caught in mist-nets that were controlled every hour from dawn to dusk. Caught birds were ringed, aged and measured according to the SEEN standards (Busse 2000). In 1968-1981 Robins were weighed with a Pesola spring balance to the nearest 0.2 g, in 1993 – to 0.5 g, and in 1995-1999 an electronic balance (with the accuracy of 0.1 g) was used. The fat score was determined according to a scale proposed by Busse and Kania (1970) and revised by Busse (2000). In retraps (birds recaptured in the same season) only fat score and weight were checked. An hour of catching was also recorded.

TERMINOLOGY AND ANALYSIS METHODS

In this study following terms were used:

– *caught birds* – in general – all individuals caught for the first time;

– *birds caught once* – individuals caught only once at a given ringing station. We assumed that these birds did not stopover at this place, they stayed at the ringing station 24 hours the longest and continued migration the following night;

– *retraps* – birds that interrupted their migration and were recaptured. Two controls (capture and recapture) must have been separated at least by one night. In our analyses data from the first and last captures were used. Birds caught second time during one day were excluded from analysis of retraps.

To get an overall pattern of migration dynamics for each day in all years jointly the percentage value of the number of caught birds was calculated in relation to the average daily number of caught Robins. Next, data were smoothed using moving average (from three adjacent days). The *stopover index* that was a percentage proportion of retraps to the number of caught birds was calculated. The Pearson correlation coefficient was applied in the analysing of relations between migration dynamics and stopover index. In this analysis three categories of days were distinguished in each season:

– *peak day* – day with the locally highest number of caught birds. Number of Robins captured on this day should be higher than 2% of the total number of birds caught in a given season,
– *adjacent days* – one day before and one after a peak day,
– *rest of days* – all days other than two categories mentioned above.

Relation between the stopover index in peak and adjacent days was analysed (the one way ANOVA) and in order to compare the distinguished categories of days the *post hoc* Tukey *t*-test was used. If two peak days were separated only by one day with lower number of caught birds, then such group of days was excluded from the analysis. Stopover index in peak days was also compared with days before and after peak day by the χ^2-test. In the analysis of stopover index at each station inter-seasonal changes were compared by one way ANOVA. The values of stopover index were also presented for different fat categories and the Pearson correlation coefficient was calculated for each station. Because of a low number of birds representing fat categories T_3, T_4 and T_5, these individuals were summed up and analysed as one group.

Table 2
Weight standardization correction values (g)

T_0	T_1	T_2	T_3	T_4	T_5
-3.11	-0.50	0	0.80	2.22	3.67

In the next step a comparison between individuals caught once and retraps was made. Percentage distribution of these two groups of birds during morning hours (from 6.00 to 12.00 *a.m.*) and evening hours (from 1.00 to 7.00 *p.m.*) was shown. Daily activity of two categories of Robins for each stations was presented at graphs and compared with the χ^2-test. Differences between initial fat score of Robins caught once and retraps were compared by the Mann-Whitney test. According to Busse (1970) fat scores were recalculated to get the *relative fat load*. Deviations of body mass averages from the average body mass of birds scored as T_2 were calculated. Resulting values for each fat score are shown in Table 2. To analyse changes in fat load between the first and last capture, differences in fat categories were calculated. Plus sign (+) was put in front of the value if fat load increased in relation to the first capture and minus (-) when a decrease in fat load was observed. Difference of fat loads between the first and last capture, called as the absolute (in grams) *fat change* (**Δ*t***), was calculated. Similar calculation procedures were used to calculate the relative (in percent) *weight change* (Δ***w***) between the first and last capture (Busse 1970). Relative fat load for birds caught once and retraps was compared at each station by the two-tailed *t*-test. In retraps comparison of stopover duration between stations was also made. Next, relative fat load in relation to stopover duration was given for each station. Variation of absolute fat changes and relative weight changes between first and last control were also presented. At Hel station only Robins that stopped over not longer than seven days were analysed because of a low number of birds staying longer. Proportion of individuals that departed with increased or decreased fat level was also calculated in relation to stopover duration.

RESULTS

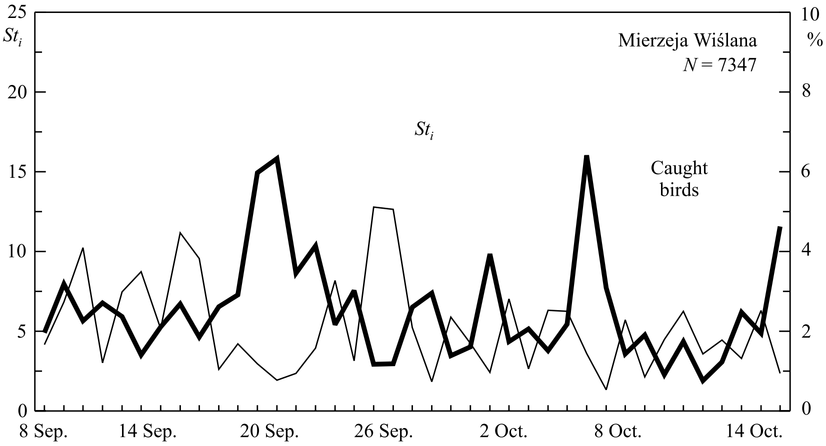
The stopover index in relation to migration dynamics

The stopover index and species migration dynamics are presented in Figure 2. At Mierzeja Wiślana the relationship between migration dynamics and stopover index was clearly marked (Fig. 3). At this station the stopover index decreased along with an increase in the total number of caught birds. At remaining stations this trend was not so clear (Fig. 3).

At Mierzeja Wiślana differences among peak days, adjacent days and the rest of days were statistically significant (ANOVA: $F = 20.80, p < 0.001$; see also Table 3). The average stopover index in peak days was lower than in remaining categories (Table 4). At Hel station differences between each category of days were statistically significant as well ($F = 13.51, p < 0.001$). Similarly, lower stopover index was found in peak days than in the other days. At Bukowo-Kopań statistically significant differences were not observed in different categories of days ($F = 1.51$, $p = 0.223$). The average stopover index in peak days was similar to its value in the remaining categories.

Table 3
Post-hoc comparison of stopover index among particular categories of days (Tukey *t*-test)

		Adjacent days	Other days
Mierzeja Wiślana	Peak days	$\boldsymbol{p < 0.001}$	$\boldsymbol{p < 0.001}$
	Adjacent days	–	$p > 0.05$
Hel	Peak days	$\boldsymbol{p < 0.001}$	$\boldsymbol{p < 0.001}$
	Adjacent days	–	$p > 0.05$
Bukowo-Kopań	Peak days	$p > 0.05$	$p > 0.05$
	Adjacent days	–	$p > 0.05$


25
St_i
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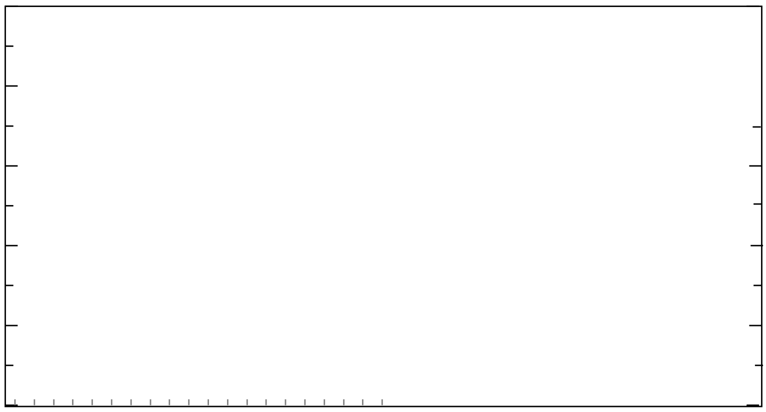
Caught
birds
8 Sep.
14 Sep.
20 Sep.
26 Sep.
2 Oct.
8 Oct.
14 Oct.



