

Hybridization as a result of spatial and reproductive interactions between species within the group of ‘yellow’ wagtails (Aves, Motacillidae) in areas of sympatry

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article info

key words

sympatry, species, reproductive relationships, hybrid, evolution, population, wagtails

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article history

Submitted: 07.12.2020. Revised:
15.06.2021. Accepted: 22.11.2021

cite as

Artemieva, E. 2021. Hybridization as a result of spatial and reproductive interactions between species within the group of ‘yellow’ wagtails (Aves, Motacillidae) in areas of sympatry. *GEO&BIO*, 21: 125–152. [In English]

abstract

The area of overlapping ranges, contact and relationships of two closely related species — the western yellow wagtail *Motacilla flava* Linnaeus, 1758 and the yellow-headed wagtail *Motacilla lutea* (Gmelin, 1774) — in the Volga region are the subject of the present study. At present, under conditions of wide sympatry, there is spatial and reproductive interaction between these closely related species — the western yellow and yellow-headed wagtails. Crossbreeding of species of ‘yellow’ wagtails gives a light-headed form of hybrids, which is a marker of the hybrid zone in the Volga region. As a result of the study of the interaction between *M. flava* and *M. lutea* in their contact zone in overlapping areas of species ranges, the following was revealed. The concept of a system of traits of the light-headed hybrid form (*M. f. beema* × *M. lutea*), marking the hybridization zone of the model species *M. flava* and *M. lutea*, is postulated. The population characteristics of this system have been determined and the possibility of their use in population and evolutionary studies of a group of species of ‘yellow’ wagtails has been shown. As a result of the spatial and reproductive interaction of species in populations, the light-headed hybrid form (*M. f. beema* × *M. lutea*) is formed, which integrates the characters of the two original species and has its own, peculiar traits, which can mark the boundaries between the western (left-bank) and eastern (right-bank) groups of populations and the boundaries of their distribution. On the basis of this, differences are formed and divergence of these groups of populations occurs, which may reflect the processes of sympatric speciation. The revealed tendencies in the variability of groups of characters in the space of the ranges of model species have a clinal character and may indicate the directions of microevolution of species. The identified hybrid zones within the boundaries of species ranges have a central position. The results of spatio-temporal divergence are *M. flava*, *M. lutea*, and their hybrid light-headed form *M. f. beema* × *M. lutea*, which may later become an independent species. In the contact zone of *M. flava* and *M. lutea*, there is an unlimited hybridization of these species.

Гібридизація як результат просторових і репродуктивних взаємин видів у групі жовтих трясогузок (*Aves*, *Motacillidae*) в областях симпатрії

Єлена Артем'єва

Резюме. Зона перекриття ареалів, контакт і взаємини близьких видів — жовтої *Motacilla flava* Linnaeus, 1758 і жовтолобої *Motacilla lutea* (S. G. Gmelin, 1774) плисок на території Поволжя є предметом вивчення в даній роботі. В даний час в умовах широкої симпатрії спостерігається просторова і репродуктивна взаємодія двох близьких видів — жовтої і жовтолобої плисок. Схрещування близьких видів жовтих плисок дає світлоголову форму гібридів, яка є маркером гібридної зони в Поволжі. В результаті проведеного дослідження взаємодії видів *M. flava* і *M. lutea* в зоні їх контакту в областях, де перекриваються їхні ареали, досягнуто наступне. Сформульовано поняття системи ознак світлоголової гібридної форми (*M. f. beema* × *M. lutea*), марковано зону гібридизації модельних видів *M. flava* та *M. lutea*. Визначено характеристики популяцій цієї системи та показана можливість їх використання в популяційних і еволюційних дослідженнях групи видів «жовтих» плисок. В результаті просторової та репродуктивної взаємодії видів в популяціях формується світлоголова гібридна форма (*M. f. beema* × *M. lutea*), яка інтегрує ознаки двох вихідних видів і володіє особливостями, властивими лише їй, які можуть маркувати межу між західною (лівобережною) та східною (правобережною) групами популяцій та межі їх поширення. На основі цього формуються відмінності та відбувається дивергенція даних груп популяцій, які можуть відображати процеси симпатричного видоутворення. Результатом просторово-часової дивергенції груп популяцій (західної і східної) є *M. flava*, *M. lutea* та їх гібридна світлоголова форма *M. f. beema* × *M. lutea*, яка в подальшому може стати самостійним видом. У зоні контакту *M. flava* і *M. lutea* відбувається необмежена гібридизація даних видів. В даний час відбувається активний процес генетичної гібридизації з утворенням проміжних гібридних форм на основі генетичного прошарку гібридів в популяціях. Дане явище може виступати в якості генетичного підживлення і механізму підтримки цілісності видів «жовтих» трясогузок за рахунок постійної міжвидової гібридизації в умовах широкої симпатрії.

Ключові слова: симпатрія, вид, репродуктивні взаємини, гібрид, еволюція, популяція, трясогузки.

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Introduction

The area of overlapping ranges, contact and relationships of two closely related species — the western yellow wagtail and the yellow-headed wagtail — in the territory of the Volga region are the subject of study in this work. At present, under conditions of wide sympatry, there is a spatial and reproductive interaction between these two closely related species (Vaurie 1959; Zaykin & Pudovkin 1993; Hewitt 2001). The study of this type of relationship is a separate line of research on biodiversity at the species and population level (Alström & Mild 2003; Baker *et al.* 2009). 'Yellow' wagtails can be the object of special evolutionary studies due to the ability to crossbreed between closely related species (allospecies and sibling species) (Zagorodniuk & Fesenko 2004; Lamichhancy *et al.* 2018).

Crossing of closely related species of 'yellow' wagtails produces a light-headed form of hybrids, which is a marker of the hybrid zone in the Volga region. Hybridization as a result of spatial and reproductive relationships of species in the group of 'yellow' wagtails (Passeriformes, Motacillidae) under conditions of their co-existence in overlapping areas of ranges remains poorly studied (Dement'ev 1937, 1941; Cramp 1988). This work is devoted to the study of spatial and reproductive interaction between the western yellow wagtail *Motacilla flava* L., 1758 and the yellow-headed wagtail *Motacilla lutea* (Gmelin, 1774) in the contact zone of their populations. One of the consequences of this process is the discovery of western yellow and yellow-headed wagtails in populations of their light-headed hybrids (Zarudny 1891; Fedorovich 1915; Artobolevsky 1924). There is a view that the western yellow wagtail gradually 'engulfs' the yellow-headed wagtail as a species and eventually it would disappear (Sotnikov 2006; Zav'lov *et al.* 2009).

