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Autumn migration of the Long-tailed Tit (*Aegithalos c. caudatus*) at the opposite sides of the Eurasian continent

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We compared autumn migration in two distant populations of the nominate subspecies of the Long-tailed Tit (*Aegithalos c. caudatus)* with assumed different migratory habits in order to reveal the difference in characteristics of their movements. We studied the Northern European (Lake Ladoga region, NW Russia) population considered to be irruptive, and the Northeastern Asian (Primorye, Russian Far East) population which is believed to migrate regularly. We analyzed year-to-year fluctuation in numbers, timing of movements, body mass, fat reserves and plumage condition in migrating birds. We found that the two studied populations shared similar characteristics of autumn migration. Apart from significant fluctuations in numbers recorded in Northern Europe and Northeastern Asia, other features were similar to what have been observed for regular migrant species. Autumn movements of Long-tailed Tits in NW Russia and in the Russian Far East were registered every year and occurred in the dates specific to each population; the median date in different years spanned a two week period. In both populations, individuals that migrated later in the season gained larger fat reserves. Birds were involved in autumn movements either at the final stage of moult or just after the end of feather replacement. Our results indicate that Northern European and Northeastern Asian populations of *Aegithalos c. caudatus* show similar patterns of migratory behaviour.

1. Introduction

Some species show a wide range of intraspecific variation in migratory status (from year-round residents and partial short-distance to regular short- and long-distance migrants) according to different geographical regions, different habitats, or both (Cramp 1998). Such variation in migration habits could reflect different genetic programs of populations (or subspecies) or/and could be a response to the environmental conditions in the breeding area during the non-breeding season (e.g., Berthold 1996, Pulido 2007).

Very little is known about the population variation in migratory behaviour across the distribution range of birds known as irruptive migrants, whose movements mainly depend on environmental conditions, an example being the nominate subspecies of the Long-tailed Tit (*Aegithalos caudatus* (L.)).

The Long-tailed Tit is a polytypic species,

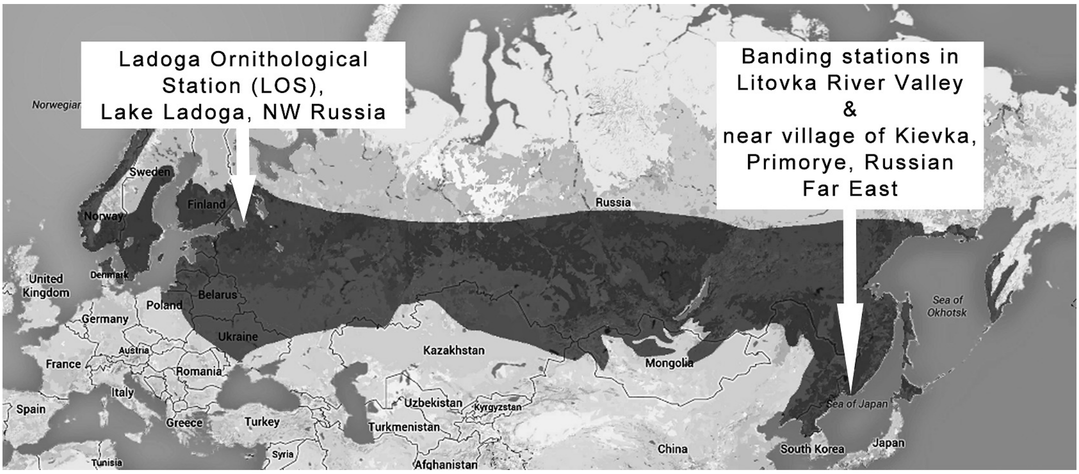

Fig. 1. The distribution range of the Long-tailed Tit *Aegithalos caudatus caudatus* and trapping sites (adapted from Glutz von Blotzheim & Bauer 1993 with changes according to Koblik *et al.* (2006) for Russian Far East and Harrap & Quinn (1996) and Svensson (1992) for Europe.

which is widespread from the Atlantic to the Pacific coast of Eurasia (Harrap & Quinn 1996, Cramp 1998, Dickinson & Christidis 2014). According to different authors the species may be split into up to 22 subspecies (Glutz von Blotzheim & Bauer 1993, Harrap & Quinn 1996, Cramp 1998, Dickinson & Christidis 2014). Most of the Long-tailed Tit subspecies are considered to be sedentary; the only one known to migrate significant distances is the nominate subspecies (Harrap & Quinn 1996, Cramp 1998).

