Hybridization of *Motacilla alba* Linnaeus, 1758, and *M. (a.) personata* Gould, 1861, in the south of Siberia

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Abstract—The authors attempt to estimate the level of hybridization of *Motacilla alba* and *M. (a.) personata* in the area of their secondary contact in the south of Siberia. Processing of the materials in several museum collections ($n = 424$) and author's own collections ($n = 347$) resulted in conclusion on the presence of introgression, in spite of limited hybridization. The data on pair composition and breeding success in the hybridization zone as well as data on habitat preferences are given. The possible reasons for the limited hybridization are discussed.

The attention of many ornithologists is attracted to the cases of hybridization of the forms which show sharp differences in plumage coloration. To gain proper understanding on of relationship between contacting populations one needs a research program based on several principal questions: Do the taxa which express the tendency to hybridize constitute unique systemic categories differing in a complex of criteria (morphological, ethological, ecological, genetic)? Only compiling with this condition we can discuss the hybridization of populations of higher ranks. Does there a gene flow exists outside the zone of the spatial contacts of the forms (Does the introgression present)? Does the selective elimination of hybrids take place in the zone of hybridization, and if so, what are the reasons? If there is no elimination of hybrids, but hybridization is limited, what factors determine its level? How does the scale of hybridization change with time? What is the role of the human activity in its dynamics?

The final result of the studying of the hybridization of the forms at the different stages of the evolutional isolation consists in revealing and explaining the mechanisms at the basis of microevolution and species formation. While the studies of hybrid zones are obviously valuable, they are still scarce [1].

In the subgenus of long-tailed wagtails (*Motacilla*) there are forms demonstrating both wide sympatry without hybridization (e.g., *M. grandis* Sharpe, 1885, *M. maderaspatensis* J. F. Gmelin, 1789) and limited hybridization in the narrow contact zone (representatives of the complex of white wagtails *Motacilla alba* sensu lato: *M. alba ocularis* Swinhoe, 1860—*M. (a.) lugens* Gloger, 1829—*M. (a.) leucopsis* Gould, 1838 and *M. a. dukhunensis* Sykes, 1832—*M. (a.) personata*

Gould, 1861—*M. a. baicalensis* Swinhoe, 1871). The last mentioned are of major interest for studying the problems of speciation. Present paper deals with relationships of white *M. alba* and masked wagtail *M. (a.) personata* in the zone of their secondary contact in the south of Siberia.

MATERIALS AND METHODS

The studies were conducted from early April to early July in 2005–2009 in the south of Yenisei Siberia (Achinsk and Kansk forest-steppe, Yenisei valley from the village of Novoselovo northward to the mouth of the Podkamennaya Tunguska River), West Sayan (the Us and Tanzybei Rivers), in the north, central and south districts of Tuva, and in South Baraba (Zdvinskii raion of Novosibirsk oblast).

The characteristics of the phenotypically pure *M. a. baicalensis*, *M. a. dukhunensis*, and *M. (a.) personata* were determined according to the pictures and descriptions of the type specimens [2] taking into account considerable variations of coloration in the allopatric parts of the range. In order to get the morphometric data and to make phenotype description the birds were caught with mist nets or collected with the following production of collection skins, part of which was passed to the Zoological Museum of MSU and Zoological Institute RAS. The authors' collection contains 347 specimens. In collected and live birds wing length, tail length, and bill length were measured using standard methods [3]. To make measurements comparable in both old and fresh museum skins we created calculation coefficients (a quotient of a fresh bird measurement to the same value of a dried specimen kept dried fro 1 to

3 years). These coefficiemts were obtained after re-measuring sample of 87 specimens and constituted 1.022 for wing lengths and 1.051 for tail lengths. In addition to our own sampe we used collection materials from the Zoological Institute RAS (ZISP) ($n = 193$), Zoological Museum of MSU (ZMMU) ($n = 188$), Tomsk State University (TSU) ($n = 31$), Institute of Systematics and Ecology of Animals SB RAS (ISEA) ($n = 6$), Institute of Zoology of the Republic of Kazakhstan (IZRK) ($n = 6$). The total number of specimens icluded into analysis is 771. The data were processed with Statistica 6.0 software. Analysis of morphometric parameters employs the Student's t-test ($p = 0.05$). The differences between the samples in their phenotypical composition were estimated with Kolmogorov–Smirnov test ($p < 0.05$).

