

Body mass, moult and migration speed of the Goldcrest *Regulus regulus* in relation to the timing of migration at different sites of the migration route

Julia Bojarinova*, Aleksandra Ilves, Nikita Chernetsov & Agu Leivits

J. Bojarinova & A. Ilves, Biological Institute of St. Petersburg State University, Oranienbaumskoje sh., 2, Stary Petergoff, St. Petersburg 198904, Russia. julia@jb2558.spb.edu (Corresponding author)*

N. Chernetsov, Biological Station Rybachy, Zoological Institute, Russian Acad. Sci., 238535 Rybachy, Kaliningrad Region, Russia. nchernetsov@bioryb.koenig.ru

A. Leivits, State Nature Conservation Centre Pärnu-Viljandi Region, Vana-Järve, Tali side, 86301, Estonia. agu.leivits@nigula.ee

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We studied body mass, fat reserves and moult data of the Goldcrest *Regulus regulus* in relation to calendar date at three sites along the migration route: Gumbaritsy, NW Russia (south-eastern coast of Lake Ladoga), Kabli, SW Estonia (eastern coast of the Baltic Sea) and Rybachy, Courish Spit (eastern coast of the Baltic Sea, Russia). We analyzed migration speed using ringing data obtained at these stations. The percentage of moulting birds involved in migration was higher in the northern site Gumbaritsy as compared with the southerly site (Kabli). During migration, body mass increased seasonally in the Goldcrests trapped in Gumbaritsy in 2001, but at the more southern trapping sites this trend was absent (Kabli) or recorded only in the later part of migration (Rybachy). Median fat reserves peaked in Gumbaritsy. Migration speed was affected by time pressure (i.e., it increased with date during migration and was more pronounced in the north) and the position of a certain part of migration route. Migration speed was significantly higher along the routes that crossed the Baltic Sea than at coastal routes. Birds that gained more fat at the time of ringing migrated with a higher speed.



1. Introduction

Patterns in seasonal timing, body mass and overlap between moult and migration, and migration speed are key characteristics of avian seasonal movements. The speed of autumn migration in birds increases with date and along the migratory route (Ellegren 1993, Fransson 1995, Bensch & Nielsen 1999), along with body mass and fuel deposition rate increase shown for several long dis-

tance migrants (Bensch & Nielsen 1999, Schaub & Jenni 2000a, b). These results indicated differences among the species studied in migration strategy, variations in time and sites where maximum fuel deposits were accumulated.

The so-called partial, short-distance migrants are insufficiently studied in this respect. Field data on dynamics of changes in body reserves have been reported for long-distance migrants (e.g., Schaub & Jenni 2000a, b) but are scarce for partial,



Fig. 1. The study sites.

short-distance migrants. Hence, we conducted a field study to gain understanding on how the migration of partial short-distance migrants is organized in time and along the migration route.

To evaluate the possible time pressure on autumn movements of partial short-distant migrants, we used the Goldcrest (*Regulus regulus*) – the smallest bird species of Europe – as a model species. The proportion of resident birds within populations increases southwards (Cramp 1998). The breeding range of this species covers vast areas from middle to upper temperate and boreal latitudes of western Palearctic (Cramp 1998), wherever the coniferous stands can be found. Autumn migration of the species across the Baltic region varies annually in timing and numbers (Remisiewicz & Baumanis 1996).

According to ring recoveries, migrating Goldcrests overwinter widely in western Europe, from the British Isles to Italy and Spain (Payevsky 1973, Hanssen 1981, Kania 1983, Pettersson *et al.* 1986, Rezvyi 1995).

In this study we present (i) data on body mass and moult status of migrating Goldcrests during autumn migration at different sites along the migration route, and (ii) analyze the speed of autumn movements, in relation to date, at different parts of the migration route in the Baltic region from Lake Ladoga (NW Russia) southwards.

2. Material and methods

2.1. Trapping sites and data collection

We used ringing data on Goldcrests captured in 2001 at three sites (Fig. 1): the Ladoga Ornithological Station Gumbaritsy (NW Russia, southeastern coast of Lake Ladoga; 60°41' N, 32°57' E), the Ornithological Station Kabli (SW Estonia, eastern coast of the Baltic Sea; 58°01' N, 24°27' E), and the Biological Station Rybachy (Courish Spit, eastern coast of the Baltic Sea, Russia; 55°05' N, 20°44' E). The distance between Gumbaritsy and Kabli is 565 km, and between Kabli and Rybachy is 398 km. These sites share the migration route of the Goldcrest. To trap birds, we used Rybachy-type traps (Gumbaritsy and Rybachy) or funnel traps and mist nets (Kabli), in habitats atypical for the Goldcrest but where this species is numerous during its migratory period. Most of the previously ringed birds recovered in Kabli and nearby in Estonia ($n = 22$) during autumn migration originated from Finland (55%) and from Russia (41%). Only one recovery is thus far known from Sweden. The origin of birds ringed to the north of Rybachy and recovered in the same autumn ($n = 158$) consists of 51% having been ringed in Estonia, Latvia and Lithuania, 29% in Sweden and Denmark, 11% in Finland, 6% in Russia and 3% in Norway. The ori-

gin of birds trapped in Gumbaritsy is unknown. We trapped only one bird ringed elsewhere: a recovery of an individual ringed the previous autumn in Germany.

