

Population Dynamics of Thrushes and Seasonal Resource Partition

O. V. Bourski, E. Yu. Demidova, and A. A. Morkovin

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, pr. Leninskii 33, Moscow, 119071 Russia

e-mail: obourski@gmail.com

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Abstract—Seasonal population dynamics was studied based on long-term observations of four thrush species and their feeding objects in the Yenisei middle taiga. Comparable estimates of dynamics were obtained by combination and mutual correction of data from route censuses, capture-mark-recapture, nest observations, and soil invertebrate censuses. The total abundance of the thrush populations in the breeding area and their energy consumption varied in proportion to the seasonal abundance of resources. The partition of resources was achieved by the ability of some species to use any kind of resources for a long period and the readiness of other species to cope with a short peak of food resource abundance.

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INTRODUCTION

The population fitness in a seasonal environment depends on how accurately annual cycles of activity are inscribed into the course of seasonal changes in the environment. In many organisms, reproduction and mortality approach the population size to concordance with fluctuations in the carrying capacity of the environment. Populations of long-lived species are relatively stable, but they also partly use a seasonal peak of productivity of ecosystems for the most energy-consuming forms of activity (Stearns, 1976; Begon et al., 1986). Passerine bird populations are renewed annually in about half (Paevskii, 1985), and both ways are relevant to them. In them, both the seasonal peak of numbers due to breeding and energy-consuming processes such as settlement, plumage change, food storage, and other means of increasing the likelihood of survival are confined to the favorable period of the year. Severe winter conditions lead to high mortality in populations at high latitudes and, as a consequence, to a relative surplus of resources in other seasons, which favors high fertility (Ashmole, 1963; Ricklefs, 1980, 2000). In the context of a highly seasonal climate, the fluctuations in resource abundance far exceed the ability of their full use by nonmigratory populations. The minimum level of annual resource is a limiting factor, and at the maximum level there is surplus food (Herrera, 1978).

Birds are one of the few animal groups capable of using a seasonal surplus of resources at high latitudes by making long-distance migrations. At high latitudes, severe winter conditions, and thus higher mortality, significantly limit the opportunities for year-round habitation. On the other hand, saturation of the communities at low latitudes leads to intense competition for resources, especially during breeding (Skutch,

1949). All of this apparently created the preconditions for the emergence of seasonal migrations (Cox, 1968, 1985; Greenberg, 1980). The mechanism of the emergence of such behavior is still hypothetical (Berthold, 1993; Salevski and Bruderer, 2007). The proportion of migrants in the European bird assemblages increases to the north in accordance with increasing seasonality (Herrera, 1978), what confirms the theory. However, this tendency is weaker in other regions of the Holarctic (MacArthur, 1959; Mönkkönen and Forsman, 2005).

The length of stay of the species in breeding and wintering area is diverse: differences seem to be related to the abundance of specific food resources (Alerstam and Högstedt, 1982). This is, however, only a general assumption, as the length of stay is difficult to reconcile with the taxonomic proximity of species.

The phenomena of the annual cycle are interrelated, and various phases usually do not overlap in time. Each phase of the cycle is preceded by a period of preparation, often including relocation and the selection of suitable habitat (Noskov and Rymkevich, 2008). The sequence and duration of phases vary on both the interspecific and individual levels. Molting has the most variable position. Depending on migration needs and the availability of resources, molting can take place in the area of breeding and can be carried into the nonbreeding habitat (Jenni and Winkler, 1994; Noskov and Rymkevich, 2008).

The costs of successful completion of a separate phase of the annual cycle may limit the success of the subsequent phases (Norris et al., 2004; Hegemann et al., 2012a, 2012b). The time required to restore the resources of the body reduces the next phase or shifts it to a less favorable season. It can be assumed that natural selection sets the optimal duration of each phase

in which the recovery of the body is effectively resourced by the external environment in accordance with its seasonal change. The alternative hypothesis (Lack, 1954) is that selection sets the timing and duration of reproduction independently, while other needs are adjusted to it and are satisfied within the rest of the year.

The verification of these hypotheses encounters great methodological difficulties. This is primarily due to the inability to measure the availability of resources accurately, especially when different species use the same resource (Hutto, 1990). Determine the identity of the bird to the local population is not easy, because individuals from different populations at different stages of their annual cycle can often be found together. In addition, the assessment of changes in abundance is highly dependent on the method and place of observation. For these reasons, most of the research is limited to the study of only one seasonal phase, usually breeding or migration.

The assessment of population numbers is usually mediated and based on a limited sample, thus inevitably involving a series of assumptions that are difficult to verify. Census methods can be based on different material: one-time audiovisual meetings, findings of nests and observations of nesting pairs, capture, and the tracking of marked birds. Each method has its advantages and disadvantages.

The route census is a type of audiovisual record that is widely used. During the long history of development of the method, perfect methods of introducing amendments for unequal visibility of individuals were developed, the main sources of systematic distortion of estimates were eliminated, and principles for the calculation and reduction of random deviations were elaborated (Ravkin, 1967; Chelintsev, 2000). Introduction of the necessary amendments makes it possible to obtain comparable data for different seasons. At the same time, the quality of the sampling assessment always depends on the number of encountered individuals or their groups (Chelintsev, 2000), such that during periods of low abundance or low visibility of the species it is extremely difficult to obtain reliable data. The possibility of extrapolation of census estimates for the entire population is determined by the representativeness of the traveled route in space and time, which is never absolute. It also increases random deviations of estimates from the true values. Along with statistical "noise," the data are distorted as a result of systematic deviations associated with weather conditions, bird behavior, differences in the experience of the observers, and other causes.

Bird capture is a significantly more labour-intensive method, and its use for census is justified only in conjunction with other tasks. It is associated with the same difficulties as the route census but to a greater extent, since it is poorly representative in space and is more dependent on the activity of birds. Despite this,

it has a number of essential benefits. It is better for identifying poorly observable, in particular, young and migratory birds (Peach et al., 1996). The processing of caught birds in most cases makes it possible to ascertain the sex, age, and the annual cycle phase of individuals. Finally, capture allows banding and individual marking of birds, making it possible to track their movements and reregister them without recaptures. Based on marking and reregistration of individuals, many variants of population analysis have been developed recently (Lebreton et al., 1992; Williams et al., 2002). Along with the numbers, they allow assessment of the survivability and productivity of populations, as well as the levels of emigration and immigration.

A census of the nests and nesting areas is applicable only during the breeding season. This period, however, is of paramount importance, as mature individuals are tied to a specific territory for a long time. Studying the contents of nests provides the opportunity to assess population changes associated with reproduction (Verner, 1985; Verner and Milne, 1990).