Hybrid forms of western yellow and yellow-headed wagtails have a strongly bleached, whitish colouration of the plumage of the head and morphologically resemble the real white-headed wagtail *Motacilla flava leucocephala* (Przewalski, 1887), an endemic, breeding and migratory subspecies, the range of which is associated with Central Asia. One of the reasons for the sharp decline in the number of this subspecies over the past 20 years is its hybridization with another subspecies of the western yellow wagtail, *Motacilla flava beema* Sykes, 1832 (Baranov 2012). However, in a number of traits, light-headed hybrids differ well from the real subspecies *M. f. leucocephala* (Artemieva & Muraviev 2012; Sundev & Leahy 2019; Ferlini *et al.* 2021). For ‘yellow’ wagtails, hybrids of the western yellow wagtail *M. flava* with the black-headed wagtail *Motacilla feldegg* Michahelles, 1830 are also known (Artemyeva & Muraviev 2012; Ferlini 2015, 2016). Interspecific hybridization with a change in range boundaries and expansion of range boundaries of original forms is also relevant for mammals (Zagorodniuk 2011) as the invasion of genomes in many species of animals and plants (Mallet 2005, 2008), including birds of different taxa (Zink *et al.* 1995; Hermansen *et al.* 2001; Frank & Scott 2011).

The aim of this work is to reveal the features of the spatial and reproductive interaction between *M. flava* and *M. lutea* in the contact zone of their populations under sympatric conditions.

Taxonomic relations of species of the genus *Motacilla*, subgenus *Budytes*

The species complex of ‘yellow’ wagtails, genus *Motacilla* Linnaeus, 1758, has been one of the most problematic taxonomic groups. Until now, the taxonomic status and systematic relationships between the species (forms?) of this group have remained completely unclear.

‘Yellow’ wagtails (*Motacilla flava* L., *Motacilla feldegg* Michah., and *Motacilla lutea* Gm.), along with closely related citrine wagtail (*Motacilla citreola* Pall.) and mountain wagtail (*Motacilla cinerea* Tunst.), form an independent subgenus *Budytes* Guw, 1817 (Suschkin 1925; Grant & Mackworth-Praed 1952; Portenko 1960).

The yellow-headed wagtail and the mountain wagtail have always been considered separate species (Dement'ev 1937; Gladkov 1954). The yellow-headed wagtail and the mountain wagtail are species in the group of ‘yellow’ wagtails, which do not raise doubts about their species status (Portenko 1960; Cramp 1988; Koblik *et al.* 2006).

Harris *et al.* (2018), based on SNP nuclear markers, showed that there is one species, *Motacilla flava*, which includes several subspecies (*Motacilla flava*, *M. lutea*, *M. feldegg*, *M. taivana*, and *M. macrorynx*).

The black-headed wagtail forms two subspecies: *Motacilla feldegg feldegg* Michahelles, 1830, which is distributed in the Black Sea coast, Crimea, and the Caucasus (western part of the range), and *Motacilla feldegg melanogrisea* (Homeyer 1878), which occurs in the Volga Delta, Caspian Sea coast, Orenburg Oblast (Zarudny 1891), Krasnoyarsk Krai (Arlott & Khrabry 2009), and Irkutsk Oblast (eastern part of the range) (Stepanyan 2003; Koblik *et al.* 2006).

E. Mayr (1968) paid great attention to the taxonomic relationship of *Motacilla flava* L. and *Motacilla lutea* Gm. In particular, he noted that ‘... the taxonomic position of *Motacilla flava* L., a highly variable population, is very difficult and important for understanding of the theory of speciation. It would be interesting to find out in detail the relationship of yellow-headed and green-headed forms (*flavissima*, *lutea*, *taivana*), is there a species difference between *M. flava* and *M. lutea*, and, finally, what are the historical and ecological features (reasons) of distribution of yellow wagtails? Although the majority of researchers recognize their systematic closeness, a systematic analysis of this issue and a detailed study of the distribution and reproduction of these birds in natural conditions is necessary’ (Mayr 1968: 117).

The second point of view on the isolation of *M. lutea* as an independent species was proposed back in the 1920s by P. P. Sushkin (1925, 1938) and J. Domaniewski (1925), who considered the western yellow, yellow-headed, black-headed, and green-headed wagtails independent species. The last three forms in some regions were sympathetic with the first, which even then did not agree with the existing

concept of allopatric and conspecific subspecies (Semyonov-Tyan-Shansky 1910). G. Johansen (1946) considered *M. lutea* as an independent and more ancient species than other 'yellow' wagtails. At the same time, a different point of view about the taxonomic status of this form is widely spread.

The yellow-headed wagtail has long been considered by ornithologists as an independent species of the genus: *Motacilla lutea* Gm. — *Parus luteus* S. G. Gmelin (1774), Reisedurch Russland; *Budytes campestris* Pallas (1776); *Budytes flavifrons* Sewertzow (1875), as well as in Russian — 'steppe' wagtail (Ruzsky 1893), 'field' wagtail — (Pallas 1811; Bogdanov 1871; Volchanetsky 1972), yellow-backed wagtail (Gladkov 1954; Ivanov 1976; Priezzhev 1978; etc.).

The taxonomy of subspecies of the western yellow wagtail *M. flava* was presented for the first time by E. Hartert (1910; Hartert & Steinbacher 1933). He listed 19 subspecies, among which the yellow-headed wagtail (*M. f. lutea*) is also mentioned. For each subspecies, the boundary of the distribution areas was indicated (Witherby 1938; Smith 1950; Meinertzhagen 1954). The systematic scheme of E. Hartert was adopted by G. P. Dement'ev (1937) and G. Niethammer (1937). In some cases, *M. lutea* is described as a mutation of *M. flava* (Grote 1937; Dementyev 1941). E. Stresemann (1926) believed that the wide range of individual variability in *M. flava* is the result of 'genetic instability'. Other authors considered the yellow-headed wagtail to be one of the morphs of *M. f. beema* Sykes (Smith 1950; Beregovoy 1970). Considering the co-occurrence of *M. f. beema* and *M. f. lutea* in the Middle Volga region, H. Grot (Grote 1937) expressed the opinion that the yellow-headed wagtail's colouration is the result of 'genetic instability', in some cases in *M. f. beema*, and in some areas of the range of this subspecies the colouration is characteristic of the British *M. f. flavissima* Blyth. A similar idea of the nature of colouration in *Motacilla lutea* was expressed by G. P. Dement'ev (1941) and S. Smith (1950), without distinguishing *Motacilla lutea* as an independent species.

Of greatest interest is the work of C. Vaurie (1957), where he gives a brief description of the types of colouration of the *M. flava* complex on subspecies forms, as well as their ranges. In one of his subsequent works, Ch. Vaurie (1959) continues to consider the yellow-headed wagtail as a subspecies of the western yellow wagtail (*M. flava lutea*). Nevertheless, the author points out that such a characteristic can be considered temporary and that the taxonomy of *M. flava* does not correspond to the structure of the 'yellow' wagtail complex. Even then, he assumed the presence of several independent species in this complex. N. A. Gladkov (1954) suggested that *M. lutea* and *M. taivana* do not fit into the scheme of subspecies *M. flava* at all, having a common range with it. He considered expedient to consider them separately as part of the *M. lutea* species, to which he also assigned the English subspecies *M. lutea flavissima* (Stepanyan 2003).