Fig. 1. The masked wagtail (I), white wagtail (VI) and different variants of the intermediate phenotypes (II–V). Ill. By Yu. I. Sheina.

RESULTS AND DISCUSSION

Phenotypical diversity in the contact zone. The complex of white wagtails *Motacilla alba* sensu lato is represented by three forms in the south of Siberia: the white wagtail *M. alba* (subspecies *dukhunensis* and *baicalensis*) and masked wagtail *M. (a.) personata*. The latter is sometimes included in *M. alba* [4–7] or treated as closely-related separate species [8, 9] or semispecies within superspecies complex of the ex-conspecies level *M. alba— M. personata—M. lugens* [10–11].

M. a. baicalensis has white throat, *M. a. dukhunensis* has black throat and white pattern on wing-covert less developed; both of them differ from *M. (a.) personata* by the color of the sides of head and neck, narrower white edges on the covert wing-feathers, as well as some size characteristics [4, 7]. In the south of Siberia white and masked wagtails show a continous row of phenotypical transitions (Fig. 1). The evidence of hybrid origin of the intermediate phenotypes has been repeatedly discussed in literature [8, 10, 12]. Detailed description of plumage coloration in phenotypical hybrids is given in our previous work [13]. We propose four color characteristics as phenotype markers: (1) the degree of black color on sides of neck; (2) black color on mustachial stripe; (3) black on ear-coverts ander eye; (4) black on throat. The first three of these are subjected to linked inheritance while the fourth one is inherited independently from the others. The use of one of the markers needs some explanation. More than 25% of females all over the range retain some elements of winter and juvenile plumage in their breeding plumage. (these include gray forehead, scaly marks on ear-coverts, suborbital pteryla and lores). Mentioned traits appear to be ancestral for all the members of *Motacilla alba* sensu lato complex characterising juvenile plumage. However, scaly black-and-white pattern on ear-coverts in males is apparently of hybrid origin. Among the 91 males of *M. alba* and *M. a. dukhunensis* from allopatric parts of range none hase ever had this trait, whereas 21.0% of mailes in hybridization zone had it.
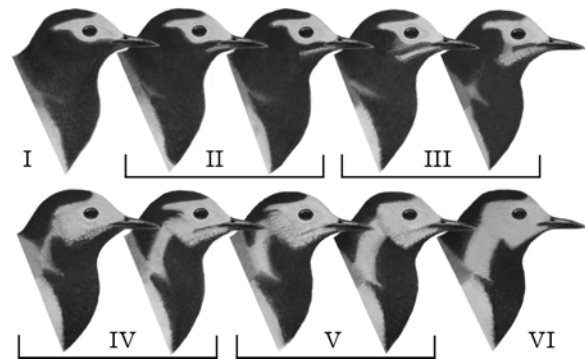
In the previous work [13] we divided phenotypes into 6 classes (see Fig. 1). We should note that such division is conventional. Masked wagtails from the zone of hybridization feature white bases of the feathers on head and neck in the same areas where *M. alba* also has white feathers. However, the black tips of the feathers of *M. (a.) personata* conceal the white area, and such bird does not differ in its appearance from the phenotypically pure one. To a certain degree of development the mentioned element of coloring is featured by all *M. (a.) personata* from the northern border of the range to the northern parts of Kazakhstan, Mongolia and from the western part of Altai eastward to the western parts of Eastern Sayan (the zone of contact with *M. alba* and adjacent territories up to 500–700 km away from it). The same trait is absent (with rare exceptions) in birds from allopatric parts of range in South Kazakhstan, Kyrgyzstan, Turkmenistan, South Uzbekistan, and Pakistan. As the given phenotype is confined to the hybrid zones, it indicates its hybrid origin, which is corroborated by the data on plastic traits variability and the results of molecular-genetic studies [14]. The attribution of "northern" masked wagtail to the phenotypically pure ones is rather conventional, although their appearance corresponds fully matches with images of type specimens.