We collected the following data in a standardized manner: date and time of capture (to the nearest hour), body mass (to the nearest 0.1 g), wing length (to 1 mm using the maximum length method; Svensson 1992), and moult stage (only for Gumbaritsy and Kabli Stations). Fat reserves were recorded by scoring the amount of subcutaneous fat deposited within the furculum of the clavícula, under the wing, and in the abdominal region (Blyumental & Dolnik 1962). In Rybachy, a 4-grade scale, and at Gumbaritsy and Kabli stations, a 10-grade scale, was used. Because the 10 levels used in Gumbaritsy and Kabli are subdivisions of the four levels used in Rybachy, we used four level scores for fat when comparing fat reserves of birds trapped at different stations. When studying the relationship between the amount of visible fat at time of ringing and speed of migration (data from Gumbaritsy) we used the original 10-grade scale.

The stages of post-juvenile moult in the Goldcrest were recorded following Rezvyi (1990): stage 1 – the onset of moult in the ventral and spinal track; stage 2 – the onset of moult in the coronal and frontal region of the capital track; stage 3 – the onset of moult in the ear region; stage 4 – the intensive moult of all contour feathers (i.e., pins, small and large brushes are present among moulting feathers); stage 5 – the moult of the wing contour feathers completed, and no pins among growing feathers elsewhere; stage 6 – the moult of the crural track completed, half of the counter feathers changed and other parts containing small and large brushes; stage 7 – the moult of tail coverts completed, spinal and ventral tracks are still at the very end of moult.

All analyses refer to first captures of the first-year birds because we captured only very few adults (0.2% in Gumbaritsy, 0.7% in Kabli and 3.1% in Rybachy). The proportion of birds for which biometrical data were recorded in autumn 2001 comprised ca. 24% in Gumbaritsy (the total number of trapped birds $n = 4071$), 50% in Kabli ($n = 2483$) and ca. 42% in Rybachy ($n = 11507$). During busy periods, we randomly selected birds for measurements. In 2001, the closing date in

Gumbaritsy was October 18, in Kabli was October 31, in Rybachy was October 29.

2.2. Migration speed

We analysed the published and unpublished data on ringing recoveries of the Goldcrest from Gumbaritsy (Rezvyi 1995), Rybachy (Bolshakov et al. 1999, 2000, 2001a, b, 2002a, b) and Kabli (unpublished data), and data on birds ringed elsewhere and recovered at these stations. Only the recoveries from the Baltic Sea region were included.

We calculated the individual speed by dividing the distance between ringing and recovery sites by the time elapsed. We used autumn recoveries that fulfilled the following criteria to exclude atypical or unreliable data (Hildén & Saurola 1982, Ellegren 1993):

- Ringing and recovery dates should be within the normal migration period of the species.
- The time between ringing and recovery should not exceed 50 days.
- The recovery site should be situated to the south from the ringing site.
- The distance should exceed 50 km.
- Dead recoveries are not included.
- The migration speed should exceed 10 km/day.

To analyze the speed in different parts of the migration route separately, we divided the recoveries into groups according to ringing and recovery places. Most data on ringed birds came from the following sites, which were used in this grouping: Luvia, Finland (61°29' N, 21°21' E), Mayachino, Russia (60°46' N, 32°48' E), Lao, Estonia (58°15' N, 24°07' E), Pape, Latvia (56°11' N, 21°03' E), Hartsö-Enskär, Sweden (58°41' N, 17°28' E), Ottenby, Sweden (56°12' N, 16°24' E), Christiansø, Denmark (55°19' N, 15°12' E), Hel, Poland (54°46' N, 18°28' E), Bukowo-Kopan, Poland (54°28' N, 16°25' E) and Mierzeja Wiślana, Poland (54°21' N, 19°19' E).

2.3. Statistical analyses

Body mass of migrating birds increases through the day (e.g., Dunn 2001, 2002) and depends on

the size of the individual (e.g., Brown 1996). Moulting process also influences body mass (e.g., Dolnik & Gavrilov 1979, Bojarinova *et al.* 1999). To compare the body mass between periods of migration we used a general linear model (GLM) with body mass as a dependent variable and period (ten-day intervals), time of trapping in the day, wing length and state of plumage (certain stage of moult reached, or moult finished) as independent factors. In Rybachy the data on moult were lacking; hence only three independent factors were included. To compare the body mass between stations, we used analysis of covariance (ANCOVA) on body mass across all trapping stations, with time of trapping and wing length as covariates.

To compare the body mass and fat reserves of birds coming to Rybachy from Sweden (across the sea) and from the Ladoga coast, Estonia and Latvia (along the coast), we used data on birds recovered in Rybachy only. We analysed body mass within generalised linear model using route (across the sea or along the coast), trapping date, trapping time (hour) and wing length as independent factors.

To analyze fat reserves we used non-parametric statistics (Mann-Whitney and Kruskal-Wallis tests) because these data did not show any standard distribution.

We log-transformed data on migration speed prior to the analysis to normalize the distribution and residual error. The normality of residuals was checked after each ANCOVA and regression analysis using a Kolmogorov-Smirnov test. Recoveries made one day after ringing do not include stop-over time and thus produce inflated speed estimates as compared with the recoveries made after several days. Therefore, in these analyses we excluded recoveries made one day after ringing. To compare migration speed between different migration routes, we used an ANCOVA with trapping date as a covariate. The reported mean values for speed and their confidence limits are the values transformed back into the linear scale by looking up their antilogarithms (Sokal & Rohlf 1998).