The purpose of our work is to establish intraspecific differences in the seasonal dynamics and annual cycles of the four thrush species during their stay in the Yenisei middle taiga and to discuss possible reasons for these differences. We will analyze the dynamics of populations based on long-term studies carried out by all of the above methods. The data from each of them do not have an unambiguous interpretation; they complement each other and work together to provide a more or less complete picture of the processes of interest. The obtained knowledge can be used in the analysis of the annual cycles of other species for which there are fewer data.

MATERIALS AND METHODS

The study area is the neighborhood of the Mirnoe Yenisei ecological station of the Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences (Turukhansky district, Krasnoyarsk territory, 62°20' N, 89°00' E). The materials were collected from 1978 to 2012. For a detailed analysis, we selected four related species that are quite common and distinctive: the fieldfare (*Turdus pilaris*), redwing (*T. iliacus*), black-throated thrush (*T. ruficollis*), and Siberian thrush (*Zoothera sibirica*).

For a rapid assessment of the thrush food supply, 50 Barber traps located in the main habitats were used. They were checked every 10 days from the second ten-day period of May to the end of September of 2011. The biomass was estimated by the size and quantity of each category of invertebrates.

Route censuses of birds were carried out every five days from early May to early October in 1979–1981 and 2010–2011 on a 12-km transect through the valley of the Yenisei. It covered common habitats in a proportion characteristic of the region. Additionally, cen-

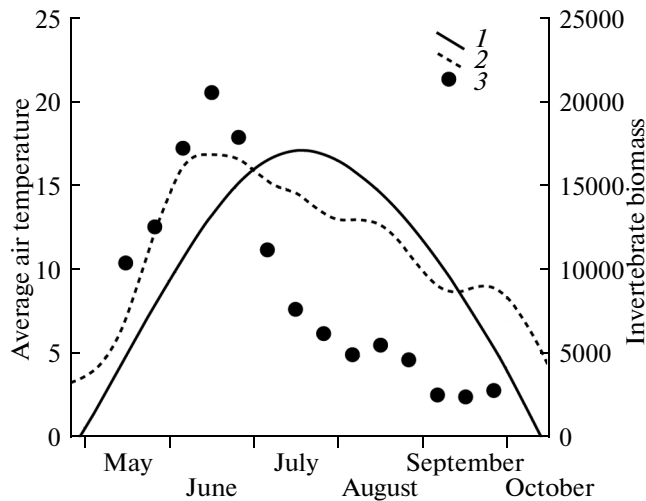


Fig. 1. Seasonal dynamics of invertebrate captures by Barber traps in 2011 against temperature anomaly. (1) Long-term average air temperature; (2) smoothed air temperature in 2011; (3) invertebrate biomass index. Weather data are provided by website Reliable Prognosis, www.rp5.ru.

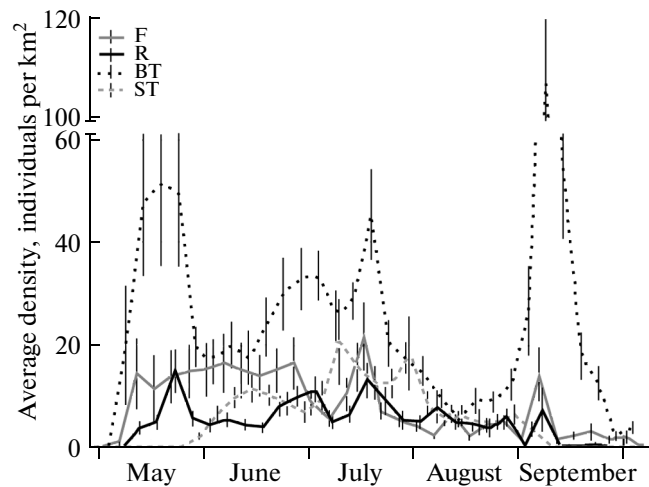


Fig. 2. Seasonal changes in regional abundance of birds on long-term data of route censuses (averages of five-day periods and their standard error). F, fieldfare; R, redwing; BT, black-throated thrush; ST, Siberian thrush.

suses in the richest habitats of the floodplain of the Yenisei were carried out in 2008–2009.

Birds were regularly captured by mist nets on a 50-ha area in the floodplain of Yenisei in 1990–2012. Nets were installed in the markup nodes with an interval of 50 m. In the 1990s, each of the 200 locations was used, but later only 60, which were in the area of greatest concentration of birds, were used. The capture season lasted from early June to the first ten days of September in 1990–1995 or from the end of May to the end of July in other years. Each net worked once per ten-day period from 20 to 12 h of the next day. During the ten-day period, 20–30 nets were opened per day in stages in the same exact order. Mist nets of 10 m in length, 3 m in height, and 14–18 mm of mesh size were used. The captured birds were treated according to standard procedures (Svensson, 1975; Vinogradova et al., 1976), including a semiquantitative description of molting. Birds were marked with a numbered aluminum ring and an individual label of three colored rings.

Nests of the species of interest were sought in the entire area of capture and in some other parts. The identified nests were examined every 2–5 days, with notation of the breeding cycle phase, the number of eggs (chicks), and the individual labels of parents.

Ordinary statistical processing was carried out in the program STATISTICA v. 8.0 (StatSoft, 2008). The survival rate of adult birds and the probability of the successful existence of nests was calculated using the program MARK (Cooch and White, 2009), and the productivity of populations was calculated according to original programs. The survival rate and productivity are used here as auxiliary parameters; the procedure and results of their assessment are considered in more detail separately (Bourski, 2011; Bourski and Demidova, 2011; Demidova, 2011).

RESULTS

Dynamics of Food Resources

Rapid assessment of the abundance of soil invertebrates was carried out within a single season with simple traps (Fig. 1). Unfortunately, 2011 was characterized by an unusually early and warm spring, which had no analogs at least over the past 40 years. Moreover, Barber traps reflect not so much the abundance but rather the mobility of ground-layer invertebrates. For example, a pronounced seasonal peak is mainly due to the massive emergence of the imago of ground beetles. Nevertheless, the biomass peak coincided with the period of maximum temperature and maximum advance of the spring temperature rise. On the whole, this result is consistent with the idea of the growth of secondary productivity of biocoenoses after primary productivity, in proportion to the amount of heat and moisture (Begon et al., 1986; Bogacheva, 1990).

Route Census Data

According to the data of route censuses (Fig. 2), three species occurred in the nesting area at the beginning or middle of May. The Siberian thrush was falling behind for almost a month. Spring migration induced increases in the numbers of birds—a high increase in the black-throated thrush and low in other species. After that, the numbers stabilized at the nesting level. During this period, the abundance of the fieldfare increased as a result of their concentration into a large colony on the census route. With the emergence of chicks as nests were destroyed and the riverine floodplain dried, the distribution of birds along the riverside forest edges was aligning, and the population density in the census band was slightly decreasing.