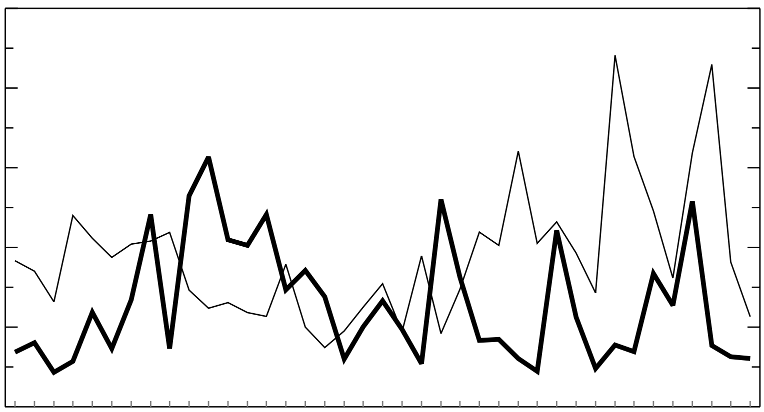


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Table 4

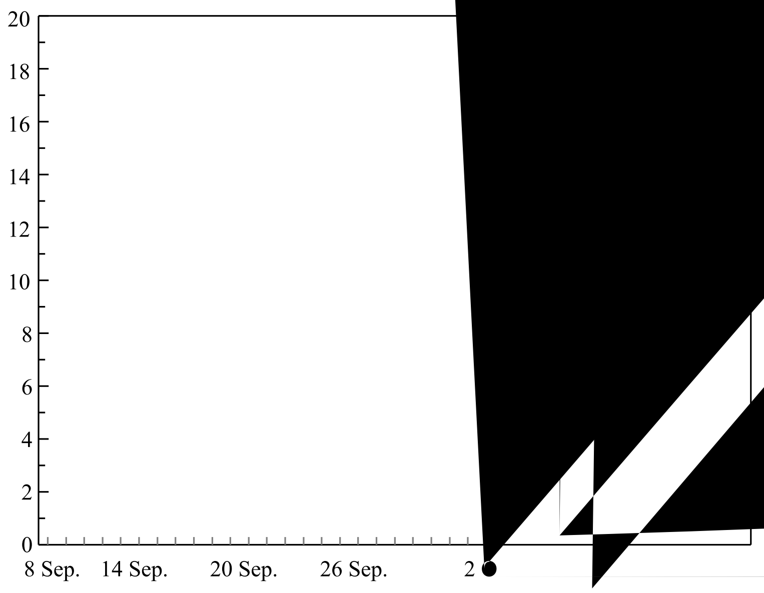
Average stopover index (pp) and deviation of sto[illegible]

	The day before peak day	
	pp	Δpp
Mierzeja Wiślana	4.36	+0.80
Hel	12.25	+4.97
Bukowo-Kopań	11.49	+1.19
Average	**9.36**	**+2.32**

The average stopover indices in subsequent [illegible]
4. At all stations decrease in value of the stop[illegible]
comparison with one day before peak day. Th[illegible]
the day after peak day. The largest difference[illegible]
noted at Hel station. Some variability in the s[illegible]
days compared to adjacent days. Decrease in t[illegible]
observed at all stations and subsequent increas[illegible]
high correspondence in course (χ^2-test: p = 0.9[illegible]

The stopover index at each station and[illegible]

Changes in the stopover index value during [illegible]
sented in Figure 4. The declining trend in the st[illegible]
Mierzeja Wiślana station (r = -0.41, $p < 0.05$). S[illegible]



Hel station ($r = 0.19$, $p = 0.258$) but it was not significant. At Bukowo-Kopań station distinct increasing trend in the stopover index was observed ($r = 0.14$, $p < 0.05$).

Statistically significant differences were found in the stopover index values between particular stations (one way ANOVA: $F = 12.07$, $p < 0.001$). The average stopover index for Bukowo-Kopań reached 9.45 and it was higher than at two other stations. The average stopover index for Hel station was 8.63 and for Mierzeja Wiślana – 5.29. Further analyses showed statistically significant differences between Mierzeja Wiślana and Hel stations (Tukey test: $p < 0.001$) and between Mierzeja Wiślana and Bukowo-Kopań stations (Tukey test: $p < 0.001$). Differences in the stopover index between Hel and Bukowo-Kopań stations were not statistically significant (Tukey test).

The stopover index values in different fat categories at each stations are presented in Table 5. A general tendency could be observed at all stations: the stopover index decreased along with fat level increase (Mierzeja Wiślana: $r = -0.97$, $p < 0.05$; Bukowo-Kopań: $r = -0.97$, $p < 0.05$). Similar trend was found at Hel station but differences were not statistically significant ($r = -0.90$, $p = 0.09$). It should be noted that regression lines, inclination observed at Mierzeja Wiślana and Bukowo-Kopań was exactly the same: b_{MW} and $b_{BK} = 0.60$ (compared to $b_H = 1.27$). At both stations the highest stopover index value was noted for the lowest fat level T_0 and at Hel station the highest stopover index value was observed in fat levels T_0 and T_1.

Table 5
Stopover index in different fat categories at studied stations

	T_0	T_1	T_2	$T_3 + T_4 + T_5$
Mierzeja Wiślana	8.33	5.69	4.66	3.46
Hel	10.52	10.99	8.23	7.22
Bukowo-Kopań	11.14	10.56	7.80	6.91

Characteristics of individuals caught once and birds later retrapped

Age structure of birds caught once and retraps is presented in Figure 5. At Hel and Bukowo-Kopań stations higher proportion of adults was noted in the group of birds later retrapped than in the group of birds caught only once. Conversely, at Mierzeja Wiślana the opposite tendency was found: within birds caught only once higher proportion of adult birds was observed.