In addition to the coloring characteristics, hybridization of the discussed forms is also indicated by their measurements. In the allopatric parts of range males of *M. (a.) personata* are significantly larger than males of *M. a. dukhunensis* (see table). In the zone of hybridization the difference is not so great, because of the size parameters averaging tendency.

Distribution in the south of Siberia and the area of hybridization. As shown above, the division of the individuals into the phenotypically pure and those with weakly expressed intermediate appearance is highly conventional, especially when dealing with the museum material. So, discussing the distribution of the wagtails in the south of Siberia, we desided to designate 3 groups of the phenotypes: individuals close to

Table. Size parameters of the males of *M. a. dukhunensis* and *M. (a.) personata* from the hybridization zone and allopatric parts of the range. The bold type stands for the values of *t*-criterion indicating the significant difference of the samplings

Length, mm		Subspecies	*n*	*x* ± SD	*Lim*	*t*
Allopatry of:	wings	*M. (a.) personata*	46	95.2 ± 2.58	86.9–101.2	**7.46**
		M. a. dukhunensis	26	90.7 ± 2.17	86.9–95.0	
	tails	*M. (a.) personata*	45	94.2 ± 3.36	85.1–102.0	**5.87**
		M. a. dukhunensis	25	89.7 ± 2.85	84.0–95.0	
	beaks	*M. (a.) personata*	43	13.1 ± 0.74	11.1–14.6	**5.39**
		M. a. dukhunensis	23	12.1 ± 0.66	10.3–13.2	
Hybridization of:	wings	*M. (a.) personata*	101	93.5 ± 2.24	86.7–100.0	1.18
		M. a. dukhunensis	23	92.9 ± 1.47	89.9–96.1	
	tails	*M. (a.) personata*	98	94.2 ± 2.49	87.3–100.0	0.99
		M. a. dukhunensis	23	93.5 ± 2.75	87.7–98.8	
	beaks	*M. (a.) personata*	57	12.3 ± 0.55	11.3–13.9	1.85
		M. a. dukhunensis	21	12.0 ± 0.74	10.4–13.5	

M. (a.) personata (I–II phenotypical class), hybrids with strictly intermediate coloring (III–IV), individuals close to *M. alba* (V–VI).