We performed the statistical analyses using Statistica 6.0.

3. Results

In 2001, Goldcrest migration began on 29 August in Gumbaritsy, on 7 September in Kabli and on 5

Table 1. Proportion of moulting birds among trapped Goldcrests during the autumn migration of 2001 at the Ladoga Ornithological Station Gumbaritsy (NW Russia) and at the Ornithological Station Kabli (SW Estonia).

Period of autumn migration	Gumbaritsy	Kabli
1–10 September	45 (<i>n</i> = 120)	10 (<i>n</i> = 21)
11–20 September	20 (<i>n</i> = 691)	17 (<i>n</i> = 401)
21–30 September	56 (<i>n</i> = 119)	11 (<i>n</i> = 285)
1–10 October	37 (<i>n</i> = 51)	0 (<i>n</i> = 302)
11–20 October	12 (<i>n</i> = 8)	0 (<i>n</i> = 207)
21–30 October	–	0 (<i>n</i> = 38)

September in Rybachy. The median dates of migration were 16 September, 22 September and 10 October, respectively. After 12 October, movements of Goldcrests were no longer recorded in Gumbaritsy, whereas at the other study sites migrating Goldcrests were trapped until the end of October.

3.1. Moulting, body mass and fat reserves

Most migrating Goldcrests trapped in Gumbaritsy and Kabli had already finished their moult. The proportion of moulting birds, trapped during the whole migration period in 2001, comprised 28% in Gumbaritsy (*n* = 989) and 8% in Kabli (*n* = 1,254). The difference between the two sites was statistically significant ($\chi^2=158.7$, $p < 0.01$). Most of the moulting birds were at the very end of their feather replacement (stage 7–75% in Gumbaritsy and 76% in Kabli).

The proportion of moulting individuals remained noticeable until the end of migration in Gumbaritsy, whereas in Kabli moulting birds disappeared by the beginning of October (Table 1). From September 20 until the end of migration, the percentage of moulting Goldcrests was significantly higher in Gumbaritsy (48%; *n* = 178) than in Kabli (4%; *n* = 832) ($\chi^2 = 272.5$, $p < 0.01$).

Body mass of Goldcrests, trapped during migration, varied from 4.5 to 7.2 g (mean 5.74 ± 0.01 SE g; *n* = 987) in Gumbaritsy, from 4.6 to 7.5 g (mean 5.76 ± 0.01 SE g; *n* = 1251) in Kabli and from 4.1 to 7.0 g (mean 5.39 ± 0.01 SE g; *n* = 4816) in Rybachy. Period of migration (ten-day inter-

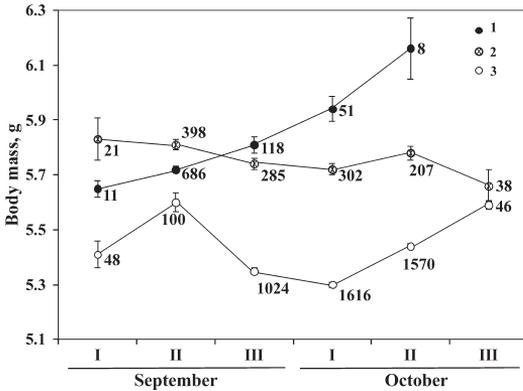


Fig. 2. Variation in body mass of migrating Goldcrests in relation to different periods of autumn passage in 2001. For each period the figure shows the least squares means ± 1 SE together with sample size after controlling for the effects of size (wing length) and time of trapping. (1) Gumbaritsy. GLM; independent factors: period of trapping ($F_{4,973} = 12.38, p < 0.001$), wing length ($F_{1,973} = 101.94, p < 0.001$) and time of trapping ($F_{1,973} = 98.67, p < 0.001$). Significant difference was detected between first and second ten-day periods of September vs. first and second ten-days periods of October (Bonferroni test). (2) Kabli. GLM; independent factors: period of trapping ($F_{5,1243} = 3.762, p = 0.003$), wing length ($F_{1,1243} = 80.77, p < 0.001$) and time of trapping ($F_{1,1243} = 209.46, p < 0.001$). Significant difference was detected between second ten-days period of September and first ten-days period of October (Bonferroni test). (3) Rybachy. GLM; independent factors: period of trapping ($F_{5,4813} = 70.66, p < 0.001$), wing length ($F_{1,4813} = 543.84, p < 0.001$) and time of trapping ($F_{1,4813} = 17.90, p < 0.001$). Significant difference in October was detected between all three ten-day periods of October (Bonferroni test).

vals), trapping time (hour) and wing length all had a significant effect on body mass at all stations (GLM; Fig. 2). The effect of state of plumage was not significant either in Gumbaritsy (GLM; $F_{1,969} = 2.93, p = 0.09$) or in Kabli ($F_{1,1239} = 0.94, p = 0.33$) and was therefore omitted from the final model. Data on moult were lacking from Rybachy; hence only three independent factors were included in the analysis. The pattern of body mass change varied during the migration season between the study sites (Fig. 2). In Gumbaritsy, the mean body mass steadily increased during the season, whereas we did not observe such a trend in Kabli. In Rybachy, we recorded this trend only in the later part of the season, i.e., in October.

The average body mass, corrected for body size (wing length) and time of capture, was significantly smaller in Rybachy than in the other sites (ANCOVA; $F_{2,7047} = 984.97, p < 0.001$).