An example of daily catching dynamics that represent daily activity of birds caught once and individuals later retrapped (data for first controls) is presented in Figure 6. At all stations most individuals of both categories were caught in the morning (from 6.00 to 12.00 *a.m.*), however birds caught once dominated (Table 6). At Hel station this difference was as high as 13.5%. The opposite was observed in the afternoon and evening (from 1.00 to 7.00 *p.m.*), when birds later retrapped dominated. Differences in daily activity between birds caught once and those later

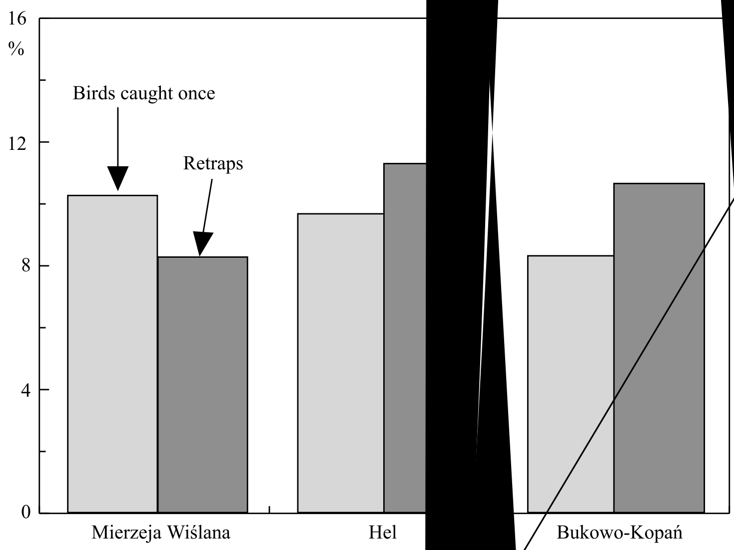
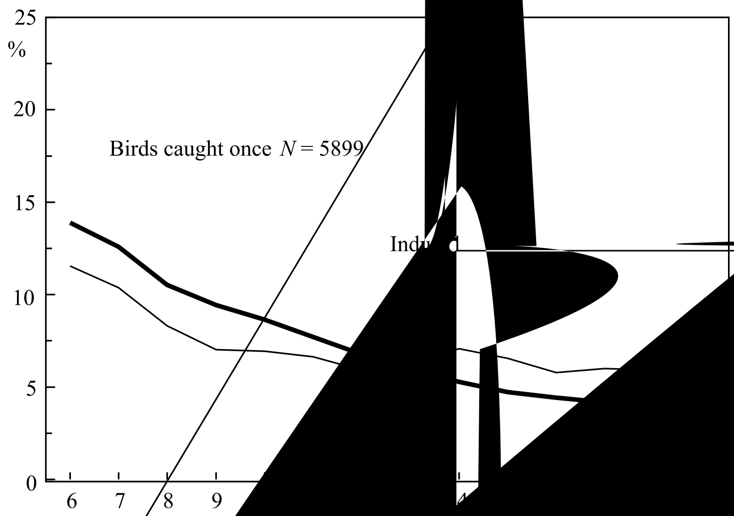


Fig. 5. Percentage of adult Robins among birds caught on [illegible] raps at each stationFig. 6.I [illegible]



retrapped were stati [illegible]
p < 0.001, Hel: p [illegible]

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Fig. 7). The average relative fat loads for birds caught once and individuals later retrapped are given in Table 7. Individuals caught once showed higher fat reserves than later retrapped birds. In retraps caught at Bukowo-Kopań and Hel stations similar relative fat loads were noted. Retraps caught at Mierzeja Wiślana station showed on average 0.47 g of fat more than birds from the other two stations. Differences in fat level of retraps caught at Hel and Bukowo-Kopań stations were insignificant (Mann-Whitney test: Z = -0.66, $p > 0.05$), while in all other cases these differences were statistically significant (Mierzeja Wiślana – Hel: Z = -4.97, $p < 0.05$; Mierzeja Wiślana – Bukowo-Kopań: Z = 4.85, $p < 0.05$).

Table 6
Percentage of birds caught once and of those later retrapped – in morning hours (from 6.00 to 12.00 *a.m.*) and in afternoon and evening hours (from 1.00 to 7.00 *p.m.*)

Station	Morning hours		Afternoon and evening hours	
	Caught once	Later retrapped	Caught once	Later retrapped
Mierzeja Wiślana	74.3	67.6	25.7	32.3
Hel	69.8	56.3	30.1	43.7
Bukowo-Kopań	76.6	70.1	23.4	29.8
Average	**73.6**	**64.7**	**26.4**	**31.9**

Table 7
Averages of relative fat load and average weight of birds caught once and individuals later retrapped

	Mierzeja Wiślana		Hel		Bukowo-Kopań	
	Fat	Weight	Fat	Weight	Fat	Weight
Caught once	0.12	16.20	-0.34	15.31	-0.29	15.80
Later retrapped	-0.01	15.91	-0.48	14.88	-0.48	15.38

Individuals caught once were heavier than those later retrapped (Table 7). Differences in weight between these two groups of birds were statistically significant at all stations (two-tailed t-test; Hel: t = 4.76, df = 1648, $p < 0.001$; Bukowo-Kopań: t = 15.43, df = 9998, $p < 0.001$; Mierzeja Wiślana: t = 4.05, df = 6689, $p < 0.001$). At Bukowo-Kopań differences in weight between birds caught once and those later retrapped were the highest and on average were equal to 0.5 grams. Weight of retrapped birds differed significantly at all stations (one way ANOVA: F = 62.31, $p <$ 0.001). Retraps caught at Hel and Bukowo-Kopań stations did not differ in weight (Tukey test: $p > 0.05$), however in the rest of cases the differences were statistically significant (Mierzeja-Wiślana – Hel: $p < 0.001$, Mierzeja Wiślana – Bukowo-Kopań: $p < 0.001$).

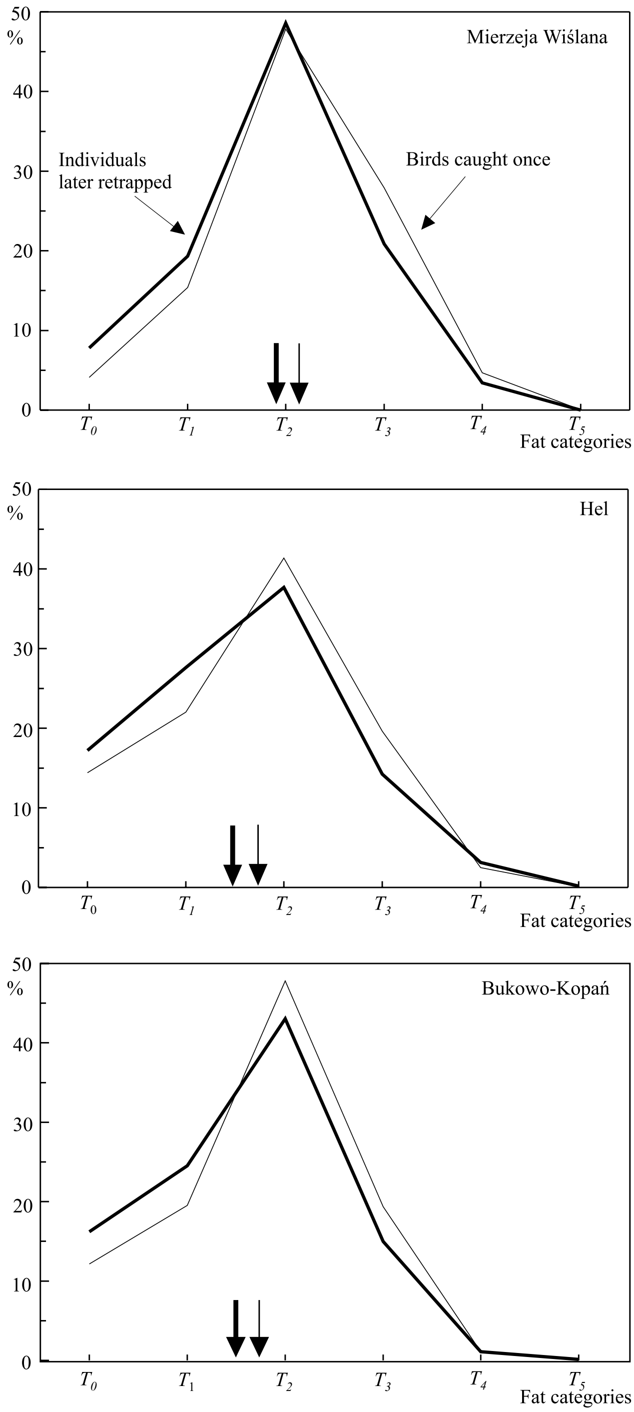


Fig. 7. Fatness classes distribution (%) in birds caught once and later retrapped individuals at each station. Arrows point at fatness averages of birds caught once (thin arrow) and retrapped later (thick arrow)