The breeding range of the nominate subspecies covers a huge area from Fennoscandia and Northeastern Europe to Northeastern Asia (Fig. 1). The migration behaviour of *A. c. caudatus* remains poorly studied. In the Baltic region of Europe, the Long-tailed Tit is considered an irruptive migrant due to great annual fluctuations in numbers during autumn migration (Zink 1982, Shapoval 1989, Glutz von Blotzheim & Bauer 1993, Harrap & Quinn 1996, Cramp 1998, Sokolov *et al*. 2004). This conclusion is supported by the fact that, in some years, Long-tailed Tits are almost completely absent from migration routes in autumn. In other years, at the same sites, the number of Long-tailed Tits observed and captured (at banding stations) can reach several tens of thousands (Ehrenroth 1976, Hildén 1977, Sokolov *et al*. 2002, 2004). It is believed that such movements are triggered mainly by environmental factors (reviews by Schwabl & Silverin 1990, Newton 2006, 2008), in particular by high population density and lack of food (Lack 1954, Svärdson 1957, Brotons 2000, Koenig & Knops 2001, Newton 2008).

In contrast, the nominate subspecies of the Long-tailed Tit in Northern and Eastern Asia (e.g., in Siberia and northeastern China) is considered a regular migrant (review by Harrap & Quinn 1996, Cramp 1998). Many authors note an increase in the number of Long-tailed Tits in October and the first half of November in different parts of the Russian Far East, followed by a decrease closer to winter (Shibnev 1975, Shokhrin 2005, Gluschenko *et al*. 2006, Nechaev 1991, Volkov & Atrokhova 2008). However, up to now no long-term data on migration of the species in this region have been presented.

The goal of this study was to compare autumn movements in two distant populations of the nominate Long-tailed Tit subspecies (in NW Russia and Russian Far East) and to determine whether a difference between movements of *A. c. caudatus* populations in the Northeastern Asia (regular partial migrant) and Northern Europe (irruptive migrant) indeed exists.

Irruptive movements are usually associated with larger year-to-year fluctuations in numbers and variation in timing compared to the regular movements (Newton 2008). Here, using long-term trapping data we test the following assumptions emerging from these general characteristics: irruptive Northern European population should demonstrate (1) higher variation in dates of movements and (2) larger year-to-year fluctuations in numbers compared to the Northeastern Asian population. In regular migrants, energy-demanding processes such as moult and migration are known to overlap only to a small extent (Jenni & Winkler 1994). The degree of moult / migration overlap is one of the key characteristics of avian seasonal movements. Some irruptive species can migrate at different stages of moult and / or suspend moult at different stages (Iovchenko & Smirnov 1990, Ree 1974 cited by Cramp 1998). We suggest that an irruptive population could be less adapted to the migrations over a large geographical scale. Therefore, we expect that the birds from the Northern European population should have (3) less fat reserves and (4) larger overlap between moult and migration compared to the Northeastern Asian one.

2. Material and methods

2.1. Trapping sites and data collection: timing of migration and numbers

For Northeastern Asia, we used long-term capture data collected during 1999–2014 in the Russian Far East (Primorye) at the banding station of Amur-Ussuri Center for Avian Biodiversity, in the valleys of the Litovka River tributaries (42º57' N, 132º53' E; Fig. 1). Mist netting was performed from August until the end of the migration in late October or early November (October 27–November 10), covering almost the whole period of Long-tailed Tit migration. The only exception was 1999, which was excluded from the analyses.

Flocks of Long-tailed Tits fly at low altitude, keeping to shrubs and trees, so that trapping by standard mist nets (height 2.8 m, length 10–12 m) reflects well the numbers of this species during seasonal movements. Because the number of mist nets varied between years (range 35–57), we calculated the annual number of birds trapped per 100 m of mist nets. For the Northern European population we used the long-term data from the Ladoga Ornithological Station (LOS), situated on the SE coast of Lake Ladoga in the NW Russia (60º41' N, 32º57' E) for years 1970 to 2014 (Fig. 1). There, the birds were captured by stationary Rybachy-type traps (Payevsky 2000) and mist nets from April to late October. Two traps were located in the coastal biotope, where movements of the studied species occur. The entrance gates of the traps were oriented in the same direction, towards the migration flow. Depending on the year, one or two stationary traps operated at the LOS during the migration period.

