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Kapitonova L.V.,* Formozov N.A., Fedorov V.V., Kerimov A.B., and D.S. Selivanova (2012) Peculiarities of behavior and ecology of the Great tit *Parus major* Linneus, 1758 and Japanese tit *P. minor* Temmink et Schlegel, 1848 as possible factors of maintaining the stability of species-specific phenotypes in the area of sympatry and local hybridization in the Amur Region // *Far East. J.Orn.* 3: 37—46.

SUMMARY

This paper discusses the ecological factors that affect the populations of the Great tit (*Parus major*) and Japanese tit (*Parus minor*) in different parts of their area of sympatry and hybridization in the Amur region. The identified factors exert their effects in different directions and strength in different parts of the vast area of sympatry of these two species. It can be assumed that they have a significant effect on the maintenance of species-specific phenotypes of the great and Japanese tits.

The referred figures and tables are in the original article in Russian, pp. 37—46

Animal species, as well as any biological systems, are characterized a finite existence. They originate, have certain periods of formation, flourishing, and decay and eventually extinct. Mayr (1971) stated that the morphological separation of forms that is not accompanied by reproductive isolation is an index of incomplete speciation. However, reproductive isolation is also likely to occur in a certain period of life of a species and, apparently, has its own characteristics and stages of development.

The fact of paraphilia in these taxa (Kvist et al., 2003) is important for understanding the situation of a secondary contact as well as local and occasional hybridization between the Great and Japanese tits in the Middle Amur Region, because these species are not closely related.

In our case, we have two already separated forms of superspecies *Parus major*, which, having come into a secondary contact, demonstrated a clear absence or weakness of their pre-zygote isolation factors. However, an intermediate hybridogeneous population between has not formed either.

More then that, as arise from our researches, the phenotypic species-specific features tends to increase within zones of relatively long-term secondary contact and proportion of individuals having a hybrid origination tends to decrease here in comparison with such occurred in the relatively young hybrid zones (Fedorov et al., 2009). Therefore understanding of both factors which stimulate hybridization in the earlier stages of contact and also ones keeping the relative isolation in the late stages contact looks important.

This paper focuses on the possible role of some ecological and ethological distinctions between the Great and Japanese tits in maintaining the species-specific phenotypes.

When studying the area of sympatry of the Great tit *Parus major* Linneus, 1758 and the Japanese tit *P. minor* Temmink et Schlegel, 1848, which occurred as a result of opposite radiation of these species, facts of their local hybridization were revealed (Smirenskii, 1977). Later, A.B. Kerimov and N.A. Formozov (1986) established a 10% (of the number of all pairs with the involvement of phenotypic *P. major*) level of formation of mixed pairs of two tit species in isolated contacting

*E-mail: < kapitonova66@yandex.ru>
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populations inhabiting the western slope of the Lesser Khingan Range (village Pashkovo, Jewish Autonomous Region (hereinafter, JAR)), the area where the species supposedly met for the first time. Later, A.A. Nazarenko et al. (1999) using a model area (village Birakan and its immediate vicinities) and the results of studies performed during six seasons (1991–1996), demonstrated a steady and «alternative» type of cohabitation of these species in the given area and, despite the unproven presence of mixed pairs, described two types of hybrid individuals and the existence of «vocal aberrants». They also showed that the situation in Birobidzhan in those years was radically different: an intense hybridization and displacement of the Japanese tit from the city were observed.

The area of sympatry occurred about 100 years ago on the territories of the Amur Region that were recently developed by humans (Smirenskii, 1986; Nazarenko et al., 1999). A.A. Nazarenko et al. (1999) identified three main parts in it, differing in the duration of contact between the two forms. Subsequently, on the basis of the results of molecular genetic studies, their boundaries were refined (Fedorov et al., 2006). The western part included the area from the southern tip of the Amur-Zeya Plateau to the east to the Bureya River; the central part encompassed the area from the Bureya River to the western slope of the Lesser Khingan Range inclusive; and the eastern part comprised the area between the eastern slope of the Lesser Khingan Range to the eastern boundary of the home range of P. major (fig. 1). Currently, the area of sympatry is dynamically expanding mainly due to the radiation of the Great tit to the east. In the 1990–2000s, new areas of sympatry with confirmed hybridizing emerged and continue to form today outside the three main parts described above (Kapitonova et al., 2011; Kapitonova, 2012).

MATERIALS AND METHODS

Mostly our own data are described and commented below.

In the period from October 2004 to December 2011, to refine the boundaries of the contact between *P. major* and *P. minor* on the left bank of the middle Reach of the Amur River, we examined 54 villages and towns (26 in the JAR, 22 in the Amur region, and 6 in the Khabarovsk Krai). When working in small settlements, we examined 60 to 100% of their territory (many villages were examined repeatedly), as well as their immediate vicinities within a radius of 1.5 km. In large settlements (towns of Birobidzhan, Obluchye, Khabarovsk, etc.), only the areas with the highest abundance of tits were examined. In the central part of the area of sympatry (village Pashkovo), the state of the group of tits was monitored using color banding at least twice a year. Birds were caught using traps with decoy birds. The latter were usually represented by *P. minor* (usually female, sometimes a female with a male). Mealworms, sunflower seeds, and crushed pine nuts served as a bait. The birds were attracted by playing the song of birds of both species with a Walkman Professional D6 tape recorder equipped with a remote speaker and Panasonic RR-U395 and OLYMPUS VN-4100PC voice recorders.