Stopover duration

Number of retraps decreased in days following the ringing day (Fig. 8). Most of retraps were caught on the next day after ringing. Proportion of these birds was different at all analysed stations. In following days no clear differences were observed among all stations.

The median stopover duration in retraps was two days at Mierzeja Wiślana and Bukowo-Kopań stations and one day at Hel station. More clearly marked differences could be observed when analysing the average stopover duration. At Mierzeja Wiślana retraps stayed the longest (on average 3.79 days) and at Hel station – the shortest (on average 2.40 days). At Bukowo-Kopań the average stopover time was 3.12 days. Stopover duration was significantly different at analysed stations (Kruskal-Wallis test: $H = 46.0, p < 0.05$); results of a detailed analysis are given in Table 8 (Mann-Whitney test).

Table 8
Comparison of stopover duration at different stations (Mann-Whitney test)

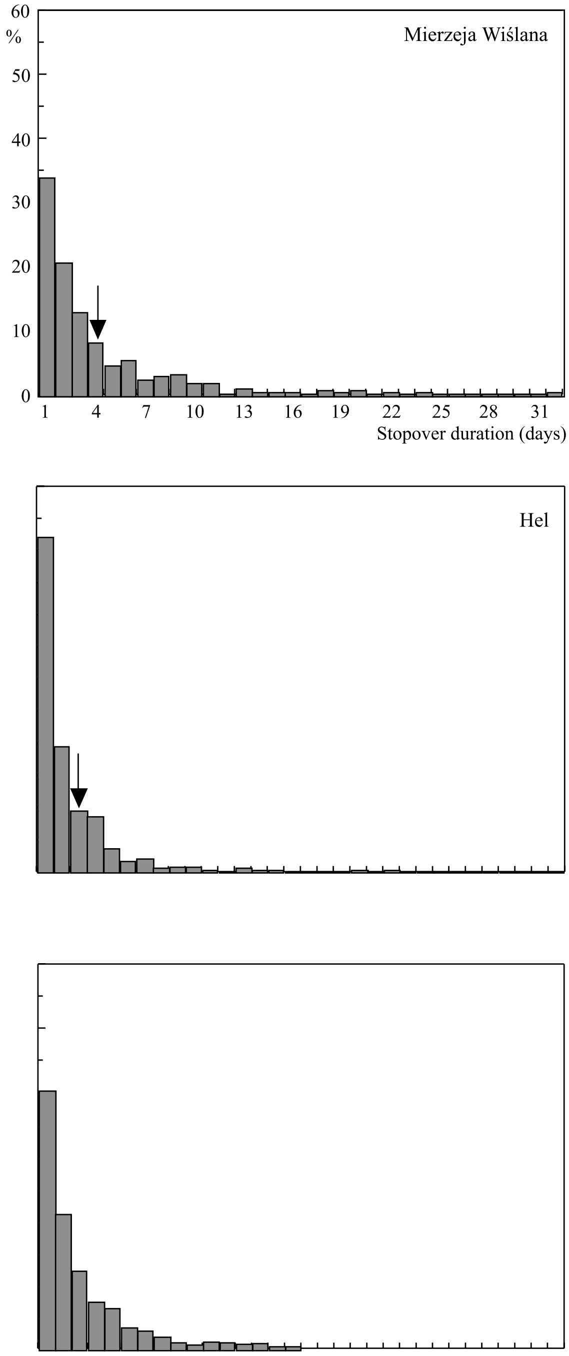
Station	Mierzeja Wiślana	Hel	Bukowo-Kopań
Mierzeja Wiślana	-	$Z = -6.31$	$Z = 2.55$
Hel	$\boldsymbol{p < 0.001}$	-	$Z = -4.98$
Bukowo-Kopań	$\boldsymbol{p < 0.05}$	$\boldsymbol{p < 0.001}$	-

Individuals with low fat reserves on the first day of stopover, interrupted their migration for longer time (Fig. 9). This phenomenon is clear at Mierzeja Wiślana and Hel stations, what is confirmed by regression coefficients in particular. Such trend can be also noted at Bukowo-Kopań station, but it is not so well marked. These results show that the stopover duration is initially determined by the relative fat load on the arrival.

Generally birds that left the study area earlier compared to the average stopover time, showed higher relative fat load on the day of first control (Fig. 9). The largest differences were observed at Hel station. In most cases birds that left station later, had lower fat reserves than initially. An exception was a group that left Hel station on the fourth day. Individuals of this group were characterised by the highest fat level at the time of the first control. Similar situation was observed at Bukowo-Kopań station on the seventh and eighth days of stopover. Again birds leaving Mierzeja Wiślana station on the eighth and ninth day showed relatively high initial fat level compared to birds that left the station just before or after both these groups. It is worth to emphasize that these groups were well represented (see Fig. 9).

Changes in fat load between the first and last control of stopover birds are presented in Figure 10. At Mierzeja Wiślana station birds that stayed longer than three days showed positive balance in fat level change, while those that stayed nine days – negative. Birds that left Hel station on the third and seventh days showed positive