In NW Russia, the data cover a significantly longer period compared to the capture period in the Russian Far East. Therefore, for NW Russia we analyze the variation in migration dates for the whole period of trapping (from 1970 to 2014) and for the period matching the capture period in the Russian Far East (Pimorye). We used data only for those years when trapping was performed at least until October 15 and therefore covered almost the whole period of movements of this species in the region. Thirty-seven years matched these requirements during the period from 1970 to 2014, and 14 years during the period from 1999 to 2014 (similar to the capture period in the Russian Far East). To calculate the timing of migration, we used data from all trapping equipment (traps and mist nets) in those years.

To assess the variation in numbers, we used only the data from two stationary traps from 1999 to 2014 (similar to the capture period in the Russian Far East). For the time intervals when both traps were in use, we calculated the average number of birds per trap. To compare the number fluctuations between the two sites where birds were trapped with different equipment, we used the relative annual number expressed as the number of birds per year divided by the median over all studied years.

Since trapping in both study areas began before the period of autumn migration, we excluded from the analysis the birds known to be locals according to previous ringing.

2.2. Trapping sites and data collection: body mass, fat reserves and plumage condition

Body mass, fat reserves and plumage condition in migrating Long-tailed Tits were analyzed on the basis of the LOS data bank and data collected in the Russian Far East (Primorye) in the vicinity of

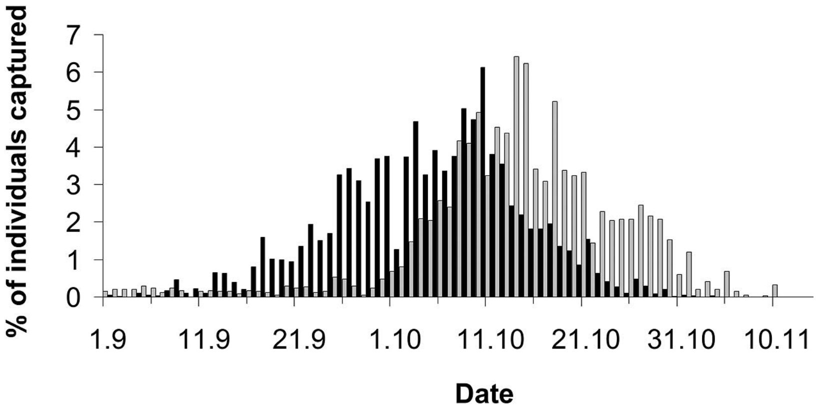

Fig. 2. The dynamics of numbers of Long-tailed Tits captured during the period of autumn migration at the LOS, NW Russia (black bars, number of years *n* = 37) and in the Litovka River valley, Primorye (grey bars, number of years *n* = 15).

the village of Kievka (42º89'N, 133º83'E) (Fig. 1). This site was situated 82 km from the banding station of Amur-Ussuri Center for Avian Biodiversity. The trapping site in the vicinity of Kievka was located in a river valley at the sea coast. Here, at the end of the migration season (late October–November) the weather is milder compared to the continental part of Primorye, with first snowfalls occurring later in the season, and the migration of many species is recorded at later dates (Shokhrin 2005). Birds were trapped there using mist nets.

We used the standard procedure of data collection. Trapped birds were ringed, their body mass was recorded to the nearest 0.1 g, and the wing length was measured to the nearest 1 mm using the maximum length method (Svensson 1992). Fat reserves were evaluated by scoring the amount of subcutaneous fat deposited within the furculum of the clavicle, under the wing, and in the abdominal region (Wolfson 1945), following a 10-score scale. Time of capture in the day was also recorded to the nearest hour.

Both first-year and adult Long-tailed Tits undergo a complete moult (Jenni & Winkler 1994) from midsummer. Primaries are replaced one after another starting from the innermost. We recorded the moult using 11 stages (Noskov & Gaginskaya 1969): the first stage corresponds to the start of moult of the innermost primary feather, and so on towards the onset of moult of the next primary. Stage 11 indicates that all the primaries are replaced, but secondaries or tertials and / or body feathers are still growing.

The data on variation in body mass and fat reserves in migrating Long-tailed Tits are presented for NW Russia for 14 years from 1970 to 2000 based on the previous analyses (Bojarinova & Babushkina 2010), and for Russian Far East (Primorye, Kievka) – for the years 2011 and 2013. In Primorye, bird trapping was conducted from September until the beginning of November.

At the LOS, analysis of plumage condition in migratory Long-tailed Tits was performed in nine years (2003, 2004, 2006–2010, 2013, 2014), when 78 to 99% (annual average of 93%) of all captured birds were examined. In Primorye, all trapped birds (73 individuals in 2011 and 761 in 2013) were examined for plumage condition.