In total, 1280 birds of both species and their hybrids were captured. We measured the basic morphometric parameters of the captured birds (the length of the wing, tail, tarsus, and beak) and described the background color of the upper and lower sides of the body as well as the configuration and size of the white spots on the rectrices. Blood specimens for genetic analysis were taken from all the samples caught.

The captured birds were classified into three categories: phenotypic *P. major* (with a yellow breast and belly), phenotypic *P. minor* (with a light ocher or light gray breast and abdomen), and phenotypic hybrids. The main criterion in this case was the intensity of the lipochrome color of the breast and abdomen of tits. This trait correlates well with the other diagnostic traits of *P. major* and *P. minor*, such as the size of the wing, tail, tarsus, and the white patch on the inner vane of the outermost tail feather (Fedorov et al., 2006). The phenotypic hybrids, in most cases, were characterized by the presence of slight yellow in the color of the abdomen. Typically, this was a continuous light yellow touch or, very rarely, patches of light yellow color on the background of light gray (or light ocher). The term «phenotypic»

in the case of *P. major* and *P. minor* means that, in reality (as was shown by molecular genetic analysis), many of them may be genetic hybrids to a certain degree. The proportion of such «hidden» genetic hybrids in the phenotypically pure populations of P. major varies in different parts of the area of sympatry (Fedorov et al., 2006, 2009; Kvist et al., 2007).

The behavioral aspects and the specific ecological characteristics of the two forms were studied by visual observations. In addition to the original data, the facts collected by other researchers during the entire period of the study of the area of sympatry served as a basis for our conclusions. When considering the issues regarding the wintering of tits in the area of sympatry, the period from late November until the second decade of March inclusive was taken as the winter.

RESULTS AND DISCUSSION

In the central part of the area of sympatry—the territory of the earliest contact of *P. minor* and *P. major* — their relationships were stable. Let us illustrate this conclusion using the group tits inhabiting village Pashkovo, Obluchye District, JAR, and its vicinities as an example. The level of formation of mixed pairs here reaches 10% of all pairs with involvement of representatives of phenotypic *P. major* for an average of four years of research. The biotopic preferences of the two forms here are clearly differentiated: *P. major* settles in settlements and sometimes in adjoining areas (within 1 km)[1] , whereas *P. minor* occupies the surrounding forests directly adjoining the settlements and only sometime penetrates them. The main contact between the two forms occurs in the areas immediately adjacent to settlements. The combination of mixed pairs «male *P. major* X female *P. minor*» prevails (Kerimov, Formozov, 1986; Formozov et al., 1993; our data).

In the areas of more recent contacts, located to the east and west of the center, the relationships between these species are different. The western part in settlements is numerically dominated by *P. major* , whereas scarce *P. minor* are found only in the environs and, as we observed, in the vicinity of villages within a radius of 1.5 km (more remote natural habitats were not examined by us) [2]. This part of the area of sympatry is characterized by the predominance of mixed pairs «male *P. minor* x female *P. major*». Note that, in this part of the area, *P. minor* settles at the habitats that were originally occupied by *P. major*.

In the eastern part of the area of sympatry, *P. major* settles in human settlements and adjacent habitats, which at the time of *P. major* radiation were already occupied by *P. minor*. The groups of tits in the settlements are mixed, the numerical ratio of representatives of the two forms in them is either equal or *P. minor* prevails, sometimes significantly. The natural habitats near human settlements are also occupied by *P. minor*, where this species is common. As was shown by A.A. Nazarenko and co-authors (1999) and S.M. Smirenskii (1977, 1986), *P. minor* inhabits secondary forests, and its radiation in the Amur region, as in the case of *P. major*, is associated with the development of this territory by humans. The dominant combination of partners in the mixed pairs in this part of the sympatric area is the same as in the western part: «male *P. minor* x female *P. major*».

The relationships between these species in Birobidzhan (the eastern part of the area of sympatry) could be traced from the time of their occurrence. As a long-term model, they may reflect the situation in the contacting groups of P. major and *P. minor* in the eastern part of the area of sympatry. Importantly, the process of «extrusion» of *P. minor* from the previously occupied settlement (presumably, due to competition with *P. major*) and the divergence of these forms in biotopic preferences was shown. The first territorial *P. major* males were recorded in Birobidzhan and the surrounding area in 1975. Before this date, the tree plantations in the city were inhabited exclusively by *P. minor* (Smirenskii, personal communication; Kapitonova

1. Single birds and even pairs of P. major can be met at a considerable distance from settlements (Kerimov, Banin, 1983); however, this is not typical for the most part of the population.

2. All unurbanized tree plantations located outside of settlements are regarded as «natural habitats».

et al., 2011). In the 1990s, a mixed group already formed here, and the process of hybridization has become widespread and the proportion of *P. minor* has begun to reduce (Nazarenko et al., 1999). By the end of the 2000s, *P. minor* has almost completely disappeared from the city, which is currently inhabited by a stable group of phenotypic *P. major*. Thus, for the short period of time, distinct differences between the forms in the selection of habitats have formed here (Kapitonova et al., 2011).

We distinguish seven factors that, in our view, determine the type and direction of modern relationships of the great and Japanese tits under conditions of sympatry.