Fig. 8. Minimum stopover duratio



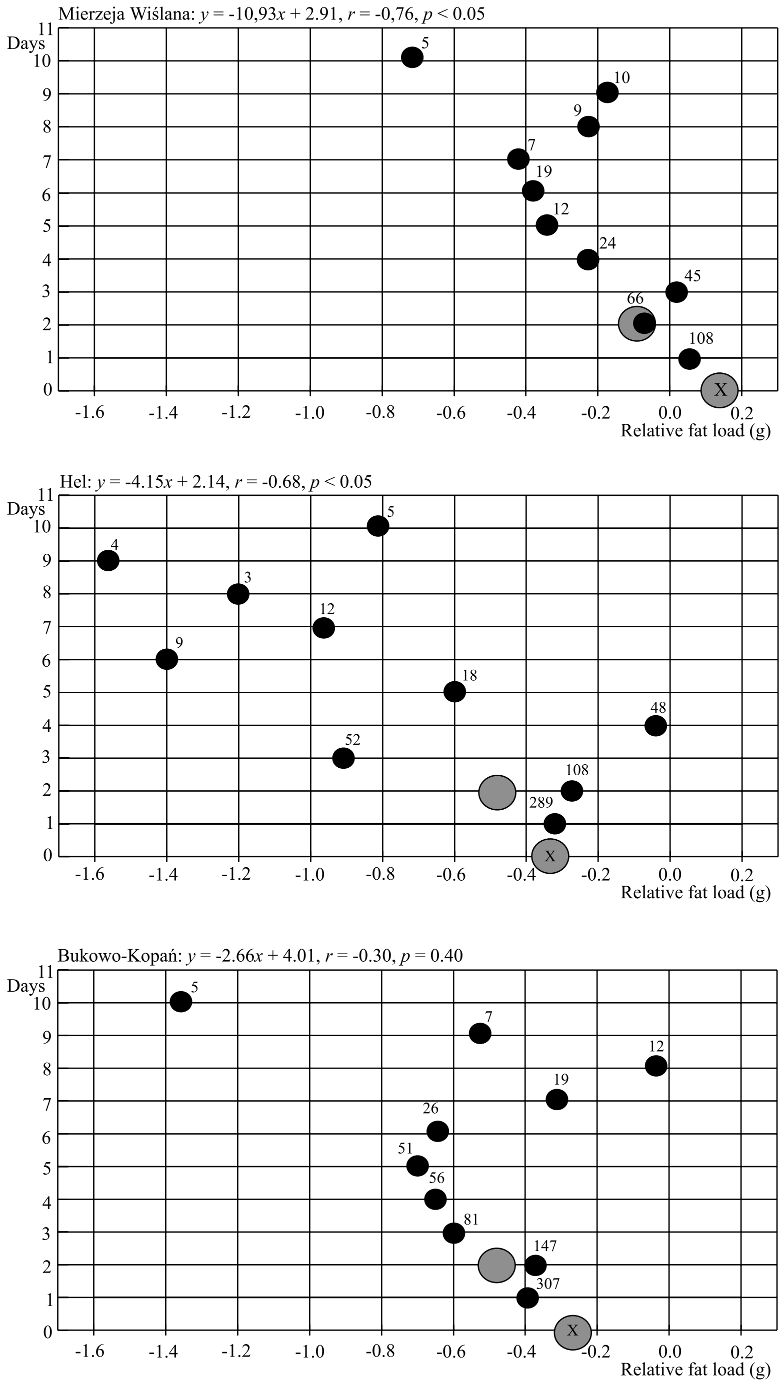


Fig. 9. Stopover duration (days) in relation to initial relative fat load of all analysed birds that stopped their migration (retrapped later – black dots) with number of individuals. Additionally, average relative fat load of birds caught once (grey dot with X) and median relative fat load of all birds that stopped their migration (grey dot) are shown

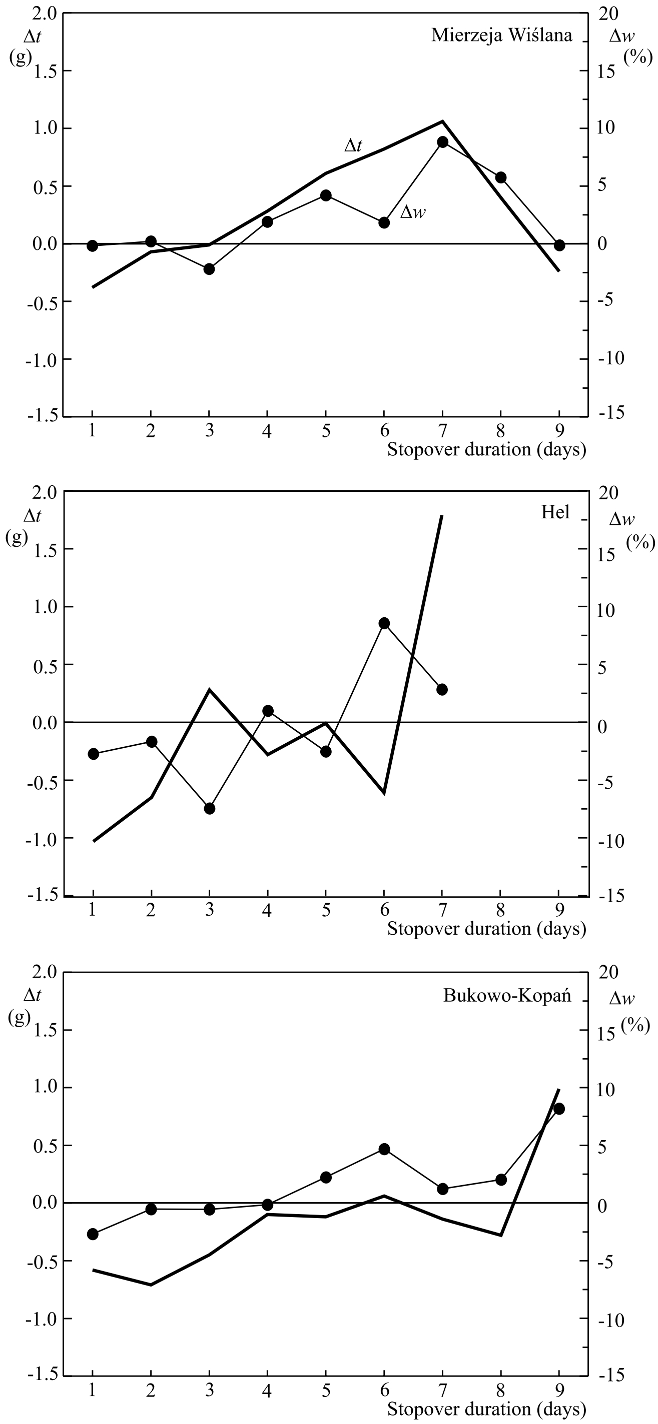


Fig. 10. Absolute fat changes (Δt) and relative weight changes (Δw) between the first and the last control of birds that stopped their migration

balance, while negative balance in fat load change was observed in individuals that left this station in other days, however its rate depended on the stopover duration. Generally this balance was lower in birds leaving station later. At Bukowo-Kopań station similar phenomenon is observed. Only group of individuals that stayed six and nine days showed increase in fat load. The results showed also that an overall pattern in fat load change was rather similar at Hel and Bukowo-Kopań stations ($r = 0.64$, $p = 0.07$). Such strong relationship was not observed in other stations (Mierzeja Wiślana – Hel: $r = 0.16$, $p = 0.68$; Mierzeja Wiślana – Bukowo-Kopań: $r = 0.05$, $p = 0.91$).

Proportion of individuals showing decrease in fat load was high in birds that interrupted migration for a short time (1-2 days) (Table 9). At Hel station this proportion was the largest in birds that stayed only one day (56%). On average it was 47% at all stations. Proportion of individuals that increased fat load was high in birds interrupting their migration for longer. Proportion of birds showing positive balance in fat load change was on average 62% at all stations in birds that stayed for eight days. All birds that left Hel station exactly on this day showed increase in fat load. At this station changes in proportion of subsequent groups of individuals occurred the fastest and were the largest as well. Proportion of birds that left Bukowo-Kopań station showing decrease in fat level fluctuated.