The variation in body mass of ringed Goldcrests recovered in Rybachy was significantly affected by the route, i.e., across sea or along coast (GLM; $F_{1,76} = 6.03, p = 0.016$), time of trapping in the day ($F_{1,76} = 4.88, p = 0.030$) and wing length ($F_{1,76} = 18.08, p = 0.001$). The effect of trapping date was not significant ($F_{1,75} = 0.32, p = 0.57$). The mean body mass of birds that had presumably crossed the Baltic Sea and arrived to Rybachy from Sweden (5.70 ± 0.06 SE; $n = 43$) was significantly higher as compared with that of birds that had arrived from Russia, Estonia and Latvia (5.47 ± 0.07 SE; $n = 37$) (Tukey's *post hoc* test; $p < 0.05$). Fat reserves of ringed Goldcrests recovered in Rybachy did not significantly differ between these two migration-route groups (Mann-Whitney's *U* test; $p > 0.05$).

Fat reserves of birds trapped during the migration season significantly differed among the three stations (median = 3 for Gumbaritsy, 2 for Kabli, 2 for Rybachy; Kruskal-Wallis test; $p < 0.05$). The percentage of lean birds (score 1) was about 5% in Gumbaritsy, 14% in Kabli and 23% in Rybachy. Median fat score varied significantly among ten-day periods of migration at Gumbaritsy and Kabli stations (Kruskal-Wallis test; $p < 0.05$), but no trend was recorded. There was no such variation in Rybachy.

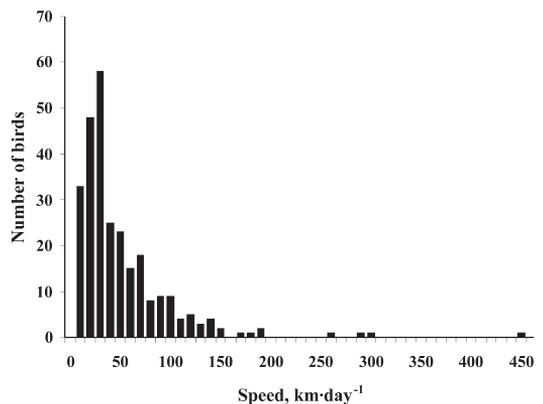


Fig. 3. Distribution of migration speed in the Goldcrest according to the data obtained from Gumbaritsy, Kabli and Rybachy stations.

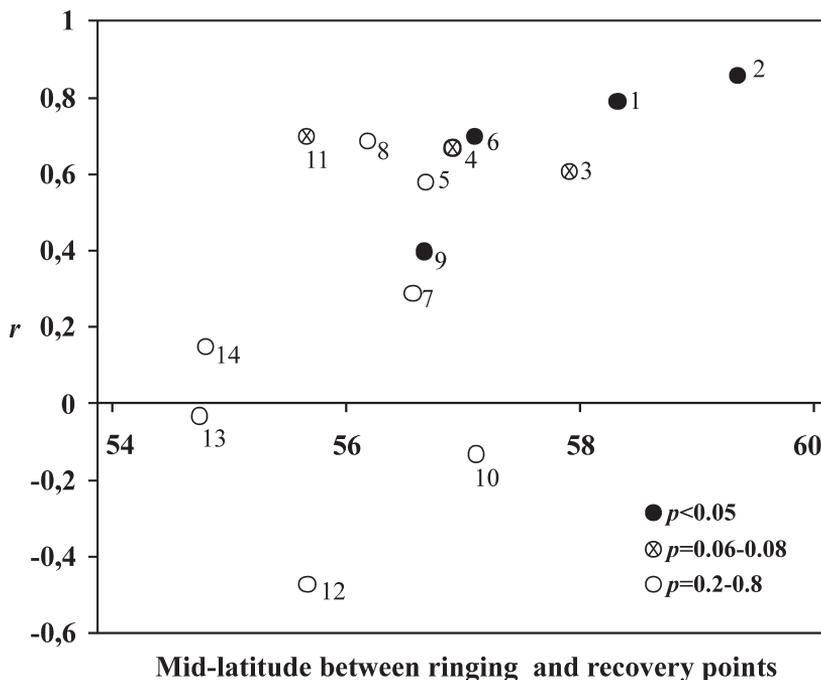


Fig. 4. Correlation coefficients (r) between ringing date and migration speed of Goldcrests for different parts of migration route. Figures in the plot refer to different migration routes: (1) Luvia (Finland)–Rybachy ($n = 9$); (2) eastern coast of Ladoga (LOS and Mayachino)–Kabli ($n = 8$); (3) eastern coast of Ladoga (LOS and Mayachino)–Rybachy ($n = 9$); (4) Hartsö-Enskär (Sweden)–Rybachy ($n = 5$); (5) Lao (Estonia)–Rybachy ($n = 5$); (6) Kabli – Mierzeja Wiślana (Poland) ($n = 11$); (7) Kabli–Rybachy ($n = 20$); (8) Kabli–Ottenby (Sweden) ($n = 7$); (9) Kabli–Pape (Latvia) ($n = 29$); (10) Kabli–Christiansø (Denmark) ($n = 7$); (11) Ottenby (Sweden)–Rybachy ($n = 8$); (12) Pape (Latvia)–Rybachy ($n = 9$); (13) Rybachy–Mierzeja Wiślana (Poland) ($n = 28$); (14) Rybachy–Bukowo-Kopan (Poland) ($n = 10$).