In a number of works, the authors continue to insist that *M. lutea* is a subspecies of *M. flava* (Bub 1981; Blozheim 1985; Cramp 1988). This point of view is also shared by a number of authors (Alström & Mild, 2003; Harris et al. 2018). At the same time, in the summary by S. Cramp et al. (1988) it is noted that within this species there are two complexes of forms 'flava' and 'lutea', and the latter includes *Motacilla flava lutea*, *M. flava flavissima*, and *M. flava taivana*. It is appropriate to emphasize here that the views on the taxonomy of the genus *Motacilla* L. are mainly based on morphological characters (morphometry and colouration) and on the specifics of their geographical distribution (Smith 1950; Beregovoy 1970; Blozheim 1985). Grichik (2005), based on the variability of colouration of the plumage of these birds, depending on many reasons (individual variability, age, and geographical distribution), also defends the point of view on the subspecies status of the forms *Motacilla flava lutea* and *M. flava taivana*. The author does not take into account that one of the discussed forms of *Motacilla lutea* Gm. exists in the centre of the range of *Motacilla flava* L. and is sympatric with various subspecies of the latter.

Jan Domanevski (1925) tried to revise the entire subgenus *Budytes*. He assumed the presence of four independent species of these wagtails: *B. flava* L., including 6 subspecies, *B. feldegg* Mich. — two subspecies, *B. lutea* Gm. — two subspecies and *B. taivana* Swinhoe (monotypic species). He justified the species status of *M. lutea* in connection with its partial sympathy with the grey-headed

forms of the 'flava' group. The point of view of L. S. Stepanyan (2003) coincides with the idea of Jan Domanevski, with the exception of only two amendments to the subspecies ranks in the western yellow and black-headed wagtails, in which the author additionally distinguishes one more subspecies. Currently, six species of wagtails *Motacilla flava*, *M. feldegg*, *M. lutea*, *M. citreola*, *M. taivana*, *M. cinerea* are distinguished in the group of 'yellow' wagtails (Babenko 1981; Bakhtadze & Kazakov 1985; Stepanyan 2003; Koblik *et al.* 2006).

Aleksandr Ivanov (1935) was the first to describe three types of age-related variation in the colouration of the head of male yellow-headed wagtails: 1) the first breeding dress of males with an entirely light green top of the head; 2) with a yellow forehead and green crown and occiput — males at the age of 2–3 years; 3) with an entirely yellow head (sometimes with a small number of green feathers on the back of the head) — birds of four years and older. The males of *M. lutea* are polymorphic in head colouration, as in *M. flava*, and this served as the basis to justify hybrid individuals (Portenko 1960; Gavrilov 1970; Bakhtadze & Kazakov 1985) and high individual variation within *M. flava* (Beregovoy 1970). A. I. Ivanov's point of view was adopted by a number of authors (Williamson 1955; Svensson 1963; Stepanyan 2003).

The differences in colouration that exist in adult males of *M. flava* living within the same territory allowed some ornithologists (Grant & Mackworth-Praed 1952) to distinguish 7 species (*flava*, *lutea*, *superciliaris*, *leucocephalus*, *personifuses*, *thunbergi*, and *feldegg*). This division of the group of 'yellow' wagtails did not receive proper recognition.

At the end of the 19th century, two works by N. A. Zarudny (1891) were published, where the author describes the hybrid forms of *M. flava* and *M. lutea*. Interspecific hybrids of *M. flava* and *M. taivana* were noted by V. G. Babenko (1981), although it was not possible to find mixed pairs themselves (Bianki 1910; Portenko 1960; Stepanyan 2003). A number of articles are devoted to the problems of hybridization of 'yellow' wagtails at intraspecific level (Smith 1950; Leisler 1968; Sammalisto 1968).

Hybridization between the species of the compared wagtails is usually not widespread; on the contrary, it is extremely rare (Beregovoy 1970; Kishchinsky & Lobkov 1979). Ch. Vori (1959) indicates the hybridization of *M. feldegg* and *M. lutea*, which is refuted by the studies of G. B. Bakhtadze & B. A. Kazakov (1985). He points out that no hybrids were recorded in the sympatry zone of *M. flava* and *M. lutea*. The appearance of 'green' feathers on the vertex ($P < 0.05$) in the contact zone between *M. flava* and *M. lutea* and partial or complete 'yellow' eyebrows is more common outside the spatial contact. The author suggests that hybridization in *M. flava* is more characteristic at intraspecific than at interspecific level. N. N. Balatsky (1992) managed to find a nest of a hybrid pair of wagtails: male *M. citreola*, female *M. flava*. When it comes to the finds of hybrids, determined only on the basis of the description of the colouration of the plumage, the question always arises, how can this be verified? It is known that females of all 'yellow' wagtails are outwardly almost indistinguishable (with the exception of the eastern forms). In this case, the only and convincing evidence of hybridization is chromosome analysis or long-term observations of individually tagged birds (Muravyov 1997, 2010; Artemyeva & Muravyov 2012).

Thus, based on morphological characters (mainly, morphometric parameters and colouration of the plumage of males during breeding season), there are currently three points of view on the taxonomic structure of the polytypic complex of 'yellow' wagtails:

1. All 'yellow' wagtails, except for the yellow-headed and mountain wagtails, are subspecies of a polytypic species.
2. There are five polytypic species: *M. flava* (*flava*, *thunbergi*, *beema*, *leucocephala*, *zaissanensis*, *plexa*, *macronyx*, *alascensis*, *simillima*, *tschutschensis*, *cinereocapilla*, *iberiae*, *pygmaea*), *M. feldegg* (*feldegg*), *M. melan melan* (*lutea*, *flavissima*, *taivana*) and *M. citreola* (*citreola*, *werae*, *quassatrix*, *calcarata*, *weigoldi*), and *M. cinerea* (*cinerea*, *melanope*, *robusta*, *schmidzi*, *flaviventris*, *clara*).
3. There are five polytypic species and three monotypic species of 'yellow' wagtails: *M. flava* (twelve subspecies); *M. feldegg* (two subspecies); *M. lutea* (two subspecies); *M. citreola* (four subspecies) and *M. werae*; *M. taivana*; *M. macronyx* (monotypic species); *M. cinerea* (six subspecies).

Since the present work did not set a special task of carrying out a taxonomic revision of the subgenus *Budytes*, studies of spatial relationships of *M. flava*, *M. feldegg*, *M. lutea*, *M. citreola*, and *M. cinerea* (Stepanyan 1990) were carried out in the zone of their sympatry in the study area, therefore the author adheres to the second point of view.