Table 1. Breeding distribution of populations over main habitat complexes on the transect

Habitat complexes	F		R		BT		ST	
	<i>d</i>	<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>	<i>p</i>
Native taiga (7.00 km)	0.0 ± 0.0	0.1	0.3 ± 0.1	3.4	9.5 ± 1.7	24.9	0.1 ± 0.1	0.6
Secondary forests (4.25 km)	0.4 ± 0.3	1.1	0.3 ± 0.1	2.5	42.3 ± 10.0	67.4	1.1 ± 0.6	4.4
Floodplain (1.15 km)	146.5 ± 27.8	98.9	44.2 ± 5.5	94.0	18.0 ± 4.7	7.8	85.3 ± 8.8	95.0
Average	13.7 ± 2.0		4.4 ± 0.5		21.5 ± 2.3		8.3 ± 0.9	

F, fieldfare; R, redwing; BT, black-throated thrush; ST, Siberian thrush; *d*, density (individuals per 1 km²); *p*, proportion in population size, %.

The postnesting increase in the numbers started in late June and reached its peak by mid-July. It was no more than a twofold increase and was not always monotonous. This was apparently due to the poor visibility of fledglings, differences in the pairs for terms of successful nesting, and the quick migration by some young birds upon becoming self-reliant. Against the background of breeding, the population number was increasing at the expense of postnesting migrations, which was highly pronounced in the black-throated thrush in the second half of July. It is noteworthy that the growth of numbers in this species outpaced the emergence times of local broods and could have indicated the emergence of the first birds from southern populations migrating to the north.

At the turn of July and August, the number of all of the species was dramatically decreasing. This decline could have been caused both by departure or movement from the nesting area and the secrecy of birds that began intensive molting. The occurrence of all of the species remained at a low level until the end of the molting season.

The Siberian thrush and redwing were disappearing from the area of observation in early and mid-September, respectively. The abundances of the fieldfare and black-throated thrush, on the contrary, were increasing and peaked in mid-September in connection with the autumn migration. In this case, the number of black-throated thrushes was significantly higher than the summer and spring levels. Both species left the nesting area by mid-October.

In addition, route censuses on the transect crossing the valley of the Yenisei showed that the species significantly differ in the use of habitats in the breeding period (Table 1). While the populations of the fieldfare, redwing, and Siberian thrush are almost entirely concentrated in the floodplain, the black-throated thrush nests mainly in secondary forests in old burned-out taiga areas.

Data from Nesting Observations

Visible changes in the numbers from the censuses reflect the effect of a complex of reasons. To separate them, a more detailed study of the floodplain popula-

tion fragments was carried out. Additional data on the nesting of the black-throated thrush were collected on burned-out areas.

The contents of the found nests were used to define the dates of the first egg laying (Fig. 3). All of the species were characterized by a modal five-day period of the beginning of layings, suggesting the synchronous start of nesting by most of the pairs. In data collected over many years, deviations of the beginning of nesting from the modal date are largely related to phenological characteristics of the year. Therefore, synchronicity within one season is even higher.

Nesting of the Siberian thrush lagged behind the others by more than ten days. The reproduction of the fieldfare, Siberian thrush, and black-throated thrush in major habitats was strictly monocyclic. The redwing and black-throated thrush in the floodplain began the second normal laying at the end of June.

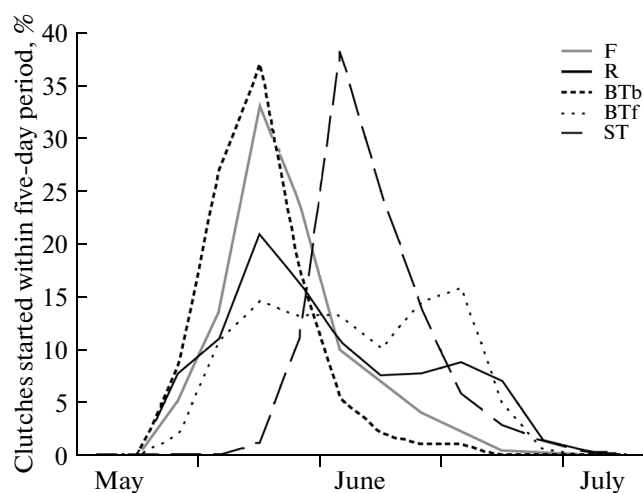


Fig. 3. Dynamics of laying starts in found nests. Notation is as in Fig. 2. Nests of black-throated thrushes are divided into two samples: BTb, in burned-out areas; BTf, in floodplain. Sample size: F, 740; R, 612; BTb, 158; BTf, 92; ST, 495 started clutches.

Table 2. Survival rate and productivity of populations within a year

Species (population)	Survival rate of adults within a year			Number of fledglings per season per pair		
	<i>n1</i>	mean	confidence interval	<i>n2</i>	mean	confidence interval
Fieldfare	1579	0.384	0.330–0.443	740	3.40	3.35–3.45
Redwing	1105	0.347	0.311–0.386	612	4.25	4.16–4.34
Black-throated thrush (floodplain)	836	0.400	0.338–0.465	158	3.96	3.79–4.13
Black-throated thrush (burned-out areas)				92	4.20	4.03–4.38
Siberian thrush	2494	0.489	0.451–0.526	495	2.71	2.64–2.78

The average survival rate was obtained by combining the estimates for the age ratio (Bourski and Demidova, 2011), where *n1* is the number of individuals, and the estimates for recaptures (Bourski, 2011) and *n1* is the number of annual intervals of observing an individual. The number of fledglings per season was defined in the simulation model of the nesting season (Demidova, 2011; Demidova and Bourski, 2012), where *n2* is the number of nests.

Calculation Based on Demographics

In the previous studies, we have established the survival rate of adults in the populations and the number of fledglings per bird pair (Table 2).

According to the data in Table 2, we calculated the expected changes in the population sizes by making the following assumptions: nesting individuals make up 100% of the nesting population; long-term dynamics is stable, so that replenishment of the nesting population at the expense of yearlings compensates adult mortality; adult survival rate does not change over seasons; the ratio of young and adult birds during the year decreases linearly; the distribution of dates of the fly-out of young birds in the population is the same as in the nests tracked in nature on the eve of a fledging.