Range of *M. a. dukhunensis* includes West Siberia and Caucasus, *M. a. baicalensis* is widespread in Tuva, Cis-Baikalia, Trans-Baikalia, and Mongolia, *M. (a.) personata* occurs from Northern Pakistan, central and western parts of Iran, Kazakhstan, Altai to Khangai, Khentii, eastern part of East Sayan, and northward to the middle Yenisei [4, 10]. Ranges of discussed forms overlap broadly in the south of Siberia (Fig. 2). Within this territory several areas of intensive hybridization with the local accumulation of strictly intermediate hybrids are known. The southern part of the contact includes territories from South-Eastern Altai (South-Chuya Range) to the western part of Eastern Sayan and Sangilen, including the Uvs Nuur Basin north to the southern slope of Tannu-Ola Range, and southward over the territory of Mongolia to South-Eastern Khangai (see Fig. 2b). This is one of the areas of intensive hybridization [18, 19, our data]. Western Sayan is inhabited only by individuals close in appearance to *M. (a.) personata* (our data). The hybrids close to *M. a. dukhunensis* and *M. a. baicalensis* occur in small numbers from the northern slope of the Western Sayan over the forest-steppe and steppe parts of the left bank of Yenisei River along the eastern parts of Kuznetsky Alatau, in Western and Central Altai, western parts of Eastern Sayan. The majority of birds in these regions belong to *M. (a.) personata* (I-II phenotypical classes) [8, 21, our data and collections of ZISP, ZMMU, TSU]. *M. (a.) personata*, *M. alba* and strictly intermediate hybrids occur in northern and north-eastern parts of Kuznetsky Alatau, in westward direction masked wagtail nests in small numbers up to Tomsk; it is common up to the eastern half of Salair Ridge, and occurs rarely in Novosibirsk; to the south it is found along the western foothills of Altai. The second known zone of intensive hybridization is located in the area between the northern and western parts of Kuznetsky Alatau and eastern part of Salair Ridge (Fig. 2b). From Kuznetsky Alatau and northern ridges of Eastern Sayan masked wagtail penetrates by the taiga westward to the middle stream of rivers of the Ob basin and northward to the mouth of the Podkamennaya Tunguska. On the contoured territory white and masked wagtails live together, however, in the western part of this territory the character of their relationship is unclear. The third, northern, zone of the intensive hybridization begins from the mouth of the Angara River in the south and spreads in the basin of the middle Yenisei to the mouth of the Sym River in the north, although single hybrids close to *M. (a.) personata* have been registered down to the mouth of the Podkamennaya Tunguska (Fig. 2a). It is quite possible that limits of the listed hybridization zones are somewhat wider and embrace the area of the north-western foothills of Altai, middle stream of the rivers of the Ob basin, as well as the Angara basin and foothills of Eastern Sayan [4], but the data and collection materials from these areas remain insufficient. According to available data, the areas outside the zones of intensive hybridization (marked with hatching in Fig. 2) are dominated by the individuals closely resembling parental form, while the rate of the strictly intermediate hybrids and representatives of the adjacent populations being low.

Level of hybridization. The scale of hybridization appears to be larger than it had been previously assumed [10]. The detailed evidence of this statement is given in the earlier work [13]. Analysis of the coloring characteristics demonstrates the presence of introgression, at least for *M. (a.) personata*. The individuals with the traits of hybrid origin (white color on the bases of the head and neck feathers, white "moustache" (Fig. 1, *II*)) occur in allopatric parts of the range of the masked wagtail in the North and Central Kazakhstan
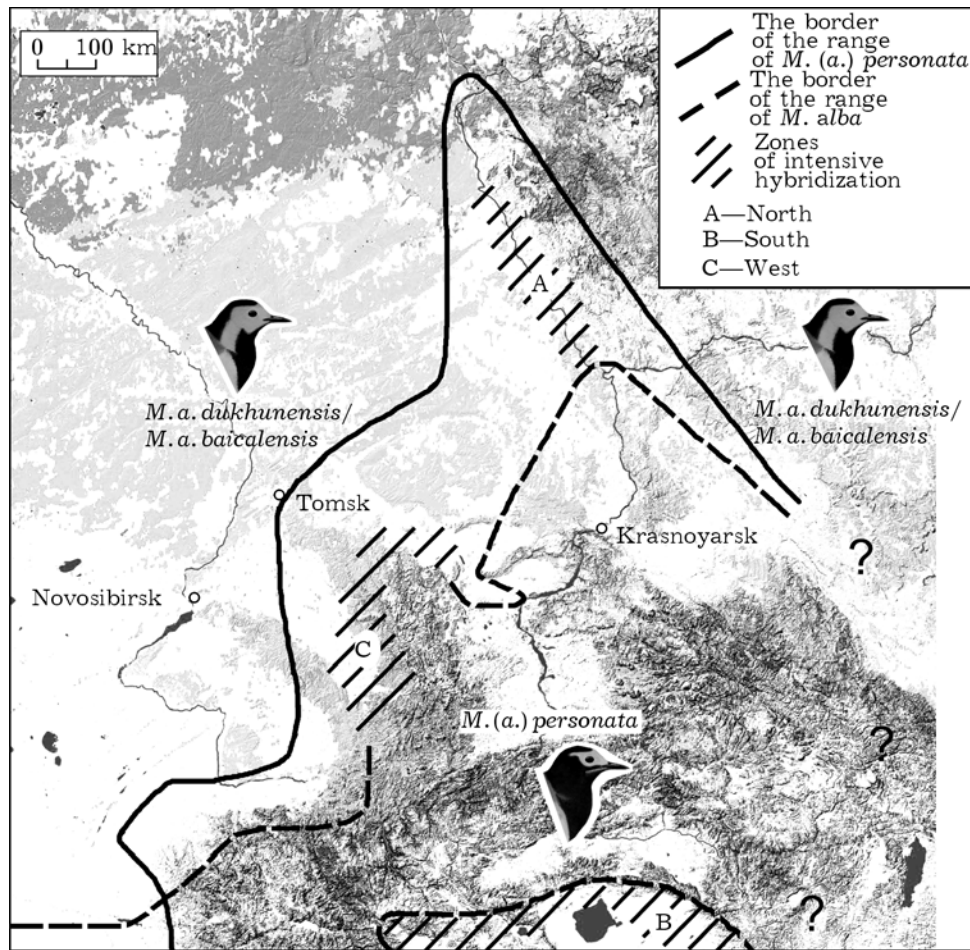
Fig. 2. Distribution of *M. alba* and *M. (a.) personata* in the south of Siberia. Composed by [4, 8, 10, 15–20, collections of ZISP, ZMMU, TSU, ISEA, our data].