2.3. Statistical analyses

For the statistical analysis of the data, conventional methods were used (Sokal & Rohlf 1998). Variation in timing of migration (dependant variable) was studied using a general linear model with "trapping site" and "year" as explanatory variables. The interaction between "trapping site" and "year" was used to test for the difference in long-term temporal trends in median migration data at two places. The fluctuations in numbers of trapped birds between two sites were compared using the Levene's test for the coefficient of variation (Van Valen 2005). We used the Mann–Whitney *U*-test to compare the relative annual numbers (expressed as a ratio of a number of birds per year divided by the median over all studied years) between two populations, and the Fisher exact probability test to compare the distributions of these parameter. Pearson and Spearman rank correlation was used for checking the relationship between body mass / fat reserves with the time of capture. The analysis of covariance (ANCOVA) was used

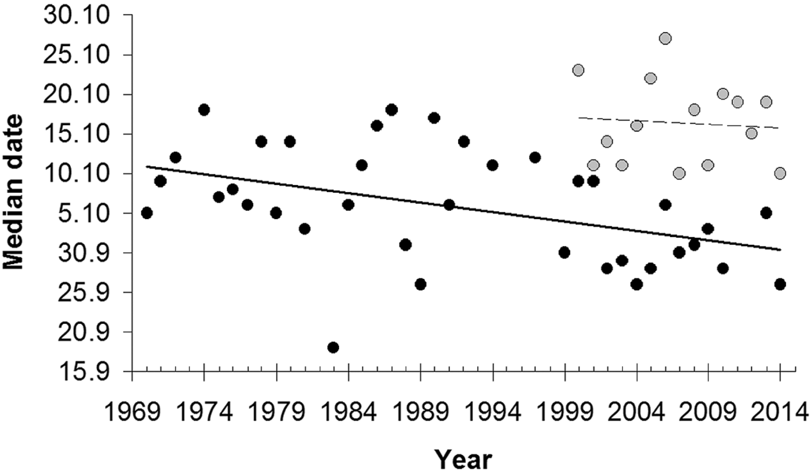

Fig. 3. Variation in the timing of movements of Long-tailed Tits at the LOS, NW Russia (black circles, solid line) and in the Litovka River valley, Primorye (grey circles, dashed line). The results of regression analysis: $F_{1,35} = 8.26$, $p = 0.007$, $y = -0.24x + 509.2$ for the LOS and $F_{1,13} = 2.23$, $p = 0.79$ for the Litovka River valley, Primorye. In the regression equation x = 1 corresponds to September 1.

to study the variation in body mass between two populations with the place of trapping as a factor variable and wing length as a covariate. Both response (body mass) and covariate (wing length) variables were log-transformed for this analysis. The variation in fat reserves was tested with Mann–Whitney *U*-test and Kruskal–Wallis test. A binomial test was used to evaluate the difference between populations in the proportion of birds with moulting primaries. Means are shown with standard error (± SE). We performed the statistical analysis using Statistica 7.0.

3. Results

3.1. The variation in timing of autumn movements

The migration of Long-tailed Tits at the LOS (NW Russia) occurred from the second ten day period of September until late October (Fig. 2). The median date of movements in the period from 1970 to 2014 varied from September 18 to October 18, and on average fell at the beginning of October (October 6 ± 1.2 days, $n = 37$). During this period, the timing of passage significantly shifted to earlier dates (Fig. 3).

Within the period from 1999 to 2014 (similar to the capture period in Primorye) the median date of migration in different years varied within two weeks – from September 26 to October 9 (Fig. 3) and, on the average, fell on October 1 (± 1.1 days, $n = 14$).

Noticeable movements of Long-tailed Tits in Primorye (Russian Far East) began no earlier than the last ten days of September (Fig. 2). Migration took place mainly in October. Annual variation in the timing of movements was rather low (Fig. 3): the median date of movements in different years varied within two weeks – from October 10 to October 27, and on average fell on October 16 (± 1.4 days, $n = 15$).

In 1999–2014, the median migration date was significantly earlier at the LOS. The “trapping site” according to partial eta-squared η^2 accounted for 33% of the variation ($F_{1,25} = 12.19, p = 0.002$). No significant effect of “year” describing the common temporal trend, or the interaction between the “trapping site” and “year” describing the temporal trend in median migration dates at the two sites were found (correspondingly $F_{1,25} = 0.61, p = 0.44$ for the “trapping site” and $F_{1,25} = 0.13, p = 0.72$ for the interaction).