Materials and Methods

During the field seasons of 2013–2019, populations of ‘yellow’ wagtails were studied in areas of co-occurrence and nesting: western yellow wagtail *M. flava*, white-eared wagtail *Motacilla flava beema* (Sykes, 1832), and yellow-headed wagtail *M. lutea* in the Volga region (European part of Russia). The model sites are located in the territory of the SPNA ‘Sandy Lake’ in the Cherdaklinsky Raion (left bank) and in the territory of the new promising SPNA ‘Flooded solonchik meadows in the Tereshka River Floodplain’ in the Radishchevsky Raion (right bank) of Ulyanovsk Oblast (Volga Region), as well as in anthropogenically transformed areas (Artemyeva & Kalinina 2019; Artemyeva *et al.* 2019, 2020a–b; Ferlini & Artemyeva 2020). Range boundaries and the spatial position of the identified areas of sympatric speciation in the three species of ‘yellow’ wagtails — *M. flava*, *M. lutea*, and *Motacilla citreola* Pallas, 1776 — were mapped.

For molecular genetic analysis, eggs from clutches and rudimentary feathers of chicks of these species were examined.

Material and geography of samples: left bank (eastern bank of the Volga River). 20.05.2013, nearby to Cherdakly, Sandy Lake, 3 eggs of *M. lutea*; 25.05.2013, nearby to Cherdakly, Sandy Lake, 3 eggs of *M. lutea*; 23.05.2015, nearby to Cherdakly, Sandy Lake, 3 eggs of *M. lutea*; 7.06.2015, 4 eggs of *M. flava*; 7.06.2015, 4 eggs of *M. flava* × *M. lutea* hybrids; 21.05.2016, nearby to Cherdakly, Sandy Lake, 3 eggs from nest No. 1 of *M. flava*; 21.05.2016, nearby to Cherdakly, Sandy Lake, 3 eggs from nest No. 2 of *M. lutea*; 21.05.2016, nearby to Cherdakly, Sandy Lake, 3 eggs from nest No. 3 of light-headed hybrids of *M. flava* × *M. lutea*; 21.05.2016, nearby to Cherdakly, Sandy Lake, 2 eggs from nest No. 4 of *M. lutea*; 21.05.2016, nearby to Cherdakly, Sandy Lake, 4 eggs from nest No. 5 of the light-headed hybrid of *M. f. beema* × *M. lutea*; 5.06.2016, nearby to Cherdakly, Sandy Lake, 4 chicks (samples of feather rudiments) from nest No. 6 of *M. flava*; 19.06.2016 nearby to Cherdakly, Sandy Lake, 2 eggs from nest No. 7 (nest with feathers in the tray) of light-headed hybrids *M. f. beema* × *M. lutea*; 19.06.2016, nearby to Cherdakly, Sandy Lake, 3 eggs from nest No. 8 (nest with wool in a tray) of *M. lutea*; 11.05.2017, nearby to Cherdakly, Sandy Lake, 2 eggs of *M. lutea*; 27.05.2018, nearby to Cherdakly, Sandy Lake, 2 eggs of *M. flava*.

Material and geography of samples: right bank (western bank of the Volga River). 11.06.2018, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, nest No. 1, embryonic feathers from 3 chicks of the western yellow wagtail *M. flava* (3 specimens); 11.06.2018, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, nest No. 2, 2 eggs of *M. flava*; 11.06.2018, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, nest No. 3, embryonic feathers from 2 chicks of *M. flava* (2 specimens); 11.06.2018, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, nest No. 4, embryonic feathers from 2 chicks of *M. flava* (2 specimens); 11.06.2018, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, nest No. 5, embryonic feathers from 2 chicks of *M. flava* (2 specimens); 9.06.2019, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, 1st nest, rudimentary feather from chick of *M. flava*; 10.06.2019, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, 2nd nest, rudimentary feather from chick of *M. flava*; 10.06.2019, nearby to Radishchevo, meadows in the floodplain of the river Tereshka, 3rd nest, rudimentary feather from chick of *M. flava*. A total of 55 samples (23 samples of *M. flava*; 19 samples of *M. lutea*; 13 samples of *M. f. beema* × *M. lutea* hybrids) were examined for molecular genetic analysis.

To compare the parameters of nests and clutches of *M. flava*, we used oological materials of this species (Catalogue of the Oological Collection of the National Museum of Natural History, NAS of Ukraine: Peklo 2018). For bioecological studies, material on finds of nests of model species was used. A total of 18 nests were examined (9 nests of *M. flava*; 4 nests of *M. lutea*; 5 nests of *M. f. beema* × *M. lutea* hybrids). The dataset ‘Records and Characteristics of Nests of the Yellow Wagtail *Motacilla flava* in the Middle Volga Region’ is deposited on ResearchGate: <https://www.researchgate.net/publication/356473899>

Isolation of DNA from biological samples (eggs, feathers, etc.). The material was homogenized using Speed-Mill (Analytik Jena) in a lysis solution (containing sodium dodecyl sulfate, 1%) using metal balls for 10 minutes; after which protease K (100 µl, mM / ml) was added and incubation was carried out at 56°C for 6 hours. Then the homogenized product was centrifuged and DNA was isolated from the obtained supernatant using the GeneJET Genomic DNA Purification Kit (Thermo Scientific).

Polymerase chain reaction. The mitochondrial cytochrome oxidase I (COI) gene was chosen as a genetic marker. Amplification was carried out using the primers BirdF1: TTCTCCAACCACAAAGACATTGGCAG and BirdR1: ACGTGGGAGATAATTCCAAATCCTG (Kerr et al., 2009). When performing PCR, the following composition of the reaction mixture (per 20 µL) was used: buffer (1X), primers (0.5 µM each), dNTPs (250 µM), taq polymerase (5 units), DNA template (1 µL), and deionized water (up to the final volume). Amplification was performed using a SpeedCycler 2 thermal cycler (Analytik Jena). Polymerase chain reaction (PCR) parameters were as follows: 5 minutes at 94°C, 30 seconds at 94°C, 30 seconds at 52°C and 40 seconds at 72°C (35 cycles total). The final elongation lasted 5 minutes at 72°C. Next, electrophoresis was carried out in 1% agarose gel in order to determine the quality of the PCR performed, after which a preparative gel was prepared, from which the fragment of interest was isolated and purified (using the GeneJET Gel Extraction Kit (Thermo Scientific)).

Fragment sequencing and bioinformatics processing. The resulting PCR products (about 600 bp in length) were purified and a sequencing reaction was performed with fluorescently labeled dideoxynucleotides triphosphate (ddNTPs), followed by purification of the set of terminated fragments. As a result of sequencing the obtained fragment of the cytochrome oxidase I gene, nucleotide sequences were obtained, which were subjected to bioinformation processing. The fragment was analyzed and corrected using the Sequence Scanner 2 software (Life Technologies Corporation) [<http://www.lifetechnologies.com>]. The alignment and construction of phylogenetic trees was carried out using the MEGA 4 software package (Tamura et al. 2007). In the MEGA 4 program, trees were constructed using the Maximum parsimony method to test the stability of phylogenetic constructs, a bootstrap test was used. For comparison, the sequences of *M. alba* (KY754516.1), *M. grandis* (JF499146.1) and *M. tschutschensis* (DQ433818.1) were selected from GenBank (Kerr et al. 2007, 2009; Johnsen et al. 2010; Artemieva et al. 2016a–b).