Behavioral differences under conditions of cohabitation

According to our observations, *P. major* differs from *P. minor* by a bolder behavior toward new objects (such as traps), as well as a higher aggression and intolerance to foreigners at their nesting sites. This behavior is very well expressed when caught in traps containing decoy birds. In most cases, *P. major* are caught much faster (maximum within 40 min) than *P. minor*. The latter are highly cautious and indecisive and do not approach the traps for a long time. Sometimes it took 2–3 h to catch *P. minor*; some individuals could not be caught in the first day at all. Let us give the description of the most time-consuming case of catching *P. minor*. In June 2006, in the Bastak Reserve (12 km northward of Birobidzhan), an attempt to capture a single male was made. In the daytime, the bird stayed at the same site of a broad-leaved forest and actively sang. A trap with a lure bird (female *P. minor*) and a recording of male's song, was set in the morning. The male did not approach to the trap all the day round (although singing became more active) and made no attempt to demonstrate the hollow to the lure female[3]. The trap with the lure bird was hanging there all the day long. Meanwhile, the male was alternately feeding and singing without flying away more than 50–80 m. The next day the trap was placed at the same place, and only 2 h later the bird was caught.

An equally cautious behavior is typical of *P. minor* that are in mixed groups of tits staying near feeders. Our observations of such a group consisting of 10 *P. major* and one *P. minor,* which stayed near one of the feeders in village Pashkovo in February 2009, showed that the male P. minor of the first year of life was constantly inferior to all males and some female *P. major* . He was waiting for a long time before taking a seed in the feeder and letting most of *P. major* go first. When he succeeded, he flied 20–25 m away from the feeder to eat the seed, which is much further than the typical distance for a male *P. major* (usually 2–10 m from a feeder). Similar observations were made in December 2010. One of female *P. minor* of the first year of life was behaving just as carefully. She waited for a long time to get to the seed in feeders and sometimes preferred to collect fallen or uneaten seeds on the ground or fed on a less favorite food, for example, fat hanging nearby. In the presence of seeds, fat was eaten by only one of nine *P. major* visiting the feeder. Both *P. minor* birds described above looked completely mobile and active, had an average fatness, and compensated the low efficiency of feeding in the feeder by its duration. It should be mentioned that we have never seen a direct aggression of *P. major* not only to *P. minor* but also to other, even smaller-size birds (for example, the Marsh tit *P. palustris*, a frequent visitor of feeders).

The reasons for this difference in the behavior of the two forms may be related to their size. *P. major* are bigger and probably stronger and, under conditions of settlements, may have advantages in the competition for resources. The advantages in linear dimensions (length of wing and tarsus) of the phenotypic *P. major* over the phenotypic *P. minor* was shown by V.V. Fedorov et al. (2005, 2009).

Seasonal differences in territorial relationships

In the Amur region, the western parts of which were inhabited by *P. major* somewhat earlier than the eastern pars, this form inhabits solely human settlements, where is nests and winters, i.e., in contrast to the European and West Siberian

3. Usually, when encountering a female, single males (both P. major and P. minor) that have a tree hollow try to carry her along with them, flying up to her to a distance of 3–5 m not closer) and flying away in the direction of the hollow. In these cases, it is almost impossible to catch the male; in our practice, we could not do it even once.

populations, behaves itself as a typical sedentary species. At the same time, *P. minor* is widespread in the natural biotopes of this region. Wandering movements and, furthermore, migrations of P. major in the Amur region were practically not reported (Nazarenko, 1999; our results in 2004-2011.) Only two records of this species outside the settlements in the post-breeding season (A.I. Antonov, unpublished data). Two birds were caught near the Bureya River estuary (Telegrafnyi Island) in the period from September 29 to October 6, 2007 (the closest settlement, village Severnoe, is located at a distance of 2.5 km from this site), and another three birds were caught on September 5, 2007, near Lake Kleshinskoe (Antonovskoe Forestry, the Khingan Reserve), which is located 10 km from the nearest village Innokentevka.

In contrast, wanderings and migrations are characteristic of *P. minor*. A well-expressed flight in the southeast direction was observed on April 10 to 20, 2005, in the Zabelovskii reserve, located in the Amur River valley 40 km westward of Khabarovsk. For 10 days, about 40 birds (1 to 11 at a time) were seen here, mostly in flocks of small birds (in other seasons, *P. minor* almost is not recorded in these areas). Only a small part of the *P. minor* population tends to lead sedentary life, wintering in the breeding areas. In village Pashkovo, for example, the proportion of wintering *P. minor* in the middle of the winter of 2005–2006 accounted for 9.1% of the total number of birds that nested here in the spring of 2005 (n = 22) (a special survey was conducted on May 17–22, 2005 and on January 21–26, 2006).

According to our data, sedentary P. major start to divide territory and form pair in winter (January and February), and some pairs or single birds retain the territory from the previous breeding season. The first *P. minor* arrive to the breeding sites starting from the second ten-day period of March, and the main flight is observed here in April, when all female *P. major* are already in pairs.

The sedentary form, P. major, begins to divide the territories and form pairs before the arrival of *P. minor* for breeding, so that all female *P. major* at this time are already in pairs. Single males, which are almost always present in groups, are displaced to the periphery of the settlement and, in some cases, form mixed pairs with female *P. minor* returning from their wintering ground (Kerimov, Formozov, 1986; Formozov et al., 1993).