3.2. Variation of autumn numbers

Autumn movements of the Long-tailed Tit were observed in both study areas each year, but the number of captured birds was highly variable: at the LOS, numbers ranged from 178 (2009) to 2,914 (2000) birds ($n = 14$); in Primorye, numbers ranged from 48 (2001) to 755 (2012) individuals ($n = 15$).

Fluctuations in numbers were similar at the LOS and in Primorye, when standardized by trapping equipment. In Primorye, the number of Long-

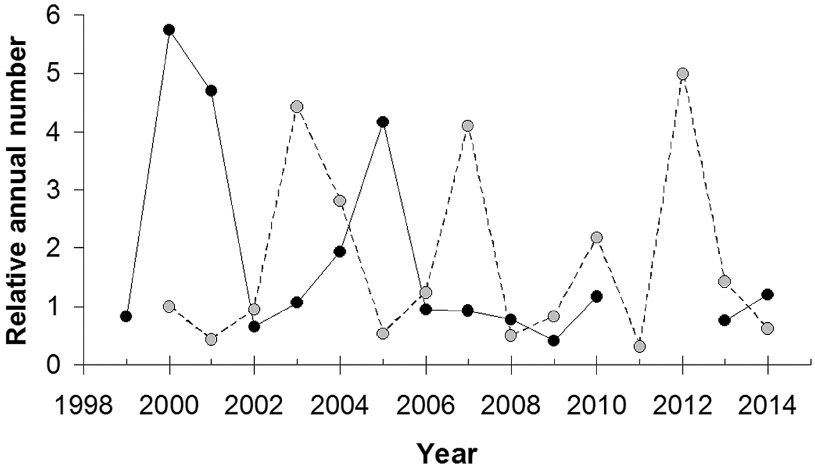

Fig. 4. Variation in relative annual numbers (expressed as a number of birds per year divided by the median number over all studied years) of Long-tailed Tits at the LOS, NW Russia (black circles, solid line) and in the Litovka River valley (grey circles, dashed line).

tailed Tits (caught per 100 m of mist nets) (mean 59.9 ± 14.0) differed by an order of 16 times in the years of maximum and minimum numbers. At the LOS, in terms of one trap, the ratio of maximum and minimum annual numbers reached 14 (mean 434.4 ± 111.1, $n = 14$). The coefficient of variation for autumn numbers in Primorye ($CV = 90\%$) did not differ significantly from the value for the LOS ($CV = 96\%$) (Levene's test for CV, $F_{1,27} = 0.06$, $p = 0.81$).

The number of migrating Long-tailed Tits was not related to the median date at either site: $r_{sp} = -0.15$, $p > 0.05$, $n = 37$ for the LOS and $r_{sp} = -0.10$, $p < 0.05$, $n = 15$ for Primorye, respectively.

The relative annual numbers did not differ significantly between two study sites (Fig. 4, Mann–Whitney U-test, $W = 100.0$, $p = 0.84$). Distributions of this value were also similar: the number of trapped birds was two times greater than the median in four years in Primorye and in three years at the LOS (Fisher exact probability test, $p = 1$), and more than four times greater in three years in both places.

3.3. Energy reserves

The average body mass of migrating Long-tailed Tits captured at the LOS and in Primorye did not exceed 9 g. Median fat scores were rather low, with scores 3 and 4, respectively (Table 1). These values for the birds from NW Russia were significantly greater compared to the values obtained for Primorye (Table 1), although the difference between means was in decimals of grams only. Among Northern European birds, 12% of birds were migrating without any visible fat, whereas 20% of such individuals were recorded for NE Asia population (the difference is significant, $\chi^2 = 41.02$, $p < 0.05$). Conversely, the percentage of birds with high fat scores (6 or higher) was significantly larger in the west (22%) compared to the east (15%) ($\chi^2 = 41.02$, $p < 0.05$).

Table 1. Body mass and fat reserves of Long-tailed Tits captured in autumn near the village of Kievka, Primorye and at the LOS, NW Russia.

Variable	Primorye, Kievka	NW Russia, LOS	Results of statistical tests
Body mass	$x = 8.48 \pm 0.02$ ($n = 834$) lim 7.3–10.1 g	$x = 8.92 \pm 0.005$ ($n = 8{,}922$) lim 6.8–10.7 g	ANCOVA, main effect (place of trapping): $F_{1,9754} = 627.5$, $p < 0.001$; $\eta^2 = 0.06$; covariate (wing length): $F_{1,9754} = 1391.9$, $p < 0.001$, $\eta^2 = 0.12$
Fat reserves	$x = 3.23 \pm 0.07$ ($n = 833$) median = 3 lim 1–8	$x = 3.91 \pm 0.02$ ($n = 8{,}859$) median = 4 lim 1–10	Mann–Whitney U-test, $Z = 10.58$, $p < 0.05$

Table 2. Median fat score of Long-tailed Tits trapped in different periods near the village of Kievka, Primorye.