Results

As a result of studying the spatial and reproductive relationships of species of ‘yellow’ wagtails *M. flava* and *M. lutea*, the analysis of the characters of their light-headed hybrid form *M. f. beema* × *M. lutea* and identified areas marked by it in the contact zone of populations of model species under sympatric conditions was carried out.

Light-headed hybrids — hybrid zone markers

This section discusses the features of the light-headed hybrid form of *M. f. beema* × *M. lutea*, described in this work as ‘light-headed hybrids,’ which is characterized by the manifestation of various groups of characters (morphological, geographical, ecological (nidological), and behavioural).

Morphological and geographical characteristics of hybrids

In the study area, in the areas of overlapping ranges of *M. flava* and *M. lutea*, sightings of their hybrids were recorded, which have a characteristic morphological feature — a strongly bleached, whitish colouration of the plumage of the head that morphologically resembles that of a real white-headed wagtail. Geographically, these hybrids are associated with the Volga region. The characteristic distinctive features of the colouration of the plumage of the head of male *M. flava*, *M. lutea* and their light-headed hybrid are shown in Fig. 1. Regions where areas of sympatric speciation are noted are shown on a map of the ranges of ‘yellow’ wagtails that co-occur (Fig. 2) (Artemieva & Muravyov 2012).

Nidological (ecological) characteristics of hybrids

Samples of nests and clutches of model species *M. flava*, *M. lutea* and their light-headed hybrid form *M. f. beema* × *M. lutea* are presented in the Appendix to this article (see below).

To compare the parameters of nests and clutches of *M. f. flava*, oological material on this species from the western regions of its range was used, which illustrates the similarity of nesting biotopes and differences in the size of nests and eggs (Catalogue of the Oological Collection of the National Museum of Natural History, NAS of Ukraine — collections of O. Kistiakivsky, V. Zubarovsky, V. Terebkov, Yu. Faidel, V. Shevchenko, and L. Kremnev) (Peklo 2018). In general, the nests and eggs of *M. flava* collected in the western areas of the range are larger than those from the Middle Volga region, which is due to the belonging of populations to different subspecies: in Ukraine, the subspecies *M. f. flava* is distributed (Panchenko 2007), while in the Middle Volga region populations are represented by the subspecies *M. f. beema* and hybrids *M. f. flava* × *M. lutea* and *M. f. beema* × *M. lutea*.

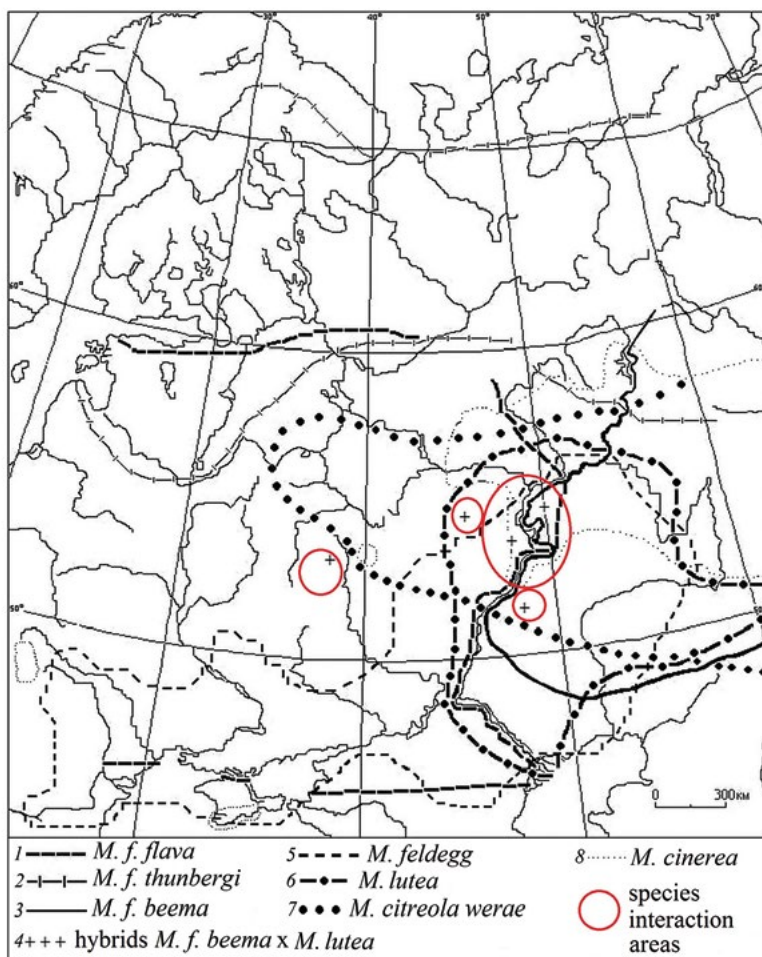


Fig. 1. Males of 'yellow' wagtails: *a* — western yellow wagtail *M. flava flava* (author's photo), *b* — yellow white-eared wagtail *M. flava beema* (author's photo), *c* — yellow-headed wagtail *M. lutea* (author's photo), *d* — light-headed hybrid form *M. f. beema* × *M. lutea* (photo by T. Kezhevatoва).

Рис. 1. Самці «жовтих» плисок: *a* — жовтої *M. f. flava* (фото автора), *b* — жовтої білоухої *M. f. beema* (фото автора), *c* — жовто-лобої *M. lutea* (фото автора), *d* — світлоголової гібридної форми *M. f. beema* × *M. lutea* (фото Т. Кежеватової).

Fig. 2. Geographical ranges and areas of spatial and reproductive interaction of species of 'yellow' wagtails in the territory of the Volga region and adjacent regions of Eastern Europe (orig.): 1 — *M. f. flava*, 2 — *M. f. thunbergi*, 3 — *M. f. beema*, 4 — light-headed hybrid form *M. f. beema* × *M. lutea*; 5 — *M. feldegg*; 6 — *M. lutea*; 7 — *M. citreola werae*; 8 — *M. cinerea*. The red circle indicates the areas of interaction of the species.

Рис. 2. Ареали і області просторового та репродуктивного взаємодії у видів «жовтих» плисок на території Поволжжя та в суміжних регіонах Східної Європи (ориг.): 1 — *M. f. flava*, 2 — *M. f. thunbergi*, 3 — *M. f. beema*, 4 — світлоголовий гібридної форми *M. f. beema* × *M. lutea*; 5 — *M. feldegg*; 6 — *M. lutea*; 7 — *M. citreola werae*; 8 — *M. cinerea*. Червоним колом позначені області взаємодії видів.