3.2. Migration speed

Migration speed of Goldcrests varied remarkably (Fig.3). Thirteen (8%) of the 155 Goldcrests recovered along the eastern Baltic coast attained speed exceeding $80 \text{ km}\cdot\text{day}^{-1}$. On the routes that possibly include crossing the Baltic Sea the number of such individuals was significantly higher, up to 32% ($n = 115$) ($\chi^2 = 24.8$, $p < 0.01$). Such birds were ringed at all three study sites only from late September, and most of them in mid-October.

Migration speed of Goldcrests was positively related to the progress of season ($r = 0.24$, $n = 264$, $p = 0.0001$). In certain parts of the migratory route (the same start and end points) this correlation might be even stronger, especially for ringing sites situated at high latitudes (Fig. 4). For the start

points situated in the southern part of the Baltic this relationship was not significant.

The type of migration route (sea crossing versus along the coast) also affected the migration speed (ANCOVA; route: $F_{1,259} = 39.30$, $p < 0.001$; trapping date: $F_{1,259} = 11.76$, $p < 0.001$). On the routes along the eastern Baltic coast it was significantly lower than on the routes that potentially include flights across the sea, i.e., from the eastern Baltic coast to/from Sweden, and from Finland to Kabli and Rybachy.

Migration speed tended to decrease from the north to the south both along the coast and across the sea (Fig. 5). Goldcrests ringed in southern Sweden and recovered in Rybachy migrated with significantly lower speed than did birds ringed in Gumbartitsy and recovered in Sweden (Bonferroni

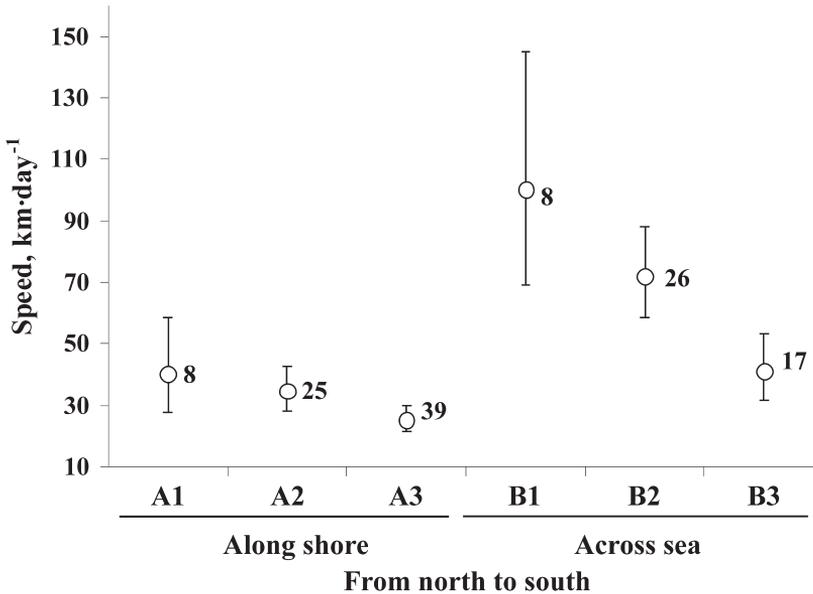


Fig. 5. Variation in migration speed of Goldcrests in relation to different parts of migration route. ANCOVA; route: $F_{5,116}=17.84$, $p<0.001$; trapping date: $F_{1,116}=6.56$, $p=0.012$. For each part of the route, the figure shows the least squares means \pm 95% confidence intervals together with sample size. Routes along the shore: (A1) eastern Ladoga coast (Gumbaritsy and Mayachino)–Kabli; (A2) Estonian Baltic coast (Kabli and Lao)–Rybachy; (A3) Rybachy–Polish Baltic coast (Mierzeja Wiślana, Hel and Bukowo–Kopan). Routes across the Baltic Sea: (B1) Gumbaritsy–Sweden; (B2) Kabli–Sweden; (B3) southern Sweden (south of 58° N)–Rybachy.

test; $p<0.05$). In ringed birds that were later recovered (data from Gumbaritsy only) the speed of migration was positively related to the amount of visible fat at the time of ringing (non-linear regression; $Y=37.3 * X^{0.4}$, $R^2=0.27$, $F=8.34$, $p=0.008$, $df=1,22$).

4. Discussion

4.1. Moulting-migration overlap

Several species show moulting-migration overlap in juveniles to a varying degree (Jenni & Winkler 1994). In Goldcrests, the annual variation in the percentage of moulting birds (between 35% and 62%) involved in migration was recorded by Johan Nilsson in Landsort, Sweden (Merilä 1997), however, the sources of annual variation still remain unclear. By comparing the data from two ringing sites along the migration route in the same year, the influence of annual variation is reduced.