Year	Periods of trapping			Statistics of the Kruskal–Wallis test
	October 1–20	October 21–31	November 1–8	
2011	1 (n = 12)	2 (n = 29)	5 (n = 31)	H = 19.7, p < 0.001
2013	2 (n = 109)	3 (n = 491)	3 (n = 161)	H = 30.7, p < 0.001

We found that fat score was positively related to the date of capture in the season at the LOS (r_{sp} = 0.36, n = 8,859, $p < 0.001$) and in Primorye (r_{sp} = 0.21, n = 833, $p < 0.001$), whereas the body mass did not change with season in either of the two places (r = –0.02, n = 8,922, p = 0.06 and r = 0.0009, n = 834, p = 0.98).

In NW Russia, Long-tailed Tits that migrated later in the season gained larger fat reserves (Bojarinova & Babushkina 2010). A similar situation was observed in Primorye (Table 2). In birds captured later in the season, the fat score was significantly higher than in those caught in earlier periods.

3.4. Plumage condition

The vast majority of birds captured in Primorye and at the LOS were at the final stage of replacing the body feathers (the end of moult; stage 11), or had completely replaced these feathers. During the final stage of moult, the longest body feathers on the edges of the dorsal and pectoral pterilia were growing.

No birds with moulting primaries were observed in Primorye (2011, n = 73 and 2013, n = 761). At the LOS, the proportion of birds with primaries still in moult was very small. It ranged from 0.2 to 5.6% in different years (n = 9) and averaged 2.1%. In nine years, there were only 83 such birds out of 3990, captured in September and October. By the time of capture, only three birds still had two primaries to replace (moulting stage 9), the rest (n = 80) had only one outermost primary to replace. The proportion of birds with moulting primaries in Primorye (0 out of 834) was lower than the value expected from the whole sample (Binomial test, one tailed, $p < 0.001$). Birds at stage 10 were captured throughout September and until October 5. Individuals at stage 9 were registered on September 18, 2007 and September 30, 2009.

4. Discussion

We studied autumn migration in two populations of the nominate subspecies of the Long-tailed Tit inhabiting the opposite sites of the Eurasian continent. We found many similarities in the characteristics of autumn movements of these populations, which have been thought to have different migratory habits. Firstly, no difference was found between the Russian Far East and NW Russia in the fluctuations of annual numbers from 1999 to 2014: the values and the distribution of the relative deviation from the median number of birds, trapped in all years, were similar. The ratio of maximum to minimum annual numbers in different years was also similar for both populations (16 for Primorye and 14 for the LOS).

It has been reported previously that for a period of 40 years in NW Russia there have been great fluctuations in numbers, the number of trapped birds changing more than 200-fold: from 7 to 1476 birds in one trap (Bojarinova & Babushkina 2010). However, over the past 15 years, there have been no such significant fluctuations in numbers. Nevertheless, in the Russian Far East and NW Russia, no matter how large were the fluctuations in numbers, migrating Long-tailed Tits were registered annually, in contrast to the Southern Baltic region, where in some years the Long-tailed Tit is completely absent among migratory birds in autumn. In other years, at the same sites, the number of observed and captured Long-tailed Tits can reach several tens of thousands (Ehrenroth 1976, Hildén 1977, Sokolov *et al*. 2002, 2004). For example, on the Courish Spit, there have been seven years (out of 47) when not a single Long-tailed Tit was captured, and another 16 years when numbers trapped ranged from 1 to 50 individuals. However, the maximum amount for the autumn period reached 20,557 individuals (in 2000) (Sokolov *et al.* 2004). Thus, in this region, the fluctuation in numbers during the autumn migration can reach four orders of magnitude. It is most likely that such variation mainly reflects fluctuations in the overall population level across a huge species range, but other environmental factors may also be involved.