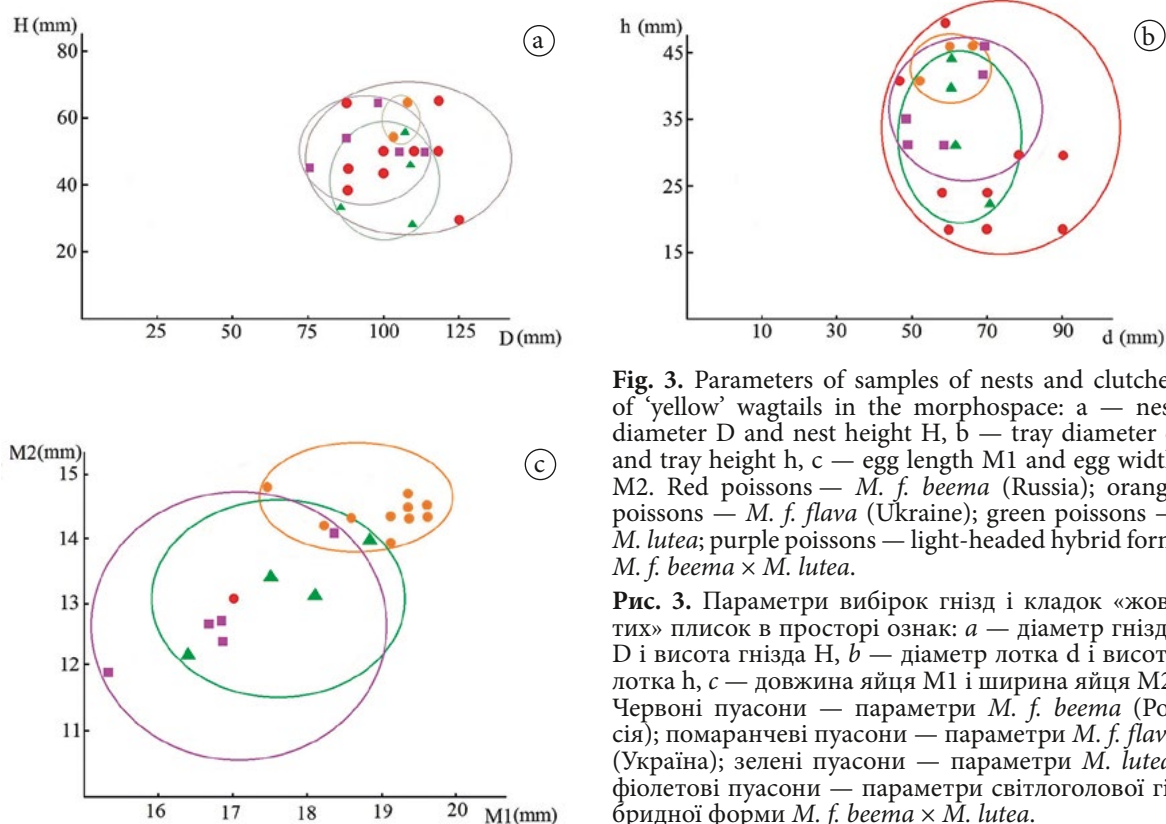


Fig. 3. Parameters of samples of nests and clutches of 'yellow' wagtails in the morphospace: a — nest diameter D and nest height H, b — tray diameter d and tray height h, c — egg length M1 and egg width M2. Red poissons — *M. f. beema* (Russia); orange poissons — *M. f. flava* (Ukraine); green poissons — *M. lutea*; purple poissons — light-headed hybrid form *M. f. beema* × *M. lutea*.

Рис. 3. Параметри вибірок гнізд і кладок «жовтих» плисок в просторі ознак: а — діаметр гнізда D і висота гнізда H, б — діаметр лотка d і висота лотка h, c — довжина яйця M1 і ширина яйця M2. Червоні пуасони — параметри *M. f. beema* (Росія); помаранчеві пуасони — параметри *M. f. flava* (Україна); зелені пуасони — параметри *M. lutea*; фіолетові пуасони — параметри світлолової гібридної форми *M. f. beema* × *M. lutea*.

Comparison of generalized values of parameters of the samples of nests and eggs shows the originality of their species: the largest nests and eggs in the western yellow wagtail *M. flava*, the smallest in the hybrid light-headed form *M. f. beema* × *M. lutea*, and average-sized nests and eggs in *M. lutea*. At the same time, the range of variation of the length and width of eggs in *M. flava* and light-headed hybrids practically coincides, while in *M. lutea* the range of variation of egg length is more stable in comparison with the width. The extreme values of the parameters of samples of nests and eggs of the model species *M. flava*, *M. lutea* and the light-headed hybrid *M. f. beema* × *M. lutea* are well distinguishable in the morphospace (Fig. 3).

The revealed atypical cases of lining of the nest tray are associated with the presence of down and feathers in the litter, without the addition of horsehair by birds during the construction of the nest. The atypical lining of the nest tray is due to the presence of mixed nesting pairs: female yellow-headed wagtails *M. lutea* build nests characteristic of their species. In the case of an extreme breeding season, a second clutch occurs (instead of the lost one), the clutches are strongly stretched in time. Examples of nests of all model species are shown in Fig. 4.

Oological (morphological) characteristics of hybrids

The oological characteristics of hybrids include the colouration and patterns of the eggshell. Parameters of eggs in clutches of *M. flava*, *M. lutea*, and their light-headed hybrids are given in the Appendix (see below).

The eggs of the western yellow wagtail *M. flava* are characterized by the following features: the background of the egg surface is greyish-beige, the pattern is dense, uniform, brownish-brown. The hairline is developed to half the perimeter of the egg.

The eggs of the yellow-headed wagtail *M. lutea* are characterized by a greyish-olive or light beige with a shade of khaki color of the background of the eggshell. The pattern of the surface of the eggshell is dense, pinpoint, brownish brown. The hairline is well defined at the infundibular end.



Fig. 4. Nests of 'yellow' wagtails: *a* — yellow white-eared wagtail *M. f. beema*, *b* — yellow-headed wagtail *M. lutea*, *c* — light-headed hybrid *M. f. beema* × *M. lutea* (with a predominance of *M. lutea* characters), *d* — light-headed hybrid form *M. f. beema* × *M. lutea* (with a predominance of *M. f. beema* characters). Photo by the author.

Рис. 4. Гнізда «жовтих» плисок: *a* — жовтої біловухої *M. f. beema*, *b* — жовтолобої *M. lutea*, *c* — світлоголової гібридної форми *M. f. beema* × *M. lutea* (з переважанням ознак *M. lutea*), *d* — світлоголової гібридної форми *M. f. beema* × *M. lutea* (з переважанням ознак *M. f. beema*). Фото автора.