Differences in biotopical confinement

Under the conditions of the Amur Region, the major part of the P. major population inhabits human settlements, whereas *P. minor* breeds in both human settlements and natural habitats. For example, in the Bastak Reserve, the southern border of which is located 10–12 km from Birobidzhan and 1 km from the nearest settlement (village Kirga), where there is a small but stable group of P. major, this species has not been recorded at all for 8 years of our research (since 2004). The only, for the 13 years of existence of the reserve, record of a single bird was made in an apiary located 13 km from village Kirga (A. Averin, personal communication). At the same time, *P. minor* is a scarce, locally common breeding, common passage migrant, and a rare wintering species in the reserve (Averin, 2007; Averin, 2010). In the line of birdhouses (20 pcs.) hung 1km from village Kirga, for three years of observations (2005–2007) we observed *P. minor* breeding with a density of 2 pairs per sq. km.

We believe that most of the *P. minor* population inhabits natural environment. As hollow-nesting birds, they are dependent on the availability of hollow trees. Hollows are most characteristic of mature and overripe forests. The main hole-forming tree species in our region are willows (*Salex caprea, S. pierotii, S. rorida,* and *S. shwerinii),* Mongolian oak (*Quercus mongolica)*, and, to a lesser extent, other representatives of the broad-leaved trees. For this reason, the characteristic habitats of *P. minor* are floodplain riparian forests, oak forests, and mature deciduous forests. Although, in general, *P. major* prefer areas with a good forest cover, both within settlements and in their vicinities, unlike *P. minor*, they can populate with a high density settlements with completely treeless environment or plantations unsuitable for breeding (coniferous sites, small-leaf or young trees). These forests are used primarily as foraging habitats. Examples of settlements completely treeless environment and

numerous groups of *P. major* are villages located along the Amur River in the Blagoveshchenskii district of the Amur Region (in particular, villages Sergeevka and Markovo). The lack of trees limits opportunities for the nesting of *P. minor* and, therefore, their further radiation in the western part of the area of sympatry. Forest stands are represented here primarily by the Asian white birch (*Betula platyphylla)*, Dahurian birch (*B. daurica)*, Dahurian larch (*Larix gmelinii)*, Scots pine (*Pinus sylvestris)*, Mongolian oak (*Quercus mongolica)*, and their combinations. In general, the western part of the area of sympatry is afforested much more poorly than other parts. The forests are highly fragmented here and interspersed by vast steppe areas. Trees in floodplains, including the Amur River floodplain, are heavily cut down, sometimes overgrown with young willows, are completely devoid of forest.

The habitats in the eastern par of the area of sympatry, in general, are favorable for *P. minor*, although its southeastern sector (the northern part of the Middle Amur Lowland) is devoid of forests, which, to some extent, affects the uniformity of distribution of both species of tits and hampers the radiation of *P. major* to the east. The forests here are diverse in the species composition. The Bira River bed on the section from Birobidzhan to its confluence site with the Amur River, is a convenient and the transit through a breeding *P. minor*.

Habitats located in the central part (the northeastern part of the Lesser Khingan Range) are the most favorable habitat for both species: the forest is diverse in species composition with a high projective cover. The Amur River bed in this section is oriented in the north-south direction, which creates a convenient way for the seasonal migrations and optimal conditions for breeding in mature floodplain forests with a relatively high participation of tree willows.

It is worth mentioning the importance of the density of location of human settlements and their size. Small settlements can accommodate small groups of *P. major* , which reduces their survival in unfavorable years. Their remoteness from larger settlements, where the abundance is maintained at a high level, hinders the influx of new invaders.

Differences in wintering success

Successful wintering of male *P. minor* in the Middle Amur Region was described by A.A. Nazarenko et al. (1999). According to our data, a certain fraction of *P. minor* spends winter in all three parts of the area of sympatry; however, their abundance decreases during the winter more significantly that the abundance of *P. major*. For example, according to our observations made over three winters (2007–2011), in the central part of the area of sympatry (village Pashkovo), out of 11 *P. minor* individuals (8 males and 3 females), recorded at the beginning of winter (in December), only one male (9.1%) wintered successfully. In general, in the study area, the differences in the number of *P. minor* recorded at the beginning and end of the winter were significant at $p < 0.01$ (Fisher's exact test). We also established single cases of sedentary life of *P. minor*: a male stayed in village Pashkovo at least from February 2009 to March 2010, and a female stayed there from May 2005 to March 2007.

In the case of *P. major*, according to our observations over three winters (2007–2011), out of the 66 individuals (43 males and 23 females) recorded at the beginning of winter (December), 65 birds (98.5%; 42 males and 23 females) wintered successfully.

Demographic aspect in the occupation of new territories by species

In the case of *P. major*, new territories are first occupied by the most mobile element of the population — young females (regarding age and gender) (Perrins, 1979). In the case of *P. minor*, according to our assumptions, the main role in settling in new areas is played by males. According to A.A. Nazarenko et al. (1999), the males wintering at the breeding sites serve as markers of the suitability of the area for breeding for the major part of the *P. minor* population returning after wintering. This is consistent with our findings, according to which over 70% of all *P. minor* wintering in the area of sympatry are males. As a result, the population-based mechanisms, different in the western and eastern parts of the area of sympatry, lead to the formation of mixed pairs of identical composition «male *P. minor* x female *P. major*».

In the east, the radiation of female *P. major* in the habitats of *P. minor* promotes hybridization; in the west, the radiation of male *P. minor* in the habitats of *P. major* maintains hybridization at a low level though does not reduce it to zero; this level apparently changes depending on the number of male *P. minor* arriving in spring, of which only few remain to winter. Since the abundance of *P. minor* in the west is smaller than in the center and especially in the east, the level of hybridization here is currently the lowest.