Thus, years of strong irruptions in this species usually coincided with favourable conditions (high air temperature) in spring across the large portion of the species' range (Sokolov *et al.* 2002, 2004). High spring temperatures may favour successful breeding across large areas, leading to increased production of juveniles that are likely to participate in autumn movements (Sokolov *et al.* 2004). As these authors suggested, the variation in numbers by several orders of magnitude cannot be due to the variation in population productivity alone, but may be connected with some environmental factors that act during autumn passage, e.g., the effect of wind on direction and route of migration. Thus, Sokolov *et al.* (2004) reported that in autumn 2000, when the earliest mass irruption of Long-tailed Tits occurred, weak and moderate easterly winds in the Eastern Baltic may have facilitated an early influx of young birds from the mainland to the Courish Spit.

The variation in timing of autumn movements in each of the study sites in the Russian Far East and NW Russia from 1999 to 2014 is insignificant: the median date in different years varied within two weeks. Such fixed timing of movements can be compared to that of regular migrants. For Long-tailed Tits from the Northwestern European population, it has been experimentally shown there is an annual cycle of migratory restlessness exhibited in captivity and influenced by photoperiod (Babushkina & Bojarinova 2011). The increase in locomotory activity in the laboratory was timed to the periods of autumn migration and spring movements, which were also recorded for the studied species (Hildén 1977, Sokolov *et al.* 2002). This fact indicates that seasonal increase in locomotory activity in the Long-tailed Tit is triggered by endogenous rhythms as in regular migrants, resulting in distant movements in some years.

The analysis of the timing of autumn movements in the Long-tailed Tit in NW Russia for the 45 year period (from 1970 to 2014) showed that the median date of migration of the species moved to an earlier date. A similar trend (though not significant) for the timing of the onset of migration was registered on the Courish Spit for the period from 1957 to 2003 (Sokolov *et al.* 2004). It was also shown that the timing of the onset of migration was associated with winter and spring NAO Index and spring temperatures in the breeding areas of the species (Sokolov *et al.* 2004). In the years with a warm spring, the timing of autumn movements in the species shifted to earlier dates.

The dependence of timing of migration in the Long-tailed Tit on spring temperatures also indirectly indicates that the beginning of autumn movements is triggered by endogenous rhythm: i.e., earlier hatching results in earlier start of autumn movements. A significant correlation between the timing of reproduction and the timing of migration has been shown previously for several long and short-distance migrants (e.g., Ellegren 1990, Morton & Pereyra 1994, Sokolov *et al.* 1999, Bojarinova *et al.* 2002, Meller *et al.* 2013).

At both sites we did not find any relationship between the annual number of birds and the timing of movements. However, for the Courish Spit, annual numbers were negatively related to the timing of passage and positively related to the NAO Index in the breeding area in spring (Sokolov *et al.* 2004). It can be inferred that early autumn passage in irruption years is a consequence of early breeding in warm springs. Warm springs at the same time favour successful breeding resulting in population increase.

We speculated that if the Northern European population was irruptive and the movements were triggered by high numbers and a lack of food, birds involved in such movements would show larger overlap between moult and migration and, therefore, high variation in plumage condition. Some irruptive species, for example first-year Siskins (*Spinus spinus)*, can migrate at different stages of moult, even in the beginning of feather replacement (Iovchenko & Smirnov 1990). Another well-known irruptive species, the Great Spotted Woodpecker (*Dendrocopos major)* shows a great variation of plumage condition during movements. As in the Long-tailed Tit, yearlings of this species undergo complete moult, but during irruptions moult is suspended or slowed down (Ree 1974 cited by Cramp 1998). Therefore, Great Spotted Woodpeckers can show a different number of renewed primaries during such movements. In both studied Long-tailed Tit populations we found no birds in the beginning or in the middle of the moult, or with any signs of suspended moult. Long-tailed Tits begin their movements at a certain stage of their annual cycle. In both populations, birds were captured either at the final stages of moult, or having already completed the replacement of feathers. At the LOS, the proportion of birds that had not yet replaced the outermost primary was negligible (2%). No such birds were captured in Primorye, which, most likely, may be explained by the fact that the birds pass this point at an advanced stage of migration. Similar differences were reported for the Goldcrest (*Regulus regulus)*: the percentage of birds in moult involved in migration was higher at a northern site in comparison with that at a southern site where birds passed through later (Bojarinova *et al*. 2008).

We predicted that if two populations were different in their migratory status they could also show differences in fat reserves. We suggested that the irruptive population (NW Russia) should have lower fuel loads compared to the assumed regularly migrating population (Russian Far East). However, we obtained the reverse result: the mean value of body mass and fat reserves of the Long-tailed Tits in NW Russia were significantly greater compared to the values obtained for Primorye.