The physiological state of migrating birds (e.g., as characterized by moulting-migration overlap) may differ in different geographical regions. The percentage of birds in moulting involved in migration was higher at the northern site (Gumbaritsy) in comparison with a more southern site (Kabli). The same phenomenon has been reported for the Great Tit *Parus major*, Chaffinch *Fringilla coelebs* and Willow Warbler *Phylloscopus trochilus* (Blyumental et al. 1967, Blyumental 1973). The pattern of changing of this value differs in two geographical regions. In both NW Russia and Estonia, most moulting Goldcrests involved in migration were at the very end of their feather replacement. We know from birds kept in captivity (J. Bojarinova, unpubl. data) that such Goldcrests usually finish their moulting within 15 days. Therefore, moulting individuals have apparently just commenced their migration but may not yet have covered a large distance. In NW Russia, moulting birds among migrating Goldcrests were present until the end of the migration season. A possible

reason for this is that these moulting individuals, involved in migration, are late-hatched birds originating from the neighbouring areas. In Kabli, the majority of recoveries from Russia (median date of recoveries 15 October) and all recoveries from Finland (median date of recoveries 13 October) were recorded in October. Therefore, we suggest that the bulk of birds trapped during this period in Estonia arrive from northern and north-eastern areas, having started their journey several weeks earlier. At their arrival to Estonia in October, these birds have already finished their moult.

4.2. Variation in body reserves and migration speed with date

The amount of fuel reserves and thus the value of body mass may be related to the strategy of the species in different parts of their migration route, such as with the presence of geographical barriers (Odum *et al.* 1961, Dolnik 1975, Karlsson *et al.* 1988, Åkesson *et al.* 1992, Berthold 1993, Schaub & Jenni 2000a).

For the Goldcrest, we found an increase in body mass with date only at the northernmost study site in 2001 (Gumbaritsy). At the other stations, this increase was not pronounced (Kabli) or was apparent only in the end of the season (Rybachy). These different patterns of mass changes can be explained by the position of the sites. As compared with birds trapped in Gumbaritsy, Goldcrests trapped at the more southerly stations apparently are a mixture of a larger number of different populations that might be at different phases of their migration. For instance, birds that had crossed an ecological barrier before trapping could be mixed with those that had not. For example, individuals that had been ringed in Sweden and had probably crossed the sea before being recovered in Rybachy, were heavier (after a correction for wing length and time of trapping) than ringed birds that probably arrived to Rybachy from Russia, Estonia and Latvia along the coast.

No seasonal trend in median fat score was recorded in 2001, even though the body mass increased with date at the northern study site (Gumbaritsy). This lack of trend may be due to the difficulties in distinguishing fat score for high fat reserves in the Goldcrest.

The increase in body mass with date found in migrating Goldcrests in Gumbaritsy suggests that, like several long-distance migrants (Schaub & Jenni 2000b), Goldcrests are increasingly time-stressed towards the end of the autumn migratory season. Our multiple-years data from Gumbaritsy showed that Goldcrest individuals that gained more fat reserves at the time of ringing migrated with a higher speed. If the body mass – and hence the amount of body reserves – are higher later on in the season, then birds can endure longer flights and show higher total speed of migration. Indeed, late-migrating Goldcrests move faster than early-migrating ones (Ellegren 1993, the present study). The correlation coefficients between the speed and trapping date, when based on all recoveries combined, was lower than those for a certain route, especially for ringing sites situated at high latitudes ($r = 0.24$ versus 0.70 – 0.86). For the ringing sites situated in the southern Baltic, this trend appeared non-significant (Fig. 4); this is a specific feature of the Goldcrest migration.

Ellegren (1993) explained the difference in migration speed between early and late migrants by the difference in speed between populations. We suggest that the accelerating effect of short days in the late season of migration may be involved in the increase of migration speed of late-migrating individuals as well. Adaptive modification of annual time programs by photoperiod is well known (Berthold 1996, Gwinner 1996). Two major effects are documented for several long- and short-distance migrants: the onset and duration of post-juvenile moult and the onset of autumn migration are advanced by a short photoperiod. This accelerated juvenile development means that late-hatched birds can prepare for autumn migration on time, but nevertheless later than early hatched individuals. Apart from this effect, there is some evidence from field and experimental studies that relatively short day length in late summer and autumn accelerate migratory fat deposition (Gifford & Odum 1965, Berthold 1996) that may result in the increase of migration speed.

Little is known about the direct influence of photoperiod on bird migration. Berthold (1984) showed that individuals of Garden Warblers *Sylvia borin* kept in long-term constant conditions showed prolonged and flattened migratory restlessness in comparison with birds kept at a shorter

day length. It cannot be ruled out that the differences in body mass and migration speed between early and late migrants might have resulted from differences in the photoperiodic conditions, in particular during the onset of migration of individuals. For example, in north-western Russia Goldcrests are normally double-brooded, and the breeding season lasts up to 2.5 months (Malchevsky & Pukinsky 1983). In this region post-juvenile moult of Goldcrests can start as late as September (Rezvyi 1990); moulting birds have been recorded until the end of October. As most Goldcrests are not involved in migration until the end of their moult (Rezvyi 1990, Merilä 1997, Bojarinova et al. 2005), such a long breeding season may result in the steady involvement of new birds in autumn migration. Late-hatched Goldcrests apparently started their movements later, during shorter days, and the effect of shortening days probably also resulted in their higher speed of migration.