Precedence in the occupation of territory

Because of the aforementioned behavioral and biotopic characteristics of the two forms, the factor of precedence in the occupation of territories by them in the area of sympatry is very important. If *P. major* distributes over a territory occupied by *P. minor*, mixed settlements of these two forms occur within human settlements. The consequence of such a contact is a high level of hybridization with numerical predominance of the residential form. Over time, provided replenishment with migrants from neighboring areas, *P. major* begin to displace *P. minor* (at different rate in different conditions). A striking illustration of the influence of this factor is the history of occupation of Birobidzhan by *P. major* (described above).

Under conditions when *P. major* radiates over a territory formerly occupied by *P. major*, mixed settlements are not formed and the differences in preferred habitats are formed immediately. Hybridization was initially maintained at a low level in a narrow band of contact on the periphery of villages and towns. For example, in the western part of the area of sympatry (south of the Amur-Zeya Plateau), where *P. minor* radiates over the territory occupied by *P. major*, out of eight males of the invading form, identified here for 3 years, only one was found breeding in the center of the village, four (50%) were found in its outskirts, and the remaining three (37.5%) were recorded at a distance of more than 500 m.

Differences in the size and density of groups

In general, the size and density of the groups of *P. major*т decreases in the direction from west to east. An exception to this tendency is the group of *P. major* in Birobidzhan. In the case of *P. minor*, conversely, the highest population density is detected in the eastern and central parts, and the lowest density is found in the west. In addition, *P. minor*, despite its high abundance, does not form settlements in towns or in natural habitats that are as dense as those formed by *P. major*. For example, in village Sergeyevka of the Amur Region (western part of the area of sympatry), on a 2-km route along the Amurskaya street we recorded nine singing territorial males of *P. major* on April 24, 2010. In the area near the northern boundary of the eastern part of the area of sympatry (Bastak Reserve), which is inhabited solely by *P. minor* and the abundance of this form here is the greatest, the population density was 2 breeding pairs per 1 km (our data for 2005–2007).

At a similar and relatively high abundance of both species in the area of sympatry, birds can form pairs with a partner of their own species, which accounts for the relatively low level of hybridization. At an unequal abundance, the less abundant species has to form pairs with the representatives of the more abundant species. The level of hybridization is determined by the demographic composition of groups of the less abundant species. This level is high if the females predominate in groups (such a situation is probable in the eastern part of the area of sympatry) and low if groups are dominated by males (western part). Let us illustrate this fact using our data as an example.

- the proportion of hybrids in the western part of the area of sympatry during the entire period of trapping was 1.1% (n = 360). The proportion of *P. major*, according to the results of counts in a model settlement in the western-most point of western part of area of sympatry (village Busse, Amur Region, May 13–14, 2009) was 84.2% (16 birds, including 11 males and 5 females), whereas the proportion of *P. minor* was only 15.8% (three males, females were absent for certain), hybrids not detected.
- in the central part, at an overall level of hybridization of 3.6% (n = 444), the proportion of the original forms and their hybrids in the model area (village Pashkovo and its vicinities within a radius of 2 km), according to the results of counts

performed on May 17–22, 2005, accounted for 47.6% (15 males and 8 females) for *P. major*, 50% (11 males and 10 females) for *P. minor*, and 2.4% (1 female) for hybrids.

• in the easternmost village in the eastern part, where the proportion of hybrids for the entire period of trapping was 7.1% (n = 519), the proportion of phenotypic *P. major*, *P. minor*, and their hybrids in the model group (Khabarovsk, the eastern boundary of the distribution of *P. major*), according to the results of catches on May 2, 2008 and May 23 and 28, 2009, was 20, 40 and 40%, respectively (n = 15). The ratio of sexes in all groups were similar (two males per one female).

The levels of hybridization in different parts of the area of sympatry were significantly different. The differences between the western and central parts and between the central and eastern parts of the area of hybridization with respect to this parameter were significant at $p = 0.03$ and $p = 0.02$, respectively (χ^2 test).

Probably, due to the selectivity of our method of trapping with the use of a decoy bird and a male singing voice recording, which reveals primarily males, the actual sex ratio is different. However, in our view, the groups of *P. major*, especially along the radiation front, were numerically dominated by females. This situation is observed in the areas of recent invasion of this form into the range of *P. minor* in the southern part of JAR (southeastern edge of the area of sympatry and hybridization), where the proportion of females for the entire period of trapping was 62.5% (n = 8). P. major in villages and towns of the southern part of JAR is represented by single birds (one or two birds per settlement, not annually).

The density of groups of *P. major* decreases eastwards. The abundance of *P. minor*, in contrast, is much lower in the western part of the area of hybridization, which is simultaneously the northern and western boundary of the distribution of this form, than in the central and eastern parts, located in the flyway of seasonal migrations. The groups of *P. minor* as such were not observed in the western part of the area.

We have found that the above-described factors are not always effective and their direction may be different in different conditions. They can both promote an increase in the abundance and radiation of species (i.e., promote hybridization) and limit these processes (i.e., limit hybridization). In the western part (on the territory of invasion of *P. minor* into the habitats occupied by *P. major*), the influence of these factors does not prevent a wide-spread radiation of *P. minor* and hybridization between the two species. A small number of mixed pairs of the «male *P. minor* x female *P. major*» type form here due to the penetration of predominantly male *P. minor* here. In the eastern part of the area of sympatry, in our opinion, the conditions are favorable for both species; however, in contrast to the west, the penetration of *P. major* into this area proceeds primarily at the expense of females. Under conditions of settlements, especially in forefront of dispersion, this promotes hybridization and formation of mixed pairs of the «male *P. minor* x female *P. major*» type. In the central part of the area of sympatry, the influence of factors creates approximately equal conditions for the habitation of both species. However, the predominance of males in the groups of *P. major* and, probably, rare cases when female *P. minor* winter in these settlements, arrive without a partner, and lose males of their own species (or in other situations), creates the conditions for the formation of pairs of the «male *P. major* x female *P. minor*» type, which are observed here and which occur more frequently than the pairs of the opposite composition.