It has been shown that the amount of energy reserves in migrating Long-tailed Tits varied significantly from year to year (Bojarinova & Babushkina 2010). We assume that small differences in the value of energy reserves and body mass found between NW Russia (using data for 14 years) and the Russian Far East (data for two years) may be associated with annual variation of these parameters. It is remarkable that fat reserves in Long-tailed Tits significantly increased during migration both in the Russian Far East and NW Russia. This increase in fat reserves during the migration season is similar to the energy reserves changes in typical long-distance migrants (Bensch & Nielsen 1999, Schaub & Jenni 2000) and a short-distance migrant – the Goldcrest (Bojarinova *et al*. 2008). Such an increase in energy reserves in late migrating birds allows them to develop a greater speed of migration compared to individuals moving in earlier periods (Ellegren 1993; Bensch & Nielsen 1999; Bojarinova *et al*. 2008), and to leave areas unfavorable for wintering. In the Long-tailed Tit, an increase in the speed of migration during the autumn season has been observed in NW Russia (Bojarinova & Babushkina 2010), and also in the Baltic region on the Courish Spit (Shapoval & Yablonkevich 1991).

According to our data, in Long-tailed Tits ringed at the LOS in October, migration speed can reach 95 km / day, with the average speed of 42.5 km / day (Bojarinova & Babushkina 2010). Many other migrant species that overwinter in Europe move with a similar speed (Ellegren 1993). The increase of energy reserves in relation to date in birds from the Russian Far East indirectly indicates that the speed of migration is likely to increase later in the season.

Whether or not the Long-tailed Tits migrate only in the first year of their life is still uncertain. Ageing of the species during autumn is possible only due to skull ossification (Svensson 1992) and is difficult at the end of the season, when birds with a completely ossified skull can be either adults or first-autumn individuals. It cannot be ruled out that some adult birds nevertheless participate in migration, but the number of such birds probably does not exceed several percent (Sokolov *et al*. 2004). In captivity, also second-year Long-tailed Tits exhibited an increase of locomotory activity in autumn and spring (Babushkina 2012).

Newton (2008) did not include Long-tailed Tits among the typical irruptive migrants of the northern regions such as boreal finches and others that depend on fluctuating tree-seed and fruit crops. However, the variation of numbers during migration, by several orders of magnitude, allows us to include Long-tailed Tits in the group of irruptive migrants. Apart from significant fluctuations in numbers during migration recorded in Northern Europe and Northeastern Asia, other features, such as small annual variation in the timing of migration, dynamics of energy reserves, limited moult / migration overlap, existence of spring return movements (Hildén 1977, Sokolov *et al.* 2002) and endogenous basis for the seasonal migration (Babushkina & Bojarinova 2011), are very similar features to what have been observed for regular migrant species.

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Pyrstötiaisen syysmuutto Euraasian mantereen vastakkaisilla puolilla

Tutkimme syysmuuttoa kahdessa toisistaan etäällä olevassa pyrstötiaisen populaatiossa, jotka edustavat samaa alalajia – *Aegithalos caudatus caudatus*. Vertailimme Pohjois-Euroopan (Laatokan alueen) populaatiota, jonka muuttokäyttäytyminen oletettiin olevan irruptiivinen (epäsäännöllinen, vaellusmainen), sekä Koillis-Aasian (Primorye) populaatiota, joka uskotaan koostuvan säännöllistä muuttolinnuista. Lajin syysliikehdintää seurattiin molemmilla alueilla vuosittain. Analysoimme vuosien välistä vaihtelua lukumäärissä, muuttoliikehdinnän ajoittumista, painoa, rasvavarojen määrää, sekä höyhenpeitteen kuntoa muuttavilla linnuilla.

Totesimme, että tutkitut kaksi populaatiota jakoivat samantapaisia syysmuuton piirteitä. Pois lukien vaelluslinnuille ominaiset suuret muuttajamäärien vuosien väliset vaihtelut, syysmuuton piirteet olivat varsin samankaltaiset kuin mitä havaitaan säännöllisillä muuttajilla. Muutonajankohdan mediaanin vaihteluväli eri vuosina oli kaksi viikkoa. Molemmissa populaatiossa myöhemmin muuttavat yksilöt olivat keränneet suuremmat rasvavarat. Syysmuutolla olevat linnut olivat joko sulkasatonsa loppuvaiheilla, tai olivat juuri päättäneet sulkasatonsa. Tulostemme valossa, Pohjois-Euroopan ja Koillis-Aasian pyrstötiaisen populaatiot ovat samankaltaisia muuttokäyttäytymisensä puolesta.

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