When calculating the population number of the black-throated thrush, we assumed that 5% of the birds nest in the floodplain, while the remaining 95% nest in the burned-out areas and similar habitats

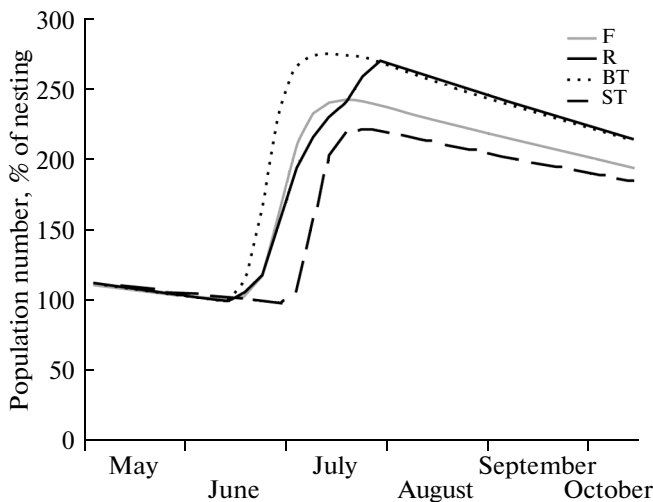


Fig. 4. Expected changes in population numbers as a result of reproduction and mortality. Notation is as in Fig. 2.

(Bourski, 2002). The available materials and formed assumptions are sufficient to calculate relative changes in the population size during the year (Fig. 4).

The jump in the number, which is associated with reproduction, was at first noted in the black-throated thrush, then in the redwing and fieldfare, and, later than others, in the Siberian thrush. The growth in the number of redwings lasted much longer, covering this period in the other three species.

Calculation According to Capture Data

To estimate the population size according to the capture data, one must divide the number of captured birds by the probability of their capture. This probability may depend on the species, sex, age, and individual annual cycle phase of the specimen, which affects its physiological condition and mobility.

The probability of capture of local birds was calculated on regular captures by nets located in the same position and operating for 16 h with an interval of 10 days from mid-May until the first ten days of September. For each day of capture, we counted the number of birds that were ringed in advance and caught or encountered after that day, which were thus reliably present in the area of capture. The proportion of birds captured that day was considered the average probability of capture (at least one time) within this ten-day period. In statistical calculations, the proportions were transformed into $\arcsin \sqrt{x}$ to normalize the distribution, and the results were again expressed as proportions of reverse transformation. Assuming that a random (Poisson) hit can be repeated on the same day, one can convert the probability of capture *p* into the average number of captures $P = -\log(1 - p)$.

The average probability of the registration of adults was determined by captures on a 50-ha site in June and early July. Intraspecific differences in the breeding period were more than doubled (Fig. 5) and explained 63.3% of the variation of the transformed indicators of probability. Siberian thrushes were captured most

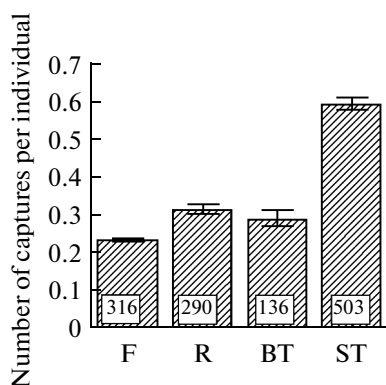


Fig. 5. Species differences in the average number of captures of an individual that reliably lives on the territory furnished with nets every 50 m over one 16-hour capture session during the nesting season (from June 1 to July 10). The boundaries of the 95% confidence interval and the number of individually tracked individuals are specified.

effectively because of their habit of flying in thick bushes close to the ground.

Among the birds whose nests were within the range of capture and whose breeding phase was known, the regression residuals of the probability of capture were studied for the dependence on the sex and nesting phase (Fig. 6). Both factors are significant ($p < 0.01$) and explain 11.9% of the variance.

Assessment of the probability of capture of young birds is hampered by the fact that fledglings at first are not very active; they rarely get into nets and then move beyond the area of capture. Nevertheless, according to 742 observations, when marked individuals of a known age were reliably in the control area before and after being captured, it was found that the frequency of their registration reaches the adult level after 40–50 days (Fig. 7). The probability of being captured grows according to a sigmoidal curve; in fledglings of the Siberian thrush, it happens somewhat faster than in other species. Logistic regression with coefficients that depend on the age and species explains 69.3% of the variation of the capture rate among young birds.

The probability of capture of adult birds after nesting is reduced because of molting. We assumed that it decreases sinusoidally and increases again as the plumage gets replaced symmetrically with respect to the date of mid-molt. On this basis, the data on symmetric stages were combined: we actually analyzed changes in the arcsin-transformed value of the probability of detection as approaching the top of molt. The method of least squares (STATISTICA v. 8.0, Nonlinear Estimation: $R^2 = 0.300$) was used to select the parameters of the sinusoidal function; the estimation of significance was provided (Fig. 8).

During molting, the detection probability significantly decreased in all of the examined species ($t > 6.5$; $p < 0.01$ for all comparisons), but it was much weaker in black-throated thrushes than in the others ($p < 0.01$). This result indicates a difference in the species regard-

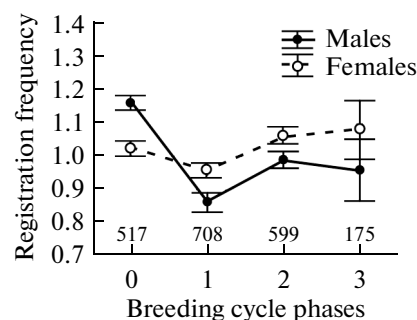


Fig. 6. Effect of the nesting cycle phase and sex on the frequency of registration (relative to the mean) of an individual that nests in the area of capture. Phases (decades): 0, nest construction and egg laying; 1, incubation; 2, hatching and feeding; 3, fledging and guarding of the brood. The boundaries of the 95% confidence interval and the number of tracked individuals are specified.

ing plumage change strategy. The extensive molt of the black-throated thrush is stretched over a longer period and is not accompanied by a significant decrease in mobility, thus allowing molt to be combined with migrations. The intensive strategy of the other thrushes makes it possible to reduce the molting period but prevents movement, at least in the middle stages.

Finally, the assessment of the population dynamics took into account all individuals of the selected species caught over nine years of regular capture on the area of 50 ha in the floodplain of Yenisei. They were classified for their belonging to the above categories, and each of them was adjusted for the probability of being caught within a ten-day period. The results are combined into

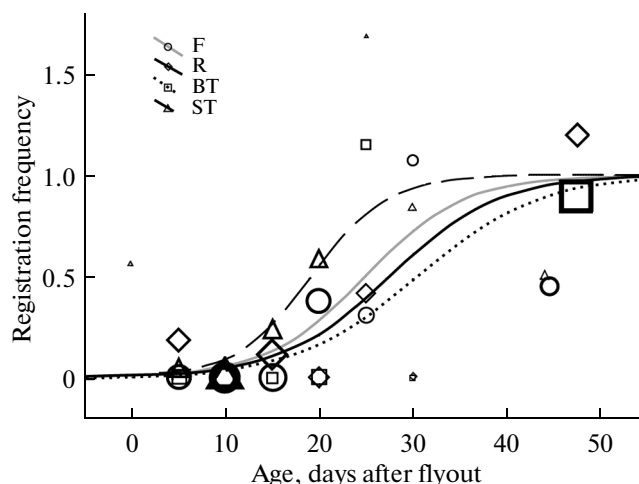


Fig. 7. Registration frequency of young birds (as compared to adults) depending on age. Logistic regression coefficients were obtained by the method of least squares (STATISTICA v. 8.0, Nonlinear Estimation). Area of icons is proportional to the number of tracked individuals (F, 200; R, 218; BT, 60; ST, 264).