(500–700 km from the area of sympatry). We suggest that their origin is caused by gene flow from the range of *M. alba*, since the degree of development of these characters decreases clinally when moving away from the hybrid zones, whereas the individuals with the clearly developed "moustache" (III phenotypical class) are found only in the area of contact. In spite of the significant level of hybridization, the distribution of the intermediate phenotypes over the whole area of sympatry does not correspond with the character of intergradation transition between the forms of subspecies rank (geographic races). The majority of the birds is closer in appearance either to phenotypically pure *M. (a.) personata* or *M. alba* with weak traces of the hybrid origin. The rate of "strictly intermediate" phenotypes is much lower, and they occur only in zones of intensive hybridization with few exceptions. The level of hybridization seems to differ in northern (Fig. 2a) and southern (Fig. 2b) parts of the contact zone. In our opinion, the available data are sufficient for comparing the situation in South-Eastern Tuva and in the middle Yenisei. The graphs of frequency of phenotypical classes have ten-

dency to differ between northern and southern populations, although the differences are statistically unreliable ($p > 0.10$). In Tuva the rate of both parental forms is higher, whereas in the north the number of the "strictly intermediate" individuals and those with weak traces of hybridization is higher (Fig. 3). The rate of parental phenotypes (I and VI) differ to the highest degree, making up 37.5% (18.5 *personata* / 18.5 *alba*) among the males ($n = 32$) and 29.4% (23.5 *personata* / 5.9 *alba*) among the females ($n = 17$), whereas in the middle Yenisei it is 21.9% (4.7 *personata* / 17.2 *alba*) for the males ($n = 64$) and 16.7% (14.6 *personata* / 2.1 *alba*) for the females ($n = 48$).