4.3. Migration speed in different parts of migration route

The average migration speed of the Goldcrests, calculated using similar criteria for recovery acceptance reported for Finnish recoveries (Hildén & Saurola 1982), is $53 \text{ km}\cdot\text{day}^{-1}$, and for Swedish recoveries (Ellegren 1993) is $57 \text{ km}\cdot\text{day}^{-1}$. We showed that the speed of Goldcrest migration significantly increases in some parts of the route, which include ecological barriers. According to our data on the routes along the eastern Baltic shore, Goldcrests migrated on average up to $40 \text{ km}\cdot\text{day}^{-1}$, but on the routes which could include crossing the Baltic Sea the average speed might increase up to nearly $100 \text{ km}\cdot\text{day}^{-1}$. Ellegren (1993), based on Swedish ringing recoveries, showed a significant positive correlation between speed and distance for 20 out of the 31 species studied, suggesting that migration speed accelerated along the route. According to our data, the trend for the speed of movements on certain parts of migration route appeared the reverse for the Goldcrest. We demonstrated a tendency for a decreasing speed from the north to the south. This decrease was more pronounced on the routes that may have included flights across the sea. The speed of move-

ments from Gumbaritsy to Sweden was significantly higher than the speed from southern Sweden to Rybachy. Because the speed of migration consists of stopover and flight periods, the decrease of speed in this region of the Baltic indicates relatively longer stopover times of migrating Goldcrests before crossing the sea barrier.

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Hippiäisen (*Regulus regulus*) ruumiinpaino, sulkasato ja muuttonopeus suhteessa muuttoajankohtaan lajin muuttoreitin varrella

Tutkimme hippiäisen ruumiinpainoa, rasvavarastoja ja sulkasatoa eri vuodenaikakohtina kolmella lajin muuttoreitin varrella sijaitsevalla paikalla: Gumbaritsy, Koillis-Venäjä (Laatokan kaakkoisranta), Kabli, Lounais-Viro (Itämeren itärannikko) ja Rybachy, Kuurinkynnäs, Venäjä (Itämeren itärannikko). Analysoimme näiltä asemilta kootulla rengastusaineistolla muuttonopeutta. Sulkasatoisten muuttajien osuus oli korkeampi pohjoisimmalla (Gumbaritsy) kuin eteläisimmällä (Kabli) paikalla. Gumbaritsyssä pyydystettyjen hippiäisten ruumiinpaino kohosi muuttosesongin kuluessa 2001, mutta eteläisemmällä paikoilla trendiä ei todettu (Kabli) tai se havaittiin vain muuttosesongin lopulla (Rybachy). Rasvavarannot olivat korkeimpia Gumbaritsyssä. Muuttonopeuteen vaikutti ajan kuluminen (ts. nopeus kasvoi päivämäärän myötä ja oli selkeämmin havaittavissa pohjoisessa) ja havaintopaikan sijainti muuttoreitin varrella. Muuttonopeus oli merkittävästi korkeampi Itämeren ylittävillä kuin rannikkolinjaa seuraavilla reiteillä. Ne yksilöt, joiden paino kohosi nopeammin rengastusajankohtana, muuttivat nopeampaa vauhtia.