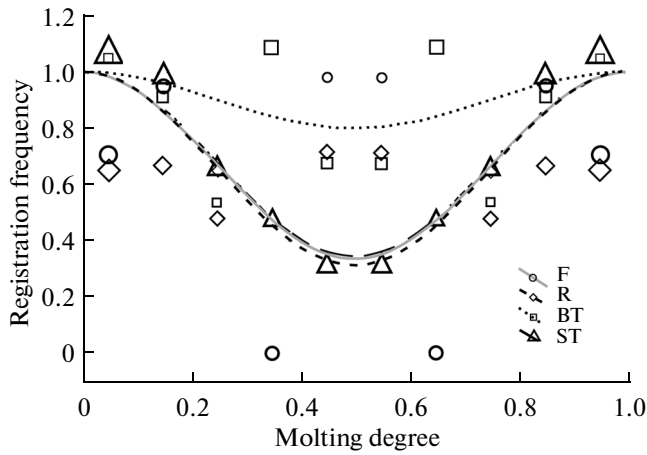


Fig. 8. Frequency of detection of an adult during molting (relative to the breeding level) depending on the molting score (molted feathers proportion). The area of the icons is proportional to the number of tracked individuals (F, 82; R, 80; BT, 104; ST, 254).

two age groups and averaged for the years of capture (Fig. 9).

Fieldfares spent an average of eight ten-day periods in the nesting site and left it after molting. Young birds left the birthplace ten days earlier, at the age of about 30 days after fledging. The actual estimates are in good agreement with the calculated ones, so that the both confirm the absence of significant movements in this period. After the first decade of August, however, the

birds did not disappear from the area of observation but rather migrated over a wide range of habitats, including the breeding areas. The decrease in the numbers provides a reason to believe that these migrations from the very start were directed towards the wintering grounds and included individuals from northern populations.

Redwings stayed in the breeding areas an average of nine ten-day periods. The median of departure of young birds occurred ten days earlier than that of adults. The departure dates are probably subject to considerable individual variation, depending on the breeding success in adults, because of the large age differences in young birds. Immediately after the appearance of broods, the numbers of young increased as a result of migrations from the surrounding areas, but it was no more than a twofold increase. On average, young redwings stayed in the control area for one or two ten-day periods longer than young fieldfares.

The breeding population of the black-throated thrush in the floodplain was formed, as in the preceding species, by the beginning of the third ten-day period of May. Unlike them, this population continued to grow with new pairs going to restart clutches after reproduction. However, the bulk of immigrants consisted of broods, the quantity and often the age of which exceeded the capabilities of local breeding. By mid-July, these birds became self-sufficient, they were moving in a northerly direction, and their number increased tenfold. By August the movements weak-

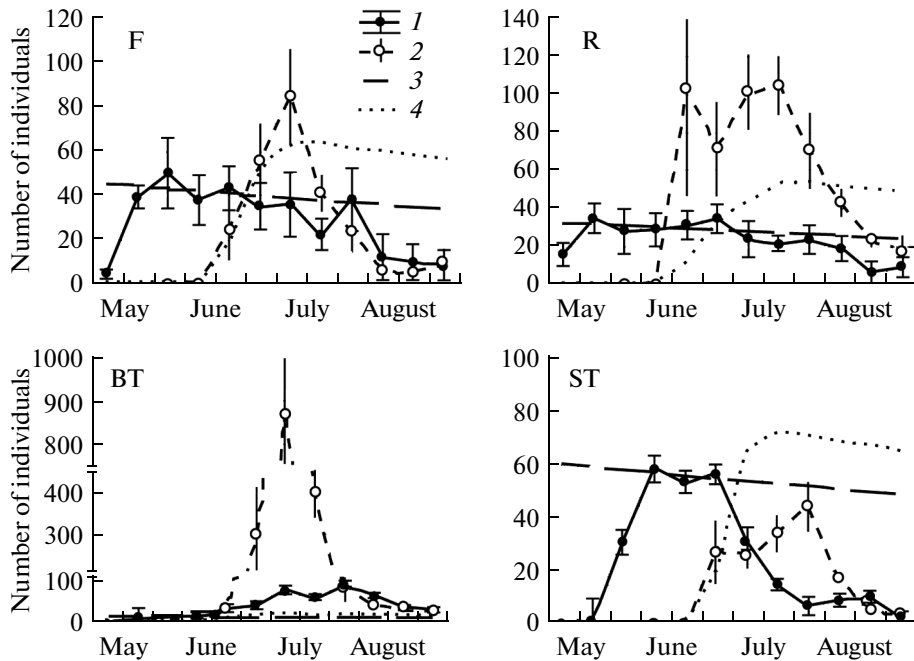


Fig. 9. Population seasonal dynamics (individuals per area of 50 ha) and confidence interval of estimates according to data of captures for 1990–1998: (1) adults; (2) young birds. The expected number ((3) adults; (4) young birds) is calculated based on estimates of the nesting level, productivity and survival. Sample: F, 719; R, 1075; BT, 1978; ST, 1802 individuals.

ened, but the number of both young and adult birds was much higher through the end of the observations than the level that was possible from local breeding. Intensive use of the floodplain habitats lasted no less than thirteen ten-day periods.

The Siberian thrush was characterized by the shortest stay in the breeding grounds: the medians of arrival and departure of adult birds are separated by only four ten-day periods between the beginning of June and mid-July. A small portion of the population delayed until the end of molting and in this case stayed near the nesting sites for about nine ten-day periods. Young birds were massively departing two ten-day periods later than their parents, staying near the nest for 30 days. Due to the hasty departure of young birds, their number was always significantly below the expected level of total productivity of the population.

In general, captures provide too high numbers of the adult population, even after adjusting, which suggests the presence of birds on passage or local non-breeding birds. Conversely, the number of young birds is generally lower than expected for the results of reproduction, because at any given time some birds have not yet reached self-sufficiency and they do not move not actively enough to get caught in nets. At the same time, other young birds have already managed to change plumage and migrate from the area of birth. Captures undoubtedly show the immigration of black-throated thrushes into the floodplain and the early departure of Siberian thrushes.

Local Movements

Evaluation of the seasonal dynamics of local populations is complicated by the flow of transit birds. Movements of various scales affect the population number increase resulting from reproduction. A judgment can be made about these movements using the dynamics of bird distribution over a profile crossing the area of capture from the bank of Yenisei to the rear of the floodplain (Fig. 10). These local movements indicate a change of habitats and the nature of the stay of birds.