Table 9

Proportion of individuals that departed with lower or higher fat deposit in relation to stopover duration (MW – Mierzeja Wiślana, HL – Hel, BK – Bukowo-Kopań)

	Stopover duration (days)							
	1	2	3	4	5	6	7	8
Proportion of individuals that decreased fat reserves								
MW	37.6	38.9	36.4	27.3	23.1	23.5	14.3	22.2
HL	55.9	42.1	28.0	34.0	44.4	12.5	0.00	0.00
BK	46.8	45.2	41.0	37.7	33.3	32.0	36.8	41.7
Average	**46.8**	**42.1**	**35.1**	**33.0**	**33.6**	**22.7**	**17.0**	**21.3**
Proportion of individuals that increased fat reserves								
MW	14.8	27.8	22.7	31.8	46.2	52.9	57.1	44.4
HL	10.3	21.5	38.0	42.6	27.8	75.0	54.6	100.0
BK	13.1	15.5	18.0	26.4	24.4	36.0	36.8	41.7
Average	**12.8**	**21.6**	**26.2**	**33.6**	**32.8**	**54.6**	**49.5**	**62.0**

Among birds that stayed eight days at most, proportion of individuals showing either increase or decrease in fat level was different at each station as well as in subsequent days. At Mierzeja Wiślana station 50% of individuals continued migration showing increase in fat level, while 17% had lower fat reserves than initially. At Hel and Bukowo-Kopań stations proportion of both these groups were similar, and were: 21% at Hel, 18% at Bukowo-Kopań, and 46% at Hel, 43% at Bukowo-Kopań, respectively. At all stations fat level decrease was observed in birds interrupting their migration for three days at maximum (Fig. 10). At Mierzeja Wiślana and Bukowo-Kopań stations increase in fat level was found on the fourth day after the beginning of stopover and at Hel station – on the fifth day.

Similar changes in bird weight in days following the stopover beginning were observed at Hel and Bukowo-Kopań stations (r = 0.72, p = 0.07). So strong relationship was not noted in other cases (Mierzeja Wiślana – Hel: r = 0.48, p = 0.27; Mierzeja Wiślana – Bukowo-Kopań : r = -0.02, p = 0.96).

At Bukowo-Kopań station changes in fat load and weight showed similar pattern (r = 0.88, $p < 0.05$). This phenomenon is not so well-marked at Mierzeja Wiślana (r = 0.72, p = 0.19; *ns*), while at Hel station is not observed at all (r = 0.04, p = 0.93).

DISCUSSION

Factors influencing stopover in migrants

Stopover depends on external and internal (physiological) factors. Strong wind and low temperature influence migrating birds to similar extent and after retreat birds should continue their migration (Rabøl and Pettersen 1973, Mehlum 1983). Internal factors cause birds to restore energy reserves (Pettersson and Hasselquist 1985, Ganness 2002, Kędzior 2002). The relation between these groups of factors has an effect on duration of flight and stopover (Jenni and Schaub 2004). Our analyses showed that body condition was a decisive factor influencing number of birds that decided to stop their flight. Birds in worse body condition (fat category T_0 and T_1) had to refuel before they continued migration. At all analysed ringing stations Robins that decided to stopover (individuals caught second time) were lean and weighed less than those caught only once. Differences in weight and fat level corresponded well with the stopover index. The largest variation was observed at Bukowo-Kopań station where proportion of stopover birds was the highest.

Body condition of landing birds depend on the covered distance and weather circumstances during nocturnal flight. Analysis of daily dynamics of birds caught in 1961-1967 may provide some information (Gross 1984). Individuals that flied over the land showed the highest activity in the morning, whereas birds that crossed the sea – in the afternoon and evening hours. Birds flying over the land cover the distance adequate to their potential and can stop if they need to restore energy reserves or when they encounter unfavourable weather conditions. In birds flying over the sea, when it is impossible to interrupt migration before reaching the coast, they usually land exhausted and weak after crossing the migration barrier. These birds after establishment of temporary territory forage very intensively to restore energy reserves. Our results showed that retraps accumulating fat before departure at each stopover site were usually more active in afternoon and evening hours than birds caught for the first time. But when a new group of birds land in a stopover site, retrapped birds might defend their territories and become more active also in the morning hours. It was surprising that only at Bukowo-Kopań the rate of retraps to birds caught only once was similar during few morning hours and increased before afternoon. It can result from habitat conditions at the stopover place.

Proportion of birds flying over the sea and land seems to be different at each ringing station. Robins caught at Mierzeja Wiślana, Bukowo-Kopań and Hel originate from several regions what is supported by ringing recoveries distribution (Remisiewicz *et al.* 1997). Our results showed that birds caught at Mierzeja Wiślana were heavier and fatter than those at Bukowo-Kopań and Hel. These Robins are not in as poor body condition as at Bukowo-Kopań and Hel where proportion of birds crossing the sea is higher (Nowakowski *et al.* 2005). Information about origin of birds migrating through the Polish Baltic coast could be supported also by age structure of caught Robins. Low proportion of adult birds is most probably caused by "coastal effect" (Payevsky 1998, Ehnbom *et al.* 1993). Young birds land immediately after crossing the sea, while more experienced adults continue their migration and stopover in more rich habitats. Lower rate of adult birds among Robins caught once at Bukowo-Kopań in contrast to Mierzeja Wiślana seems to confirm the hypothesis about Fennoscandian origin of birds stopping over at this site. Adult Robins after crossing the sea could stopover in more rich or less crowded sites than the ringing area. If they decided to stop their flight at this site they would have to stay longer to rebuild fat reserves. Birds flying over the land and caught at Mierzeja Wiślana have better body condition. Suitable habitat and lower competition between individuals at Mierzeja Wiślana cause that proportion of adults among retraps is lower that at Bukowo-Kopań.

At Mierzeja Wiślana and Hel the stopover index was significantly lower in peak days than in other days. This could result from a better body condition of birds migrating in the peak days. Similar phenomenon was observed in the Redstart, Blackbird (*Turdus merula)*, Song Thrush and Redwing (*Turdus iliacus*) at Helgoland. Birds caught in peak days were heavier than those from other days (Dierschke and Bindrich 2001). However, at the analysed stopover sites the lower stopover index in peak days is rather a result of higher competition between individuals. Limited capacity of habitat causes that birds that have just landed in certain area compete for space and food. In species establishing temporary territories individuals caught in peak days could be more likely to continue migration when landing at a crowded stopover place (Jenni and Schaub 2004). More birds interrupted migration on the days preceding peak days than on the peak days. On the days adjacent to peak days stopover sites were filled up with foraging Robins. We expected that relation to be observed at all analysed stations but it was not recorded at Bukowo-Kopań. At this site the stopover index was similar in peak and adjacent days (day before and after a peak day). After crossing an ecological barrier lean and weak birds may have strong need to restore fat reserves (Jenni and Schaub 2004). As a result of competition between individuals, birds that find space and food can forage very intensively for all day and depart next night in contrast to birds that have to stay longer to replenish fat stores. These retraps dominate next day when a new group of birds come. Daily activity of retraps at Bukowo-Kopań in relation to birds caught once seems to support such mechanism. Age structure showed that percentage share of adult birds was higher in retraps than in birds caught once at Bukowo-Kopań and Hel. High social rank of adults, in contrast to young birds, enables them to defence territories successfully. As a result of competition the adults could stay longer and forage more effectively than the young birds.