The sufficiently large number of genetic hybrids (almost 40%) in the populations of the eastern part of the area of sympatry (Fedorov et al., 2009), was the result of the stage of intensive hybridization, which is characteristic only for the areas where *P. major*, with similar requirements to the selection of breeding grounds, occupies anthropogenic habitats previously inhabited by *P. minor* at a time when its abundance is smaller than the abundance of *P. minor*. The intense hybridization begins to reduce when the abundance of P. major in the mixed groups begins to exceed the abundance of *P. minor*. The stabilization of hybridization at a level of 10% of the mixed pairs of the total number of pairs with participation of Great tits takes place after the disappearance of the majority of *P. minor*

from the settlements and formation of biotopic differences between the species.

Currently, the disappearance of *P. minor* form settlements does not threaten the survival of this species in the Russian part of the area of sympatry, because the major part of the population inhabits natural habitats, where *P. major* are almost absent. However, it is unclear what may happen to these species if *P. major* form migratory and breeding in the wild parts of populations in the Amur region (similarly to what is happening in the European Russia and Western Siberia), which will compete on a large scale with the migratory *P. minor*? It is also unclear how the relationships between these species will form (or are already being formed) if P. major penetrates into the Chinese part of the Amur Region (the habitats of the sedentary part of more southern *P. minor* populations).

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Nazarenko A.A.* (2012) New details on the early stage of Great tit (*Parus major)* and Japanese tit (*Parus minor*) settlement of the Amur River basin, and inception of hybridization between them // *Far East. J. Orn.* 3: 47—52.

SUMMARY

The first specimen of Great tit from Amur River basin was collected on the Shilka River in the eastern Trans-Baikal in May, 1855 by R. Maack (1859), and breeding by Japanese tits was strictly proved in 1869 at Lake Khanka, in southwest Ussuriland (Przhewalski, 1876), but not any further north. Examination of high-quality colour photographs of the type specimen of P. *m. bargaensis* (Yamashina, 1939), collected on 22 April, 1935 on the eastern shore of Lake Dalainor (in the western foothills of the Great Khingan Mountains), has conclusively shown that it was a hybrid between *P. major* and *P. minor.*

The referred figures and tables are in the original article in Russian, pp. 47—52

The relationships between the populations *major* and *minor* of the «great» tits in the middle Amur Region, one of the textbook examples of Mayrian evolutionary biology (Mayr, 1968), is unique in its multifaceted elaboration, in particular, in terms of time/space, the use of modern methods of molecular genetics and systematics, ecological assessments, and just field observations. There were two independent field teams, «Vladivostok's» in 1991–1996 (Nazarenko et al., 1999; Kvist et al., 2002; P ckert et al., 2005, etc.) and «Moscow's» in 1970–2012; the latter was headed by N.A. Formozov (Formozov et al., 1993; Fedorov et al., 2006, 2009; Kapitonova et al., 2011, et al.). Their contributions, in my view, well suplement each other.

I would like to specially mention the recent article (Kapitonova et al., 2011) as directly pertaining the «space/time» problem. It is based on the material unique in scope, which was carefully analyzed and considered in relation to specific areas and time. It emphasizes the stability of the dispersal trends against the background of a dynamic, including unstable, abundance of local populations. These are very realistic estimates, which allows regarding them as a conceptual model to explain, for example, the early history of the emergence of *P. major* and *P. minor* populations in the Amur River basin.

Acquaintance with publications by R.K. Maack (1859) and N.M. Przewalski (1876) helped to clarify the details of the time and place of localization of the populations of these species in the Amur River basin in the middle of the 19th century. In connection with the annexation of the Amur Region to Russia (1858), the Siberian Division of the Imperial Russian Geographical Society carried out a number of complex, as we would say today, expeditions to study the geology, wildlife, and population of the Amur River basin (Zakharenko, 2008). The expedition to survey the Amur River from its sources in 1855 was headed by R.K. Maack. The main preparations for the expedition were performed in April–May in Nerchinsk, the largest town in eastern Trans-baikalia at the time. The first birds were also collected here.

As was customary at that time, the ornithological chapter of Maack's book (pages 113–151) included data on the birds from other, previously places visited: Irkutsk, Lake Baikal, and Yakutia, including the Viljui River valley. As an ethnographer, he carefully described the details of life of the aboriginal population, including houses.

*E-mail: < birds@idss.dvo.ru >
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For example, even then the barn swallow *Hirundo rustica* nested on Yakut yurts (Maack, 1859, page 132), and the magpie *Pica pica* had clearly bent to human settlements and was encountered in all Tungus villages along the middle Amur River valley (l.c., p. 125).

The Great tit is mentioned in this book once only. The specimen was collected on May 5 (May 18, New Style) 1855 in Shilka near the Nerch River estuary (l.c., page 125). However, it is important to make an important ecological note: anyone who gets into the settlements in the Trans-Baikal region for the first time is impressed by the lack of woody shrubs and even trees in them. I had an opportunity to see, on the internet, a series of excellent photos of Nerchinsk and its immediate vicinities made before the Revolution. It was a completely naked city, with pastures beginning on its suburbs, with obvious signs of overgrazing. Such settlements could hardly be a favorable environment for the Great tit.