Analysis of the neutral molecular markers (ND 2 and Control region) demonstrate a significant level of hybridization in the south of Siberia and poor isolation of *M. alba* from *M. (a.) personata* [14]. The majority of haplotypes of the masked wagtail from Tuva is identical to those of the individuals with the phenotypes *M. a. dukhunensis* and *M. a. baicalensis* from West Siberia and Cis-Baikalia. At the same time *M. (a.) personata* has unique haplotypes in the allopatric areas of
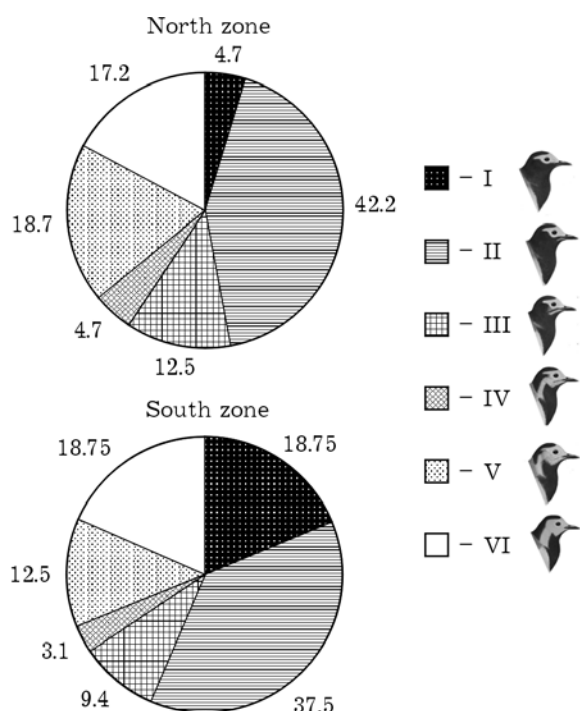
Fig. 3. Occurrences of phenotypical classes of the males in the north (*n* = 64) and south (*n* = 32) zones of hybridization.

Fig. 4. Composition of the pairs, times of hatching (*), and success of hatching in the mixed population in Tuva, 2009.

the range in South Kazakhstan. Most likely *M. (a.) personata* borrowed the mitochondrial haplotypes of *M. alba* as a result of hybridization. Similar example is known for the hybrid zone of the bank vole (*Clethrionomys glareolus*) and the northern red-backed vole (*Clethrionomys rutilus*) [22].

Thus, at the joint of the ranges the white and masked wagtails are engaged into hybridization, however, the hybrid zones are significantly smaller in area than the allopatric areas of distribution. The hybridization zones are unlikely to occupy the entire sympatry area, on the larger part of which the individuals close to either white or masked wagtail dominate, with single individuals of the adjacent forms and strictly intermediate hybrids. The phenotypical influence of hybridization is experienced by parental populations (at least the populations of *M. (a.) personata*). The level of hybridization differs somewhat in the northern and southern parts of the contact area. The character of distribution of the intermediate phenotypes indicates the existence of the factors limiting hybridization. Below we examine them.

Biotopical preferences. There are no strong differences in the biotopical preferences between the discussed forms. All of them occupy similar habitats in the nesting period: flood plains of the rivers, shores of water bodies, and urban landscapes. A great flexibility of the wagtails in choice of the nest locations determines the wide range of the suitable biotopes and creates the premises for symbiotopy. However, in Altai, Kazakhstan, Tuva and Western Sayan masked wagtail prefers
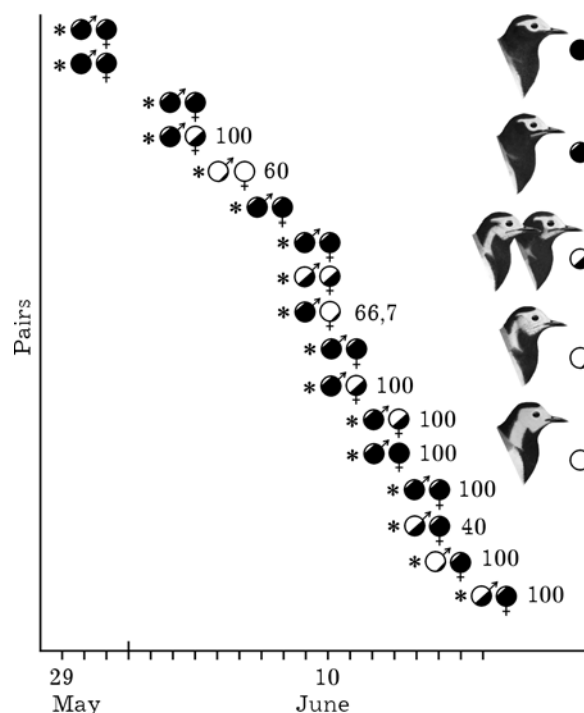
mountain and foothill areas, whereas in taiga and in open landscapes it builds its nests only in the human-made structures. White wagtail, on the contrary, avoids the mountain areas and nests in taiga along the river banks far from the villages. Only in taiga, steppe, and mountain territories poorly developed by humans, the conditions for habitat segregation are created [4, 8, our data]. All discussed forms readily nest in the anthropogenic landscape, which plays role of ecotone in this case and favors the individuals of hybrid origin, even if they are less competitive.