Light-headed hybrids *M. f. beema* × *M. lutea*, in contrast to the original species *M. flava* and *M. lutea*, have different features of the background coloration and pattern of the eggshell surface. The background of the surface of the eggs is grey-milky-beige, light-grey-milky or whitish, the pattern is sparse, greyish-olive. The eggs are smaller and generally darker than those of *M. f. flava* and *M. f. beema*, but larger and paler than in *M. lutea* (in general, in appearance, it is closer to *M. lutea* than to *M. f. flava* and *M. f. beema*). Sometimes a wide dark-brown thickening, a spot or a ring at the infundibular end of small dark striated elements of the shell pattern is expressed.



Fig. 5. Coloration and patterns of eggshells of model species of 'yellow' wagtails: *a* — western yellow wagtail *M. flava*, *b* — yellow-headed wagtail *M. lutea*, *c* — light-headed hybrid form *M. f. beema* × *M. lutea* (predominance of characters from the female *M. f. beema*), *d* — light-headed hybrid form *M. f. beema* × *M. lutea* (predominance of characters from the female *M. lutea*). Photo by the author.

Рис. 5. Забарвлення і малюнок шкаралупи яєць модельних видів «жовтих» плисок: *a* — жовтої *M. flava*, *b* — жовтолобої *M. lutea*, *c* — світлоголової гібридної форми *M. f. beema* × *M. lutea* (переважання ознак від самки *M. f. beema*), *d* — світлоголової гібридної форми *M. f. beema* × *M. lutea* (переважання ознак від самки *M. lutea*). Фото автора.

There is no hairline or it is displaced, in the form of a loop. The pattern is brown or dark brown, dense, with a rather large spot. Sometimes a very dense pattern is developed, thickening at the infundibular end into a common dark spot.

Examples of clutches of all model species are presented in Fig. 5.

Behavioural characteristics of hybrids

In *M. flava* and *M. lutea*, two peaks of daily nesting activity are well pronounced — in the morning (from 4:00 to 11:00) and in the afternoon (from 16:00 to 19:00), from 12:00 to 16:00. Birds can fly off to feed and rest to the nearest body of water. In hybrids of yellow white-eared and yellow-headed wagtails *M. f. beema* × *M. lutea*, on the other hand, there is a pronounced twilight nesting activity (from 20:00 to 24:00). Territorial males actively sing on the nesting site at dusk, after sunset. The color of the head plumage in males is very light, whitish ('grey-haired') and is clearly visible from a distance at dusk. Light, whitish, 'grey-haired' plumage of the head has a signal value. In addition, the sound signals of light-headed hybrids also have important signaling significance. A. B. Kistiyakovsky (1967) and E. N. Panov (1973, 1989, 1993) attached great importance to the study of visual and verbal characters in the process of sympatric speciation of sibling species in birds.

The spectrum of behavioural repertoire of species of the group of 'yellow' wagtails in the space of their ranges under conditions of wide sympatry reflects the mechanisms of reproductive isolation of forms of species and subspecies ranks and is the result of microevolution of the group. Currently, studies have shown that in order to resolve controversial issues in the taxonomy of closely related bird species, complex approaches and methods of study are required, including ecological and ethological ones (Panov 1973). The study of model species *M. flava*, *M. lutea*, and their light-headed hybrids in natural communities should be carried out in ecological and behavioural aspects (phenology of arrival and nesting, mating, peculiarities of choosing a suitable nesting biotope, nesting and size of the nesting site, incubation, acoustic signaling, etc.). Many authors propose to solve the problems of intraspecific and species systematics of polytypic complexes of birds using sonograms of recordings of their voices (Panov 1973).

Observations and study of behaviour (ethology) in birds (postures of mating, courtship, aggression, etc.) are one of the important directions in resolving controversial issues within one or several taxa (Panov 1993). Territorial behaviour: in the zones of spatial contact of the compared species, there are quite pronounced species-specific requirements for the nesting place (Panov 1993). Mating behaviour: observation and study of behaviour in birds (postures of mating, courtship, aggression, etc.) is one of the important directions in resolving controversial issues within the framework of one or several taxa (Panov 1989). Sound signaling has an important place in communication of birds at the intraspecific level, which allows them to maintain contact with each other, guard the nesting area, warn neighbouring nesting pairs of danger, etc. Sound signaling in birds has a species-specific character, which, in turn, at the interspecific level is one of the conditions of reproductive isolation (Panov 1993). An important role in relations at the inter- and intraspecific levels is played by mating acoustic signals, which have a clear specific, situational significance and difference, being the basis of sound communication in joint group nesting settlements (Panov 1989).

Discussion

Ecological and genetic characteristics of light-headed hybrids

Previously, it was shown that the very existence and distribution of *M. lutea* directly depends on the phenomenon of interspecific and intraspecific hybridization of these forms (Sotnikov 2006; Pavlova *et al.* 2003; Artemieva *et al.* 2016a–b), and also some authors prove that all intraspecific forms of *M. flava* are either subspecies or races (Alström & Ödeen 2002; Alström & Mild 2003; Alström *et al.* 2018; Harrisa *et al.* 2018).

Selected sequences from GenBank for *M. alba* (KY754516.1), *M. grandis* (JF499146.1), and *M. tschutschensis* (DQ433818.1), which constitute the outgroup for comparison of the obtained results (Figs. 6–7), confirm the taxonomic independence of the studied forms of ‘yellow’ wagtails.

Light-headed hybrids *M. f. beema* × *M. lutea* are first generation hybrids that act as markers of hybrid zones of interaction between *M. flava* and *M. lutea* under sympatric conditions. The unusual appearance of the hybrid — the appearance of a clearly pronounced whitish colour of the head — is a phenotypic trait that is not traced in any of the parent taxa and it is explained by the complementary action of the genes of pigments of the head plumage, that is, the grey phenotype in *M. flava* and the yellow phenotype in *M. lutea*, which is probably due to the interaction of the corresponding alleles of the head plumage colouration gene.

Phenotypic and genotypic structure of *M. flava*

The colour of the plumage of the upper part of the head of male western yellow wagtails *M. flava* varies geographically in a wide range from white to black. However, in most of the range, their head is coloured bluish-grey or lead-grey. *M. f. flava* predominates in the southern part, while *M. f. thunbergi* in the northern part of the range. Moreover, throughout the entire area of its distribution, *M. f. thunbergi* occurs sympatrically with *M. f. flava* and crossbreeds freely with it. In the entire area of the north-eastern part of the range, specimens with intermediate characters are found, demonstrating all variants of transitions between these forms. In some places, individuals with intermediate traits even numerically dominate over the original, pure phenotypes (Sotnikov 2006). The available information on the ecological specificity of the *thunbergi* form indicates a more frequent nesting of these birds in peat bogs and raised sphagnum bogs, while *flava* individuals usually settle in floodplain meadows. A large number of cases of joint nesting of *thunbergi* individuals in mixed settlements with *flava* in floodplain habitats and in fields are known (Sotnikov 2006). Despite this, biotopic preferences, food supply, sound signaling, and behavioural features of *flava* and *thunbergi* are generally quite different, which makes it possible to consider these forms at species level, which is confirmed by a comparative analysis of mitochondrial DNA (Sotnikov 2006).