The distribution of model populations across habitats of the Yenisei floodplain changed over the annual cycle phases. When breeding, fieldfares preferred edge forests of the riverine bank. Black-throated thrushes inhabited forests of the central floodplain. Siberian thrushes occupied both of these habitats, while redwings also readily nested in mature willow forests of the low floodplain.

During the postbreeding dispersal, the preferences of all of the species in one way or another shifted to the low floodplain. These changes were minimal in the Siberian thrush and stronger in the fieldfare, but they did not extend beyond the reproductive capabilities of the model population. The number of redwings in the low floodplain doubled, assuming immigration from adjacent areas. The number of black-throated

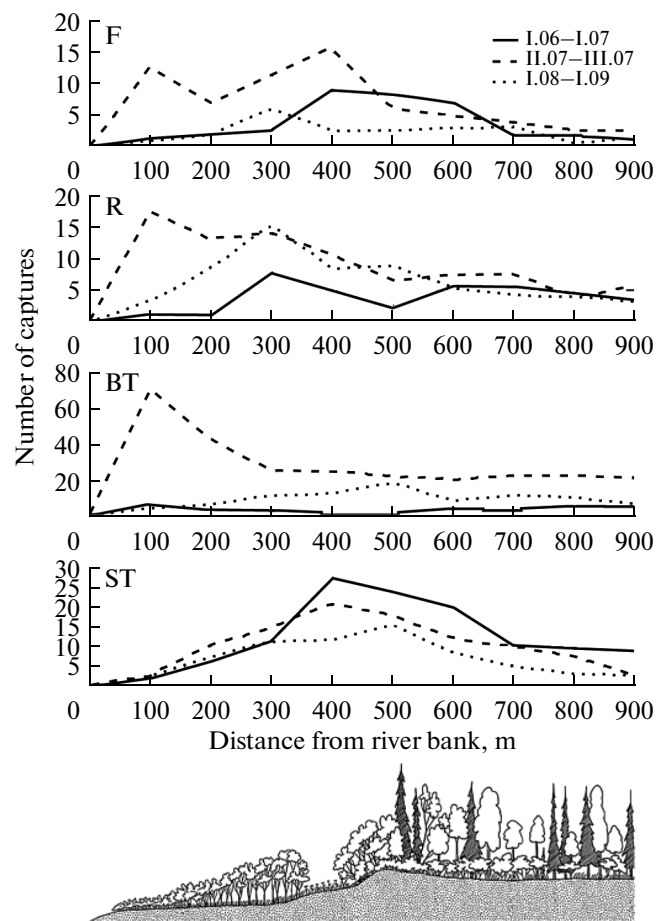


Fig. 10. Distribution of population density (captures per 100 net-days) along the landscape profile across the Yenisei River floodplain during the breeding season (I.06–I.07), dispersion (II.07–III.07), and fattening (I.08–I.09).

thrushes was manifold increasing from the end of June at the expense of nonindigenous birds. They were concentrating in young willow forests along the riverside and were moving to the north.

In August and early September, the distribution changed again and was more like the breeding one. Frontal willow forests no longer enjoyed preference. The abundance of fieldfares and redwings became the highest in the mature willow forests. Black-throated and Siberian thrushes occupied the habitats of the floodplain levee and, to a lesser extent, habitats of the central floodplain.

Long-Distance Movements

Censuses on the routes covering the entire regional spectrum of habitats (Fig. 2) made it possible to track seasonal changes on a larger scale.

The three considered species were active mainly in the habitats of the developed floodplain of Yenisei. Some pairs of redwings nested in the valleys of streams and in the richest secondary forests. Fieldfares were

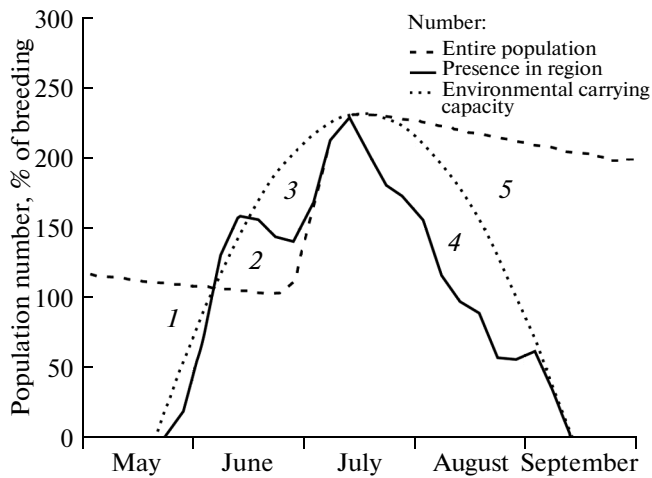


Fig. 11. Seasonal use of food resources on the example of the population of the Siberian thrush. Differences between the expected and actual estimates of numbers are due to arrival (1), passage (2), additional expenses for reproduction (3) and molting (4), and departure (5).

encountered widely but in small amounts in the forest edge habitats outside the floodplain during the spring and pre-migratory movements. Siberian thrushes outside the floodplain were noted sporadically and only during the flight.

The fourth species, black-throated thrushes, was breeding mainly in taiga burned-out areas and secondary forests of watersheds. In mid-summer, however, the birds were leaving their breeding habitats, spreading to other sites and migrating massively. The route censuses revealed the following features of the behavior of the local population: immediately after one nesting cycle the birds were leaving their breeding habitats in the taiga burned-out areas; from mid-summer the range of used habitats expanded; abundance of the species increased sharply near the banks of the large river regardless of the habitat; the proportion of birds registered in the flight increased in the riverside habitats. According to the data of captures, individuals migrating in a northerly direction were predominant. In addition, the proportion of individuals with features of the red-throated thrush (*T. ruficollis ruficollis*), which were unusual for the breeding population (*T. ruficollis atrogularis*), was increasing in the post-breeding period. These findings confirm long-distance movements of birds from south to north for the use of resources available in the second half of the summer.

The concentration of birds along the landscape borders that create a temporary barrier for the movement, already indicates the fact of long-distance movements. This concentration in the second half of the summer is also typical of other species, which may be associated with the post-breeding dispersal. However, as a result of these movements, the number of fieldfares reduced several times (Fig. 2), therefore we

suggest it as a pre-departure movement in a southerly direction.

The fact of the departure in the form of a nocturnal migration did not cause significant changes in the distribution of birds. The above observations allow concluding that the departure took place without any prior movements in the Siberian thrush and largely in the redwing, as well as in part of the fieldfare population that was staying in the breeding area until October. In September, black-throated thrushes, judging by the censuses, were involved into movement to the south, gradually passing into the departure.