At Bukowo-Kopań birds stayed for a shorter period of time than at Mierzeja Wiślana. Individuals that due to competition do not establish temporary territory in the ringing station vicinity could scatter within larger area at Bukowo-Kopań because of similar habitats along most of western Polish coastline. Telemetric study provided that Robins could search optimal territory to forage from several hours to two days after landfall. They can scatter at least within 1.0-1.5 km. Lean and exhausted birds can stay in stopover area but individuals in better body condition might search for better, optimal place (Chernetsov and Bolshakov 2006, Chernetsov 2006). Because such exploration movements after landing need also energetic expenditure, birds usually stay in a new place only for a short time. We could also assume that at Bukowo-Kopań when the stopover site is occupied by foraging birds the new migrants have to scatter on wider area.

An increasing trend in the stopover index from the end of September was observed at Bukowo-Kopań. In contrast to Hel and Mierzeja Wiślana more birds caught at Bukowo-Kopań decided to stopover in October than in September. It can be a result of change in migration strategy with the progress of migration season (Ehnbom *et al*. 1993, Csörgõ and Lövei 1995, Jenni and Schaub 2004). Two migration strategies were described in Robins caught in southern Sweden (Karlsson *et al*. 1988, Ehnbom *et al*. 1993). "Long-stage" migrants caught in southern Sweden need large fat reserves to flight over the Baltic sea, while "short-stage" ones do not cross the sea. Birds landing at Bukowo-Kopań after crossing the sea belong to the "long-stage" migrants described in Sweden. Swedish "short-stage" migrants do not attain Polish Baltic coast because they do not cross the Baltic sea. Thus, the "short-stage" migrants caught at the Polish Baltic coast come from eastern Europe. Another explanation is that in the course of migration season the "short-stage" migrants could change their strategy to the "long-stage" one because finding abundant habitats can be more difficult with the progress of the season. In many species individuals that migrate later in the season accumulate more fat and seem to travel at a higher speed (Jenni and Schaub 2004). At inland station Urasa, localized in the southern part of Sweden, both in fat and weight some increasing trends after the second decade of September were observed in retraps. Moreover, Robins showed a tendency to deposit more fat the longer they stayed and with the progress of migration season (Ehnbom *et al*. 1993). Higher stopover index at Bukowo-Kopań can be explained by two phenomena: the higher (starting from the end of September) share of "long-stage" migrants that come from Sweden and winter in southern Europe or the change of migration strategy from "short-stage" to the "long-stage" one in Robins originating from eastern Europe that direct to the west.

Stopover duration

Birds may differ in migration strategy and stopover ecology in relation to ecological barrier that have to be crossed. Passage over the land where appropriate habitats occur allows to interrupt migration when fat reserves have to be restored. Bird migrating over ecological barriers (*e.g.* sea, mountains, desert) need high fat reserves for a longer flight (Karlsson *et al.* 1988, Ehnbom *et al*. 1993, Keşaplı Can and Bilgin 2005). Two groups of birds that differed in fat level and stopped their flight before crossing Sahara were distinguished (Titov 1999a). Fatter birds stayed for about 1-2 days and in favourable conditions continued their migration. Weaker birds stayed longer to rebuild fat reserves. In Blackcaps (*Sylvia atricapilla)* that stopped their flight during spring migration in Israel the increase in body mass was at first low but after attaining liminal weight it rapidly increased (Gannes 2002). The birds attained liminal weight after three or four days. The low growth in the first days was caused by rebuilding organs that were resorbed during flight over Sahara (Biebach 1998, Karson and Pinshow 1998, 2000, Piersma 1998 after Gannes 2002). Another mechanism was observed in birds staying at small isolated stopover sites like Helgoland (Dierschke and Bindrich 2001). Despite the fact that body mass and fat level of birds before crossing small ecological barriers were lower than in the case of large ones, due to high birds densities body mass might have not increased in the first 1-4 days after arrival. Such phenomenon could have depended on limited food resources but also on competition for food among stopover birds.

At Polish ringing stations we have also some group of birds that differ in fat balance. At Mierzeja Wiślana 50% of individuals departed when they increased in fat level, while at Hel and Bukowo-Kopań only about 20%. These disproportions can result from different food resources and also competition between individuals. At Hel Peninsula where rich habitats are rather limited, more birds departed on the next day. Different food availability at Bukowo-Kopań and strong competition between individuals caused that only small number of birds were able to rebuild fat reserves. Thus, high proportion of retraps departed with lower fat level. In Central Anatolia only two from 20 retrapped Blackcaps gained considerable amounts of fat, whereas in most of Willow Warblers (*Phylloscopus trochilus*) the increase in fat level was observed (Keşaplı Can and Bilgin 2005). Such behaviour of Blackcaps could be a result of reduced food availability and strong competition between individuals. Decrease in fat level can be explained by energetic costs of territory occupation or searching an optimal area to settle (Szulc-Olech 1965, Chernetsov and Bolshakov 2006). Individuals of the Northern Waterthrush (*Seiurus novoboracensis*) gained weight usually after few days when they had found their own territories (Rappole i Warner 1976 after Cherry 1982). At coastal Swedish station Falsterbo even if birds stayed for longer periods the increase in fat level was not observed. Most of birds stayed less than five days and decreased in fat load and weight (Ehnbom *et al.* 1993). Our analyses showed that not always a decrease in fat level is observed in the first day of stopover. Moreover, the growth in fat load was observed in more than 10% of birds during the first day and later in subsequent days the increasing trend was noted. It can rather depend on the occupation of territory abundant in food and not on the stopover duration. In the Sedge Warbler (*Acrocephalus schoenobaenus*) the fastest increase in weight was observed while foraging in richer habitats, whereas the stopover duration was the shortest (Grandío 1998). Robins that were feeding in the territories of *ca* 30 m in diameter increased in weight faster than those foraging in larger areas (Titov 1999b). Another explanation could be different feeding strategy of some species. In White-crowned Sparrows (*Zonotrichia leucophrys*), that are not territorial during migration the increase in weight was observed in the first day of stopover (Cherry 1982). Thus, the increase in fat level in retrapped Willow Warblers shown in Central Anatolia may be an effect of different stopover strategy of these trans-Saharan migrants (Keşaplı Can and Bilgin 2005). Unfortunately, the mechanism of gaining fat during stopover of different species is still unknown and many factors might have an effect on this phenomenon.

Our results show that birds with low fat level stayed longer than individuals with the higher one. Fat level as well as habitat and foraging conditions are decisive factors influencing the departure sequence of stopover birds. It was well defined at Hel station where during the first two days of stopover a strong selection was observed and birds in better body condition departed as the first ones. Only Robins in weaker condition stayed longer (two ore more days). At other stations it was not so clear. It is also difficult to explain why more birds departed from Hel station with the increase in weight but not always with the higher fat level. But these individuals departed one or two days after the fattest group. Maybe in some individuals initial fat level does not reflect body condition. Beside fat, such components as water content and protein reserves may have an effect on weight. Results obtained by Zakala and co-authors (2004) showed that in the Sedge Warbler visible fat deposit does not reflect all gained fuel. Metabolism of glycogen may be responsible for differences between fat and weight. Detailed analysis of the relation between fat level and weight could help in analysis of this mechanism.