According to E.V. Kozlova (1930, p. 222), in the mid 1920's the Great tit was a scarce species in the southern Transbaikalia. Although the birds kept near villages, they nested exclusively in riparian poplar forests, including the mountain terrains. In winter, the birds migrated to more southern areas, up to the almost treeless Gobi-Altai. Today, they spend the winter mainly in settlements, including Chita, and occupy adjacent forests and woodlands in the spring (Shchekin, 2007).

These facts suggest that, there could hardly exist a highly productive population of the species in eastern Transbaikalia at the time of Maack, which could ensure a population excess. In addition, both Shilka and Amur Rivers rounded the Greater Khingan Range in the north and flowed through a remote mountain taiga area, which was then almost uninhabited. Naturally, Maack has no opportunity to examine three Chinese towns that existed at that time on the right bank of the Amur River upstream of its place where it crosses the Lesser Khingan Range. Neither is there any evidence of former habitation of the Great tit in the north of the Manchuria (Yamashina, 1939). Nevertheless, small numbers of these birds were observed by G. Radde in the spring of 1858 (Radde, 1863) near the Bureya River mouth, but not further eastwards, because the Great tit was not found at all in the Lesser Khingan Range, where Radde spent two years (1858 and 1859), conducting stationary research and collecting specimens, basing in the Cossack village that was later named in his honor (Zakharenko, 2008). It can be assumed that this was a failed attempt of this species to spread to the east, and the later settling along the Trans-Siberian Railway took place in fact.

It is also interesting that stationary studies in Birakan village and the results of counts performed in a number of other settlements, including Birobidzhan, showed that the «modus vivendi» of the Middle-Amur population is different from that of the Transbaikalian population (see above) (Nazarenko et al., 1999). In the Middle Amur Region, the birds not only winter in settlements but also nest there with a high density (l.c., fig. 3, p. 376). This difference can be explained not only the fact that now these settlements abound in green wood but also by the fact that various buildings in the residential sector and the numerous technical and engineering facilities, including those located near the railway, create ideal conditions for building nests, although in most cases these nests are inaccessible for inspection (Nazarenko et al., 1999, p. 373). In adjacent forests, which are presented today mostly by brush woods, there is a severe shortage of hollows. This conclusion is made not only on the basis of the low density of Great tits in them but also on the fact that the same hollows are occupied annually, even if they are of a poor quality (very tight and close to the ground, or filled with water during heavy rains).

In general, it was the perfectly favorable environment created by humans in the Middle Amur basin that contributed to the fast growth of the Great tit population and its territorial expansion in recent decades, which was convincingly demonstrated by L.V. Kapitonova et al. (2011). For me, the disinclination of Great tits to disperse in the southern direction remains a complete mystery.

The Japanese tit. The environment potentially suitable for this species already existed in the middle Amur River valley (the most southern portion of its course) during the expedition of R.K. Maack: he noted the ubiquitous presence of oak and other broad-leaved trees on the high banks of the river and the presence of large oak woods among vast tall-grass meadows (later called the Amur prairie) in the valley east of the Lesser Khangan Range. During the same trip, he explored the forests in the Greater Khekhtsir near the Ussuri River estuary. and once worked there in June 1859 (Maack, 1861). But neither there nor in the middle reaches of the Ussuri, which places it right coast is mountainous and directly adjacent to the river, and where, as now, was to be oak stands (Nazarenko et al., 1999, p 380), he found this species.

In the book by N.M. Przewalski (1870, p. 52), there is only a general mentioning of this species in the Ussuri region. However, the book describing the results of his first trip to Inner Asia (Przewalski, 1876), more specific comments can be found (p. 52): «... By voice and way of life, the described tit not differ from our *P. major*» (?). And further: «In the Ussuri region, *P. minor* occurs quite often: in the middle of June, I often found fledged immatures on Lake Khanka» (p. 52). It is known, however, that the only area where he collected specimens and worked for certain in summer is the mountain-forest area to the west of Lake Khanka between villages (stanitsas at that time) Turii Rog, on the border with China, and Kamen'-Rybolov. In addition, he explored the valley of the lower reaches of the Lefu River (now the Ililstaya River) on the Khanka Plain. It was in May–June 1869, and it is here where he began his return to Russia.

Meanwhile, a careful reading of books by Maack and Przewalski, together with his above quote regarding the comparison of the great and Japanese tits, suggest that young Przewalski, as a naturalist, was markedly inferior to Maack. The latter gives surprisingly accurate and sharp observations of birds. Undoubtedly, Przewalski knew well large birds, including the game birds. In general, the northern boundary of the Japanese tit range in the Ussuri region was apparently located in the vicinities of Lake Khanka in those years.

The time when hybridization between the Great and Japanese tits began

In March 2006, thanks to assistance of Dr. Edward Dickinson, c/o The Trust of Oriental Ornithology, I was provided with an opportunity to examine color photographs (of a very good quality) of the type specimen of *Parus major bargaensis* Yamashina, 1939 (collection No. 19037, museum No. YIO-00128) at the depositary of the Yamashina Institute for Ornithology, Japan. It is known (Yamashina, 1939, p. 481) that this specimen (adult male from a pair) was collected on April 22, 1935, in a treeless terrain on the eastern shore of Lake Dalainor near the confluence of the Khailar River, flowing from the western slope of the Greater Khingan Range. The wing length of this specimen is 73.0 mm (l.c., p. 481), which corresponds to the minimum value of this trait in *major* males formally outside of the contact area with a *minor* population (Nazarenko et al., 1999, p. 374, table). The color of the bottom of this specimen is very light, almost white, with a slight yellowish tinge. The outermost tail feathers, according to the two pictures, carry broad and long white stripes.