In the spring, at the time of arrival, the species again had different tactics. Siberian thrushes and redwings appeared on their breeding territories immediately after arrival. Black-throated thrushes and especially fieldfares did not occupy them at once, spending considerable time in movements over the region. For example, flocks of fieldfares used to appear in the meadows around the Mirnoe village on May 6 and stay there until the end of the month (Rogacheva et al., 1991). They occupied the nesting sites in the floodplain not earlier than the third decade of May. In case of cold snaps and snowfalls, pairs were leaving unfinished nests, flocked together, and moved back to the meadows for a few days. Such behavior was also observed in black-throated thrushes.

DISCUSSION

Population Dynamics and Environmental Carrying Capacity

As was shown by observations, animal food resources vary gradually during the year, following a sinusoidal rhythm of received solar radiation. By mid-July the average daily temperature reaches a seasonal maximum; the primary production of ecosystems passes a seasonal peak, having created a plant biomass, the use of which soon leads to a peak of secondary production and provides a maximum abundance of food available for thrushes. It is then followed by a steady decline in their stocks. General ideas about the seasonal dynamics of the population of the migratory species of birds intuitively paint us a step curve: spring arrival—nesting “plateau”—reproductive rise—post-breeding “plateau”—overall departure.

The above facts do not support that notion. The seasonal peak in abundance of each population occurs at maximum productivity—in mid-July. The use of resources increases during the season and then decreases gradually, reflecting the seasonal changes in productivity of habitats. This correspondence is provided by adaptive changes of the annual cycle, which are clearly traceable on the example of the population of the Siberian thrush—the most closed among those studied (Fig. 11).

Differences in the estimates of abundance and the expected capacity of the environment, besides statisti-

cal errors, are due to additional needs of birds in each phase of the annual cycle. During passage, the population uses the resources of the territories that lie along the route of the flyway. In turn, after arrival at the breeding site, they have to share the resources of their territories with the passing northern populations. During the breeding period, birds expend extra energy for territory protection, nest construction, the formation of reproductive products, incubation, and feeding of the nestlings (Dol'nik, 1995). These expenses, including food for chicks, gradually increase until midseason in accordance with the growth of productivity of ecosystem. In the post-breeding period, food resources are required to cover the expenses of molt. Birds compensate the decrease in the stocks, which is gradual at first and then sharper, by the time spent on foraging, which can be prolonged after breeding is finished. In the end, the lack of food reduces the quality of the conditions of stay in the breeding area in comparison with the wintering area, such that it becomes a categorical reason for departure. In particular this limitation is expressed most sharply in the Siberian thrush: it leads to such adaptations of the annual cycle as the early departure of most of the adult birds prior to molt and the accelerated molting of juveniles.

Intrapopulation differences among individuals in time required for passing the annual cycle phases explain the gradual character of changes in the numbers. As is known (Paevskii, 1985), many species differ in arrival time between males and females, yearlings, and older birds. Within each cohort, the timing is ranked by the tolerance of individuals to adverse conditions. Stronger individuals, arriving first, increase their chances of productive breeding, while those that are weaker lag behind and thus reduce the likelihood of death of extreme conditions, so selection supports individual differences in the time schedule. The same is probably typical for departure dates. Individuals breeding the first time can also reduce the breeding season there by prolonging the period of highest survival and increasing the likelihood of successful breeding in the future. Thus, the gradual character of changes in the population size in the breeding area can be achieved by natural selection at the individual level, allowing the population to gradually "embed" into seasonal changes of conditions. For the first time, our results appear to provide an unbiased estimate of the decrease in the bird population size during the departure period. They strongly support a very early start and a gradual development of the process long before the time when the last individuals leave the nesting area.

The obtained results make it possible to provide approximately similar curves of seasonal changes in the carrying capacity of the environment for other species, given that they use resources not only to maintain the population size but also for other purposes. These curves are difficult to construct because the populations are closed to a lesser extent, as it fol-

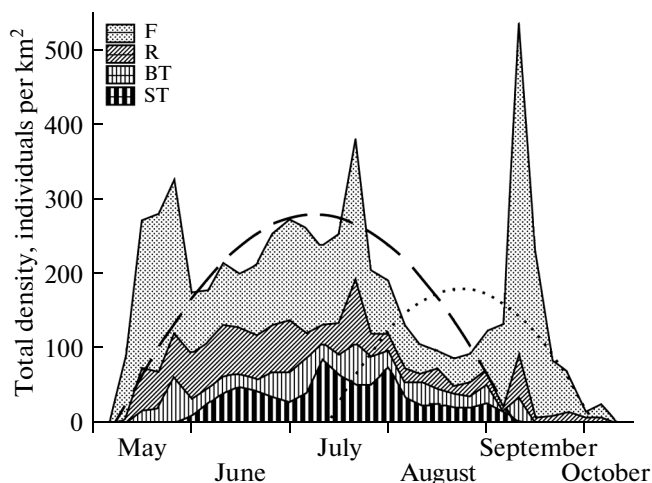


Fig. 12. Seasonal subdivision of regional food resources available for thrushes in middle taiga for the four studied species. The dashed line schematically shows abundance of available invertebrates, and the dotted line shows ripening of berries. The density of species populations and notation are as in Fig. 2.

lows from the analysis of the breeding distribution (Table 1) and post-breeding movements (Fig. 10). However, we can obtain a general idea of the dynamics of their resources using the census data, making some adjustments for the probability of detection (Fig. 12). First, as in captures, molting birds are less likely to get into the census band, and their omission is not compensated by a decrease in the detection range (Chelintsev, 2000). Secondly, migration peaks of diurnal migrants cause overestimation of the dynamic population density, because censuses are carried out in the morning, when movements are the most noticeable. Aside from this, the census data are consistent with other estimates while being representative for the region as a whole. They show that discrepancies in the carrying capacity of the environment and the number of users are small; moreover, for the magnitude and time they match population expenses on activity associated with reproduction and molting.

Interspecific Differences

The tolerance limits for a low abundance of food obviously differ greatly between the studied species, which determines the duration of their stay in the region. As compared with the Siberian thrush, other species are much less demanding in this respect. The feeding habits of the redwing allow it to winter in a much harsher climate than the wintering grounds of the Siberian thrush. The same features make the redwing able to arrive earlier, maintain the balance of the population at the expense of a long reproduction, and to stay longer in the breeding area. The stay of the fieldfare is extended probably as a result of feeding on berries in late summer and the consumption of animal

food in open habitats unsuitable for breeding in spring. During these periods, it is not reproduction but rather a decrease in mortality that has a positive effect on the population balance. Therefore, selection should favor a long stay in the breeding area for the of species with a higher mortality in the winter area. The largest range of conditions is suitable for the black-throated thrush, which switches to feeding on berries in the second half of summer and not only disperses over all the habitats but also starts long movements within its breeding range. In spring, its diet apparently consists of last year's berries, until they are replaced by invertebrates from the first glades in taiga burned-out areas, where snow melts earlier and conditions for breeding appear.