It seems that in the northern part of the contact zone the level of hybridization increased in the last 100 years due to the masked wagtail moving north along the valley of the Yenisei River. In the middle of the 20th century the northern limit of its distribution was registered at the town of Yeniseisk [4], however, today its range reaches the mouth of the Podkamennaya Tunguska (our data). Probably, this move to the taiga territories was triggered by intensive industrial development in the 20th century in the middle Yenisei, since in the zone of taiga masked wagtail prefers to nest in the anthropogenic landscape. The individuals from the expanding population are always short of con-specific partners on the periphery of the range, which also serves as an important premise for hybridization [23].

Display behavior. The limitation of this publication does not allow us to compare in detail the display behavior of white wagtails, so a separate paper is planned to cover ethological aspects. We should note that the
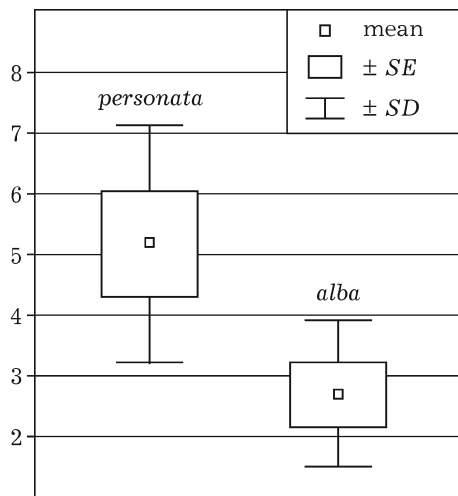
Fig. 5. Length of the testes of the wagtails ($n = 5$, *M. (a.) personata* and phenotypically close hybrids; $n = 5$, *M. alba* and phenotypically close hybrids) caught on April 26–30, 2009, in Southern Tuva.

majority of the EBA in all forms in the group of *Motacilla alba* sensu lato (*M. (a.) lugens*, *M. a. leucopsis*, *M. a. alba*, *M. a. yarrellii*, *M. a. baicalensis*, *M. (a.) personata*) are very similar [4, 6, 24–27, our data], with some peculiarities noted only for *M. a. ocularis* for the pose of impression in males [25]. There are some differences in vocalization between white and masked wagtails [7], however, as our observations indicate they do not inhibit their communication. To this moment we have not found any ethological barriers in cases of both territorial and mating display behavior, which is confirmed by the breeding pairs of various compositions.

The pair composition and success of reproduction in Southern Tuva. According to our observations, hybrids of both sexes are fertile (Fig. 4). The pairs with a hybrid and phenotypically pure members as well as hybrid/hybrid pairs have normal offspring. Data on successful breeding (number of chicks/number of lain eggs) were obtained for the 10 pairs of different composition. Seven out of them showed 100% breeding success, three pauirs—40.0–66.7%. No relation is found between sex or phenotype of a bird and survival rate of its offspring: only in one pair with low breeding success the male had hybrid phenotype, and another pair of the same composition had 5 chicks, and the success of hatching was 100%. We should take into account that our data are obtained from the zone of accumulation of hybrids. We cannot exclude the possibility of lower reproductive success of hybrids outside the zone of sympatry. We need more additional date to make proper conclusions.

Pair forming. There is an evidence that in Tuva males of the white and masked wagtails become sexually active at different, though overlapping, time. In our opinion, it is related to the earlier arrival of males of the masked wagtail to the nesting sites. In late April the testes of *M. (a.) personata* were significantly bigger than in *M. a. baicalensis* ($p = 0.04$) (Fig. 5). At this time the majority of the males of *M. a. baicalensis* were still in the flocks, they rarely sing, did not show any signs of antagonism to each other, and did not react to the playback of song. At the same time males of *M. (a.) personata* began to occupy nesting sites and mark them.