In this context, it is important to note that, of the nine Great tit specimens collected by me on June 20–22, 1992, in the vicinities of the town of Shimanovsk, which is formally located outside of the contact area of these species, one specimen was classified into the category «light major» (see below). It is remarkable that this specimen had a minor haplotype (Pöckert et al., 2005, table 1, N 1276, p. 160); i.e., was a hybrid. With allowance for these data, the representative specimen bargaensis can be classified as a hybrid between major and minor of the «light/white major» category (Nazarenko et al., 1999, p. 373), and it can be assumed that the hybridization between the two species began at least in the mid-1930s.

It is difficult to interpret the place of this finding. However, it is known that, during autumn migrations, the birds can fly sufficiently far away from their breeding areas (Kozlova, 1930; Kapito-

nova, 2012). In addition, strictly speaking, the western boundary of the minor population in the middle Amur River basin before that time remains unknown. It can be only noted that, in the same article (Yamashina, 1939, p. 481), four minor specimens are mentioned (two adult males and two young birds collected in the period between August 1 and 19, 1935, in the vicinities of the town of Aihon, on the other bank of the Amur River opposite to Blagoveshchensk. It is also symptomatic that the population of the Great tit in the southeastern Transbaikalia, on the basis of the trait of a paler back and abdomen, was distinguished as the subspecies *P. major kapustini* Portenko, 1954, which is not recognized now. It would be highly desirable to perform a molecular genetic screening of this population.

To conclude, I have to give a critical commentary on the recently published article by L.V. Kapitonova (2012), because its contents may mislead an unqualified reader. This article reviews the cases of vagrancy and introduction of the Great and Japanese tits in different places and areas on the eastern boundary of Asia and the importance of «ecological routes» (railways) in this phenome-non. The author of this article also decided to track (in real time as well) the dispersal of the Japanese tit in the Central Sikhote-Alin. She misread the article by L.M. Shulpin (1931), attributing to him the discovery of a nonexistent finding of this species in the middle Sikhote-Alin. Let me quote her: «In the basins of Botchi and Kopi Rivers, *P. minor* was recorded by L.M. Shul'pin (1931) in 1928 as one of the southern species coming far to the north along the eastern and west Sikhote-Alin. Note that Shul'pin mentioned a significant transformation of these areas by humans» (Kapitonova, 2012, p. 603). However, L.M. Shul'pin never worked in the Central Sikhote-Alin in general and in the basins of Kopi and Botchi rivers in particular!

In his article (Shul'pin, 1931), he clearly indicates where and when he worked in 1926-1928. In 1928, the area of his work was the extreme north of the Sikhote-Alin Mountains (near Lake Kizi) and the sea coast northward of De Kastri Bay. In these areas, the Japanese tit has not yet nested to date. In fact, L.M. Shul'pin in 1927 made the northernmost (at the time) record of this species near the sea coast, in the vicinity of Tetyukhe village (now Dal'negorsk), which belongs to the southern Primorye. Referring to A.A. Emel'yanov (1929), who collected bird specimens in the basins of Kopi and Botchi rivers, located northwards, he especially emphasizes the lack of this tit in his collections. Let me quote him: «Among the species unknown there [Kopi, Botchi] but found by me in this trip [Tetyukhe], I should mention ... *Parus major wladivostokensis* ...» (Shul'pin, 1931, p. 597). Indeed, in 1908–1910, in this region, which was well developed already in that time, the Japanese (White-bellied then) tit was not found (Chersky, 1915, pp. 232, 233).

Finally, I would like to give a brief commentary on the role of the Komsomolsk–Vanino–Sovetskaya Gavan township railway as an «ecological route» for the dispersal of the tit species discussed. This railway crosses, almost at a right angle, the Sikhote-Alin Mountain Range between its central and northern parts. It has regularly operating since with 1947. Today, at least 10 railway stations with perfect features of «ecological islands» can be specified between the end points: they are separated from each other by an average of 40 km, has well planting of greenary, and their environs are represented by meadows or pastures, and diverse woodlands that have nothing to do with the dark coniferous taiga that grew here earlier.

I have chosen Vysokogornyi township, which is located in the axial part of the Sikhote-Alin range, as a model. For seven monitoring seasons (2004–2012., with a two-year skip), neither the Great tit nor the Japanese tit have been recorded here in late June–early July, even with their songs being specially played. However, in another model area (Sovetskaya Gavan–Gatka village), the Japanese tit was found immediately and was then regularly observed there over the years. However, strangely enough, during a thorough surveyof Vanino township as such, including the large holiday village in its vicinities, which was performed in 2004, none of the two species was identified here. In the same year, at the end of June, we also visited Gurskoe village/station

(formerly Khungari), which is the western foothills of the Sikhote-Alin Range. The Japanese tit was detected immediately; however, the size of this local population was small. The prelimina-ry results of studies of these «ecological islands» were published earlier (Nazarenko et al., 2006).

Thus, an «ecological routes» can be effective only when there is a sufficiently potent population pool takes place in the region, which may to create an excess of population. Apparently, this is not yet the case in the Lower Amur region.

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