The food resources of thrushes are generally similar (Ptitsy..., 1954; Clement and Hathway, 2000), but their availability for the species differs. Seasonal changes in their abundance are so large and rapid that each species is able to use only part of their seasonal range (Fig. 12). The major difference between the thrush species in the quality of preferred resources presumably lies in the duration of their guaranteed availability. The existence of the black-throated thrush and fieldfare is based on the consumption of vegetable food. Taiga berries and bird cherry extend the length of stay of the black-throated thrush in the breeding area for the entire snow-free period—more than five months. The fieldfare, according to our observations, stays for a long time when the harvest of rowan is high, but usually it migrates in advance to areas with milder winters. In the breeding period, between the old and the new harvest, these two species shift to feeding on invertebrates (earthworms, insects, etc.). Reproduction and the seasonal population peak fall within the period of the availability of this food. The abundance of soil invertebrates, however, is excessive in the summer and allows the existence (stay) of other consumers. The redwing, being a more carnivorous species, stays at the nesting site for more than four months. But at the peak of seasonal productivity of ecosystem, the reproduction of the redwing also is not as fast as the increasing abundance of invertebrates. The excessive food is consumed by the Siberian thrush, a tropical migrant with high demands for the quality of resources and the shortest stay in the breeding habitat. Of course, in the middle of the season, its reproduction also lags behind the increase in the availability of resources. However, this abundance is not long enough to provide a complete breeding cycle to an even more specialized species of birds.

Thus, the prolonged stay of thrushes in the nesting area suggests mixed feeding. Feeding mainly on animal food provides for the moderately long stay of a species that is ready to live on scarce resources in spring and autumn. A species demanding the abundance and quality of feed is provided with it only during the seasonal peak. As a result, pronounced seasonality allows joint use of common resources by various species. Some of them easily tolerate the lack of

resources while there is a possibility of their long-term use. Other species are adapted to short-term use of the same resources as they are found in abundance.

Productivity and its dynamics differ in habitats. We assume (Bourski, 2002) that taiga forests are characterized by a relatively flat dynamics, whereas the seasonal drop in productivity is more pronounced in burned-out areas overgrown with small-leaved saplings. Floodplain habitats have the highest productivity and its seasonal peak value. Therefore, species with short-cycle summer activity are found mainly in floodplain habitats with a particularly high level of productivity and seasonal peak.

Ways to Adapt to Pronounced Seasonality

In the case of coincidence of individual phases, the population size in the breeding area would have changed stepwise: at the time of arrival, the flyout of chicks from nests, and especially the departure. We find a significantly different picture in each species. First, the “steps” of changes in the numbers are blurred by individual variation. A significant contribution to the variety of timing is introduced by a “decision” about departure before or after molting, probably depending on the result of breeding. Individuals who have not succeeded by the end of the fertile period may leave the area before molting. Successful parents usually end up feeding the brood much later, at the beginning of molting, and are forced to postpone the departure until it ends or to suspend molting at the early stages. These three possible alternatives have their own advantages and can stretch the departure of the population for two to three months. Second, downward deviations in the numbers from the resource abundance account for the additional costs of food energy for reproduction and molt. Third, the fly-over of northern populations may also smooth the changes in the resource consumption rate. Finally, the use of the local berry harvest can be stretched or postponed to a more convenient time in the annual cycle. Thus, seasonal changes in the population size are defined by resources not only in moments of arrival, the peak of breeding, and departure, but during the entire period of stay in the breeding range.

The pronounced seasonality results in the short duration of the seasonal productivity peak persisting at the same level, which is possible under the increasing continentality of the climate. What features of the annual cycle contribute to survival in such conditions? Let us imagine that the reproductive parameters of the species (clutch size, renesting ability, etc.) have been formed in the breeding range lying mostly within an area with temperate seasonality. Under increasing seasonality, the population growth would lag behind ecosystem productivity growth, which is why there appears an excess of unused resources at the peak of the season. On the other hand, the duration of the breeding season will decrease, the population size will

be reduced, and subsequently the excess of resources in midseason will become more noticeable. The population size of such a species will be limited to the proportion of resources that are available for a long period. In our example, these features characterize the redwing population inhabiting the rich floodplain habitats.

The use of short-term resources is possible for species that can compensate for annual mortality within a short breeding season; these species are tropical migrants characterized by a high survival rate during the year. Species that stay in tropical communities for most of the year are adapted to high levels of resource abundance and intense competitive relations that lead to specialization (Morse, 1971). Exactly such a situation is created for a short period at high latitudes under increasing climate continentality, where the productivity of the richest ecosystems or their components may exceed tropical analogs. This creates the prerequisites for it to be inhabited by tropical migrants. Having relatively high feeding specialization and competitiveness, these species, like the Siberian thrush, can penetrate far to the north through the richest habitats.

Another means of using the seasonal excess of secondary production of ecosystems—the ability to survive most of the year via the consumption of less calorie vegetable food—is found in the black-throated thrush and fieldfare. It makes it possible to extend the stay in the breeding range before and after the peak abundance of invertebrates and to maintain population balance by reducing the mortality rate. Changing the diet also likely involves a loss of specialization and a decrease in the competitiveness and efficiency of resource use. At the same time, it facilitates development of mobility, seasonal habitat change, wide movements, search for ephemeral resources, and wintering in a relatively harsh climate. Obviously, this path is more versatile in high latitudes, where higher seasonality reduces the productivity of ecosystems.

Of course, the balance of the number and the carrying capacity of the environment does not mean that the population completely consumes all potential food as soon as it appears. When food is abundant, birds spend only about 2 h per day for feeding, but this time increases manifold at critical periods (Dol'nik, 1995). Studies have shown that insectivorous birds reduce the prey population only by a few percent (Korol'kova, 1966). However, this food is the most accessible and nutritionally valuable. Population growth is likely to cause the birds to take less accessible and valuable food, which will inevitably increase the search costs and will subsequently reduce the survival rate and productivity of the population. Thus, regulation of the numbers by density-depending factors maintains a relatively low level of consumption in the equilibrium population. A heterogeneous environment complicates spatial expansion and reduces the numbers below the equilibrium point. In a harsh and unstable climate, the gap between the numbers and abundance of resources increases. Pronounced seasonality

increases this gap even more. Nevertheless, over an evolutionarily significant time, any population repeatedly faces regulation depending on the abundance of resources in all seasons. Selection fits the population dynamics to seasonal changes in the direction most favorable for the species in accordance with the rest of its adaptations. Therefore, the peculiarities of species adaptation to the seasonal dynamics of the same resources are different in thrushes.

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