References

- Åkesson, S., Karlsson, L., Pettersson, J. & Wallinder, G. 1992: Body composition and migration strategies: a comparison between Robins *Erithacus rubecula* from two stop-over sites in Sweden. — *Vogelwarte* 36: 188–195.
- Bensch, S. & Nielsen, B. 1999: Autumn migration speed of juvenile Reed and Sedge warblers in relation to date and fat loads. — *Condor* 101: 153–156.
- Berthold, P. 1993: Bird migration: a general survey. — Oxford University Press, Oxford.
- Berthold, P. 1996: Control of bird migration. — Chapman & Hall, London.
- Berthold, P. 1984: The endogenous control of bird migration: a survey of experimental evidence. — *Bird Study* 31: 19–27.
- Blyumental, T.I. 1973: Development of the fall migratory state in some wild passerine birds (bioenergetic aspect). — In *Bird migrations: ecological and physiological factors* (ed. Bykhovskii, B.E.): 125–218. Wiley & Sons, New York.
- Blyumental, T.I., Vilks, E.K. & Gaginskaya, A.R. 1967: Geographical variation in molt in the Great Tit (*Parus major* L.) in the Baltic region. — *Proceedings of the Zoological Institute* 40: 203–216. (In Russian)
- Blyumental, T.I. & Dolnik, V.R. 1962: Evaluation of energetic parameters of birds in the field. — *Ornithologia* 4: 394–407. (In Russian)
- Bojarinova, J.G., Ilves, A.I. & Leivits, A. 2005: Autumn migration of the Goldcrest (*Regulus regulus* L.) in NW Russia and Estonia: a comparative analysis. — In *Ornithological research in the Ladoga region* (ed. Iovchenko, N.P.): 82–101. St. Petersburg University Press, St. Petersburg. (In Russian with English summary)
- Bojarinova, J.B., Lehtikoinen, E. & Eeva, T. 1999: Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. — *Journal of Avian Biology* 30: 437–446.
- Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. 1999: Results of bird trapping and ringing by the Biological Station “Rybachy” on the Courish Spit in 1998. — *Avian Ecology and Behaviour* 2: 105–150.
- Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. 2000: Results of bird trapping and ringing by the Biological Station “Rybachy” on the Courish Spit in 1999. — *Avian Ecology and Behaviour* 4: 85–145.
- Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. 2001a: Results of bird ringing by the Biological Station “Rybachy” on the Courish Spit: long-distance recoveries of birds ringed in 1956–1997. — *Avian Ecology and Behaviour* Suppl. 1: 1–126.
- Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. 2001b: Results of bird ringing by the Biological Station “Rybachy” on the Courish Spit: long-distance recoveries of birds ringed in 1956–1997. — *Avian Ecology and Behaviour* Suppl. 2: 1–150.
- Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. 2002a: Results of bird trapping and ringing by the Biological Station “Rybachy” on the Courish Spit in 2001. — *Avian Ecology and Behaviour* 8: 109–166.
- Bolshakov, C.V., Shapoval, A.P., Zelenova, N.P. 2002b: Results of bird trapping and ringing by the Biological Station “Rybachy” on the Courish Spit in 2001. — *Avian Ecology and Behaviour* 9: 67–114.
- Brown, M.E. 1996: Assessing body condition in birds. — In *Current Ornithology* (ed. Nolan, V. Jr. & Ketterson, E.D.) 13: 67–135. Plenum Press, New York.
- Cramp, S. (ed.) 1998: The Complete Birds of the Western Palearctic. — CD-ROM, Oxford University Press, Oxford.
- Dolnik, V.R. 1975: Migratory disposition in birds. — *Nauka, Moscow*. (In Russian)
- Dolnik, V.R., Gavrilov, V.M. 1979: Bioenergetics of molt in the Chaffinch (*Fringilla coelebs*). — *Auk* 96: 253–264.
- Dunn, E.H. 2001: Mass change during migration stopover: a comparison of species groups and sites. — *Journal of Field Ornithology* 73: 419–432.
- Dunn, E.H. 2002: A cross-Canada comparison of mass change in birds during migration stopover. — *Wilson Bulletin* 114: 368–379.
- Ellegren, H. 1993: Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. — *Ornis Scandinavica* 24: 220–228.
- Fransson, T. 1995: Timing and speed of migration in North and West European population of *Sylvia* warblers. — *Journal of Avian Biology* 26: 39–48.
- Gifford, C.E. & Odum, E.P. 1965: Bioenergetics of lipid deposition in the Bobolink, a transequatorial migrant. — *Condor* 67: 383–403.
- Gwinner, E. 1996: Circadian and circannual programmes in avian migration. — *Journal of Experimental Biology* 199: 39–48.
- Hanssen, O.J. 1981: Migratory movements of Scandinavian Goldcrests *Regulus regulus* (L.). — *Fauna Norvegica Ser. C, Cinclus* 4: 1–8.
- Hildén, O. & Saurola, P. 1982: Speed of autumn migration of birds ringed in Finland. — *Ornis Fennica* 59: 140–143.
- Jenni, L. & Winkler, R. 1994: Moulting and Ageing of European Passerines. — Academic Press, London.
- Kania, W. 1983: Preliminary remarks on the migration of North European Goldcrests *Regulus regulus*. — *Ornis Fennica* Suppl. 3: 29–30.
- Karlsson, L., Persson, K., Pettersson, J. & Walinder, G. 1988: Fat-weight relationship and migratory strategies in the Robin *Erithacus rubecula* at two stop-over sites in south Sweden. — *Ringling and Migration* 9: 160–168.
- Malchevsky, A.S. & Pukinsky, Y.B. 1983: Ptitzii Leningradskoy oblasti i sopredelnykh territoriy (The birds of Leningrad Region and adjacent areas). Vol. 2. — Leningrad University Press, Leningrad. (In Russian)

- Merilä, J. 1997: Fat reserves and moult-migration overlap in Goldcrest, *Regulus regulus* – A trade-off? — *Annales Zoologici Fennici* 34: 229–234.
- Odum, E.P., Connel, C.E. & Stoddard, H.L. 1961: Flight energy and estimated flight ranges of some migratory birds. — *Auk* 78: 515–527.
- Payevsky, V.A. 1973: Atlas of bird migrations according to banding data on the Courland Spit. — In *Bird migrations: ecological and physiological factors* (ed. Bykhovskii, B.E.): 1–124. Wiley & Sons, New York.
- Pettersson, J., Sandström, A. & Johansson, K. 1986: Wintering areas of migrants trapped at Ottenby Bird Observatory. — *Special report from Ottenby Bird Observatory* 6: 1–276.
- Remisiewicz, M. & Baumanis, J. 1996: Autumn migration of Goldcrest (*Regulus regulus*) at the eastern and southern Baltic coast. — *Ring* 18: 3–36.
- Rezvyi, S.P. 1990: The Goldcrest (*Regulus regulus* L.) — In *Linka vorobiinih ptitz Severo-Zapada SSSR* (Moult of Passerine of north-western USSR) (ed. Rymkevich, T.A.): 137–139. Leningrad University Press, Leningrad. (In Russian)
- Rezvyi, S.P. 1995: The Goldcrest (*Regulus regulus* L.). — In *Atlas of bird migration according to ringing and recovery data for Leningrad region* (ed. Noskov, G.A. & Rezvyi, S.P.): 150–164. Leningrad University Press, Leningrad. (In Russian)
- Schaub, M. & Jenni, L. 2000a: Fuel deposition of three passerine bird species along the migration route. — *Oecologia* 122: 306–317.
- Schaub, M. & Jenni, L. 2000b: Body mass of six long-distance migrant passerine species along the autumn migration route. — *Journal of Ornithology* 141: 441–460.
- Sokal, R.S. & Rohlf, F.J. 1998: *Biometry*. Third edition. — W.F. Freeman and Company, New York.
- Svensson, L. 1992: *Identification Guide to European Passerines*. Fourth edition. — Fingraf, Södertälje.