Summing up, the decisive factor to stopover is poor body condition that can be a result of distance covered the night before landing. Stopover duration and sequence of departing birds depend on food availability, size of stopover site and competition for food resources. Interactions between these factors are different at all analysed stations. Higher proportion of birds interrupting their flight at Bukowo-Kopań and Hel than at Mierzeja Wiślana is caused by longer distance birds covered previous night and different migration strategy. At both of these stations proportion of birds from Fennoscandia is higher than at Mierzeja Wiślana, where more birds coming from inland are caught. At Mierzeja Wiślana, the higher proportion of birds departing with the increase in fat level may depend on the richest habitats among studied stations or different migration strategy of stopover birds.

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REFERENCES

Åkesson S., Karlsson L., Pettersson J., Walinder. 1992. *Body composition and migration strategies: a comparision between Robins (Erithacus rubecula) from two stopover sites in Sweden*. Vogelwarte 36: 188-195.

Busse P. 1970. *Measurements of weight and fatness in migrating populations of birds. Operation Baltic. Paper No. 23.* Not. Orn. 11,1: 1-15.

Busse P. 1972. *Autumn migration of Redstart, Phoenicurus phoenicurus (L.) along the Polish coast of the Baltic.* Acta orn. 13, 6: 193-241.

Busse P. 2000. *Bird Station Manual.* SE European Bird Migration Network, Gdańsk.

Busse P., Kania W. 1970. *The Operation Baltic 1961-67*. Acta orn. 12, 7: 231-267.

Catry P., Encarnação V., Araújo A., Fearon P., Fearon A., Armelin, Delaloye P. 2004. *Are long-distance migrant passerines faithful to their stopover sites?* J. Avian Biol. 35: 170-181.

Chernetsov N. 2006. *Habitat selection by nocturnal passerine migrants en route: mechanisms and results.* J. Ornithol. 147: 185-191.

Chernetsov N., Bolshakov C. V. 2006. *Spatial behaviour of some nocturnal passerine migrants during stopover.* Acta Zool. Sin. 52 (Suppl.): 599-601.

Cherry J.D. 1982. *Fat deposition and length of stopover of migrant White-crowned Sparrow.* Auk 99: 725-732.

Csörgõ T., Lövei L.G. 1995. *Autumn migration and recurrence of the Thrush Nightingale Luscinia luscinia at stopover site in central Hungary.* Ardeola 42, 1: 59-68.

Dierschke V., Bindrich F. 2001. *Body condition of migrant crossing a small ecological barrier.* Vogelwarte 41: 119-132.

Ehnbom S., Karlsson L., Ylvén R., Åkesson S, 1993. *A comparison of autumn migration strategies in Robins Erithacus rubecula at a coastal and an inland site in southern Sweden.* Ring. & Migr. 14: 84-93.

Gannes L.Z. 2002. *Mass change pattern of Blackcaps refuelling during spring migration: evidence for physiological limitations to food assimilation.* Condor 104: 231-239.

Gross M. 1984. [*Daily activity of the Robin Erithacus rubecula L. during autumn migration over the Polish Baltic coast*]. M. Sc. thesis, Univ. of Gdańsk, Poland. (In Polish).

Grandío J.M. 1998. *Comparison of body mass, body mass increase, stopover residence time and abundance of the Sedge Warbler Acrocephalus schoenabaenus between two areas of the Txingudi marsh (northern Spain)*. Ardeola 45, 2: 137-142.

Jenni L., Schaub M. 2004. *Behavioural and Physiological Reactions to environmental Variation in Bird Migration: a Review.* In: Berthold P., Gwinner E., Sonnenschein E. (Eds). *Avian Migration.* Springer-Verlag, Berlin-Heidelberg: pp. 155-171.

Karlsson L., Persson K., Pettersson J. 1988. *Fat-weight relationships and migratory strategies in the Robin Erithacus rubecula at two stopover sites in south Sweden*. Ring. & and Migr. 9: 160-166.

Keşaplı Can Ö., Can Bilgin C. 2005. *Stopover ecology of some passerines at Ankara (Central Turkey).* Ring 27, 2: 127-136.

Kędzior K. 2002. *Stopover of migrant Blackcap (Sylvia atricapilla) on autumn passage through the Polish Baltic coast.* Ring 24, 2: 31-47.

Khoury F. 2004. *Seasonal variation in body fat and weight of migratory Sylvia Warblers in central Jordan*. Vogelwarte 42: 191-202.

Maksalon L. 1983. *Autumn migration of Song Thrush through Polish Baltic coast.* Not. Orn. 24: 3-29.

Mehlum F. 1983. *Resting time in migrating Robins Erithacus rubecula at Store Faerder, Outer Oslofjord, Norway.* Ser. C. Cinclus 6: 62-72.

Moore F.R., Yong W. 1991. *Evidence of food-based competition among passerine migrants during stopover.* Behav. Ecol. Sociobiol. 28: 85-90.

Nowakowski J.K., Remisiewicz M., Keller M., Busse P., Rowiński P. 2005. *Synchronisation of the autumn mass migration of passerines: a case of Robin Erithacus rubecula.* Acta ornithol. 40: 103-115.

Payevsky V.A. 1998. *Age structure of passerine migrants at the eastern Baltic coast: the analysis of the "coastal effect".* Ornis Svecica 8: 171-178.

Pettersson J., Hasselquist D. 1985. *Fat desposition and migrating capacity of Robins Erithacus rubecula and Goldcrest Regulus regulus at Ottenby, Sweden.* Ring. & Migr. 6: 66-77.

Rabøl J., Petersen F.D. 1973. *Length of resting time in various night migrating passerines at Hesselo, southern Kattegat, Denmark.* Ornis Scand. 4: 33-46.

Remisiewicz M., Nowakowski J.K., Busse P. 1997. *Migration pattern of Robin (Erithacus rubecula) on the basis of Polish recoveries.* Ring 19, 1-2: 3-40.

Szulc-Olech B. 1965. *The resting period of migrant Robins on passage.* Bird Study 12, 1: 1-7.

Szumiło M. 1987. *[Analysis of stopover phenomenon during autumn migration in Robin (Erithacus rubecula L.) through the Polish Baltic* coast]. M. Sc. thesis, Univ. of Gdańsk, Poland. (In Polish).

Titov N. 1999a. *Home range in two passerine nocturnal migrants at a stopover site in autumn*. Avian Ecol. Behav. 3: 69-78.

Titov N. 1999b. *Fat level and temporal pattern of diurnal movements of Robins (Erithacus rubecula) at an autumn stopover site.* Avian Ecol. Behav. 2: 89-99.

Weber T.P., Fransson T., Houston A.I. 1999. *Should I stay or should I go? Testing optimality models of stopover decisions in migrating birds*. Behav. Ecol. Sociobiol. 46: 280-286.

Zakala O., Shydlowskyy I., Busse P. 2004. *Variation in body mass and fat reserves of the Sedge Warbler Acrocephalus schoenobaenus on autumn migration in the Lviv province (W Ukraine).* Ring 26, 2: 55-69.