Although our data are insufficient to make final conclusions, we traced the tendency to earlier breeding of masked wagtails in Tuva (see Fig. 4). The latest nesting males were represented by white wagtail and hybrids close to it in appearance. In our opinion, there some hiatus in times of nesting of pairs of different phenotypical composition reflecting the beginning of male sexual activity. Thus, the times of pair forming overlap widely but not entirely, which can serve as a mechanism supporting a certain level of isolation.

In northern area of contact the brooding begins 18–24 days later than in Tuva (our data). Although we do not have information on the time of pair forming in this area, we can make certain conclusions on the reasons for a higher level of hybridization in the middle Yenisei, provided that the assumption on the significance of the arrival dates to the nesting sites is true. The time of arrival of the wagtails to the taiga habitats is determined by presence of food resources, which become available later there than in Tuva. Near Krasnoyarsk the spring migration goes in two stages. Local birds appear in late March–early April. The second peak of spring migration begins in late April–early May and lasts until early June (our data). At this time the mixed flocks are watched consisting of *M. alba* and *M. (a.) personata*, apparently originating from the area of hybridization, since a significant number of the individuals wear hybrid features. It appears that white and masked wagtails arrival to the northern parts of the contact area is more strongly synchronized with climate conditions than in Tuva resulting in a larger overlap in dates of the pair forming in the north and, consequently, in a larger rate of mixed pairs.

CONCLUSIONS

We believe that the masked wagtail is at an early stage of isolation and differs from the other members of the complex *Motacilla alba* sensu lato primarily in its coloring and size characteristics. The breeding range of this form in the south of Siberia is surrounded by range of white wagtail (represented by two geographical races), however, the zones of intensive hybridization are significantly smaller than the territory of their allopatric distribution. In spite of introgressive hybridization, the distribution of the intermediate phenotypes differs from normal intergradation transition between "typical subspecies", which is likely to indicate an existence of a certain level of reproductive isolation. Our

data did not confirm the assumption of presence of ethological barriers. The survival rate and reproduction of the hybrids do not differ from those of parental forms, however, our data were obtained in areas of accumulation of the hybrids, so we cannot exclude that outside the zone of sympatry the hybrids have the rate reproductive success equal to that of the parental forms. There are certain differences in the habitat preferences, however, they are able to result in habitat segregation only in the territories poorly developed by humans. The anthropogenic landscape in this case can play the role of ecotone, providing favorable conditions to the hybrid individuals, even if they are less competitive. We suppose that hybridization is limited primarily by the differences in the dates of arrival and beginning of sexual activity in males.

The industrial development of the Yenisei valley drove the masked wagtail into the taiga zone, which resulted in the increased level of hybridization due to forced symbiotopy and larger overlap in dates of beginning of sexual activity.

The presence of the limited hybridization indicates that this situation cannot be regarded as a case of appearance of the secondary intergradation zone between populations of subspecific level. In our opinion, the masked wagtail belongs to a separate evolutionary branch (conforming the definition of semispecies in terms of biological concept) including *M. (a.) personata* and *M. (a.) alboides* Hodgson, 1836, inhabiting Pakistan, Northern India, Northern Myanmar [26], and Northern Vietnam [14]. In addition to the similar traits of coloring topography of these forms, this conclusion is corroborated by data on hybridization of *M. (a.) personata* and *M. (a.) alboides* in Northern Pakistan [28], as well as on existence of clinal morphological transition between them in Eastern Iran [29]. Clearly transitional individuals from Southern Kazakhstan, Kyrgyzstan, Turkmenistan, and North-West China are studied in the collections of ZISP, ZMMU, IZRK. The evolutionary affinity of *M. (a.) alboides* and *M. (a.) personata* is also confirmed by molecular-genetic data [14].

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