The forms *M. f. flava*, *M. f. thunbergi*, *M. f. beema*, and *M. f. leucocephala* are likely the result of intraspecific genotypic cleavage of *M. flava*. In this case, two schemes of such splitting are possible: by the type of incomplete dominance and by the type of complementarity. The considered diagnostically important inherited trait is the colour of the plumage of the ear region. Inheritance pattern with incomplete dominance: *M. f. flava* — grey ear (heterozygous genotype Aa), in *M. f. thunbergi* — black ear (homozygous dominant AA genotype), in *M. f. beema* — white ear (homozygous recessive genotype aa). When crossing in populations of phenotypes with black and white ears, heterozygous phenotypes with grey ears are constantly renewed in the first generation of hybrid individuals. In subsequent generations of hybrids, there is a constant split according to the genotype and phenotype — 1 AA (homozygous dominant black-eared *thunbergi*) : 2 Aa (heterozygous grey-eared *flava*) : 1 aa (homozygous recessive white-eared *beema*). Inheritance pattern with complementarity: *M. f. flava* — grey ear (genotypes A_bb), in *M. f. thunbergi* — black ear (genotypes A_B_), *M. f. beema* — white ear (genotypes aaB_), in *M. f. leucocephala* — completely white head (genotype aabb); alleles of this gene can be designated as follows: A — presence of pigment, aa — absence of pigment, B — black colour, bb — grey-blue (grey) colour. The ratio of genotypes and phenotypes in populations by area is 9 A_B_ (*M. f. thunbergi*) : 3 A_bb (*M. f. flava*) : 3 aaB_ (*M. f. beema*) : 1 aabb (*M. f. leucocephala*).

In isolated populations in certain part of the *M. flava* range, over time, a pattern of dominance of certain genotypes and the corresponding phenotypes of individuals may develop: in the northern parts of the range, the *thunbergi* form prevails, in the eastern areas of the range the *beema* form prevails, while in the mountains and steppes of Central Asia populations of the *leucocephala* form were formed facilitated by geographical and ecological isolation, which prevented the active drift of genes from neighbouring areas of the range and contributed to the accumulation of recessive alleles. The

Central Asian white-headed subspecies *M. f. leucocephala* probably has a completely recessive genotype (aabb), which is characterized by a complete loss of pigmentation in the plumage of the head. Due to the striking features of morphology, biology, and ecology, this form deserves to be assigned a species status. Certain ratios of genotypes and phenotypes throughout the geographic range can mark the areas of hybridization of these phenotypes.

Phenotypically, the forms *plexa* and *tschutschensis*, which are widespread in Eastern Siberia and in the north of the Far East, are similar in dark head colouration to the *thunbergi* form, however, genotypically these forms are completely different and have their own evolutionary fate, being, probably, independent species belonging to the eastern complex of 'yellow' wagtails (Pavlova *et al.* 2003).

The southern European form *M. f. dombrowski* Tschusi differs from *M. f. flava* with a darker colouration of the top of the head and a blackish colouration of the ear coverts, and probably also has a genotype of the A_B_ complex, like *thunbergi*; therefore, it is incorrect to consider this form as an independent taxon (Bakhtadze & Kazakov 1985).

Hybrids are known not only between subspecies of *M. flava*, but also between specific forms. Two closely related species — *M. flava* (subspecies *M. f. macronyx*) and *M. taivana* Swinh., 1863 — form hybrids in the Lower Amur region in their common habitats, their ranges overlap in a large area from the city of Amursk to Udył Lake (Babenko 1981; Stepanyan 2003). The area of distribution of *M. taivana* extends from the basin of the river Vilyuy and valley of the river Vitim to the east to the northern and western coasts of the Okhotsk Sea, to the north to the 64th parallel. To the south, it was recorded nesting in Primorye up to the 45th parallel. The area of distribution of *M. f. macronyx* extends from the Eastern Sayan to the east to the coast of the Okhotsk Sea and the Japan Sea, to the north up to about the 60th parallel, to the south to the state border of the Russian Federation (Stepanyan 2003).

Groups of identified hybrids *M. f. macronyx* and *M. taivana* have the following quantitative ratios: 5 (grey top of the head, several green feathers, no eyebrow — *M. flava*) : 2 (green top of the head, several grey feathers, yellow eyebrow — *M. taivana*) : 1 (green-grey top of the head, pale yellow eyebrow — *M. taivana* and *M. f. macronyx*).

Hybrid individuals with a large bias towards *M. f. macronyx* were found upstream of the Amur River (nearby to Komsomolsk-on-Amur). On the contrary, birds caught downstream (Udył Lake) have an appearance characteristic of *M. taivana*. Crossbreeding of *M. taivana* and *M. f. macronyx* was recorded on one of the islands of the Amur River near the confluence with the river Gorin. Under sympatric conditions (joint nesting settlements), *M. taivana* and *M. flava* keep apart, preferring different nesting biotopes (Babenko 1981).

Phenotypic and genotypic structure of *M. lutea*

The taxonomic position of *M. lutea* is rather controversial. Many authors expressed an opinion about the advisability of including the form *M. lutea* in the species *M. flava* on the grounds that it regularly nests in mixed colonies with grey-headed yellow wagtails, and their females practically do not differ from each other (Zarudny 1891; Vaurie 1959). However, subsequent studies have shown that this form is more correct to be considered as an independent taxon, since in three isolated parts of the range of the yellow-headed wagtail populations — the British Isles; Middle and Lower Volga, Ural River and the coast of the Okhotsk Sea, the lower reaches of the river Lena, Indigirka and Sakhalin Island (Gladkov 1954) — in which a large or significant part of the males have a yellow, dirty green or olive green colour of the forehead and crown. These populations are listed as a separate species *M. lutea* Gm. (= *Budytes luteus*) (Gladkov 1954; Portenko 1960), consisting of three subspecies, corresponding to the isolated areas of the range listed above: *flavissima*, *lutea*, and *taivana* (Beregovoy 1970; Stepanyan 2003; Pavlova *et al.* 2003).

The colour of the head of male yellow wagtails from two homogeneous populations was investigated: in the region of Ivdel (Ural), the subspecies *M. f. thunbergi* with a lead-grey head and in the

Baymak region (Bashkiria) the subspecies *M. f. flava* with a bluish-grey head; as well as from three polymorphic populations: the Ural river 80 km below the city of Orenburg; river Akhtuba, Lower Volga, and the middle course of the river Ilovlya near the station Zenzevatka of the Volgograd region. The three latter populations are represented by individuals with head colouration as in *M. f. flava*, *M. lutea*, and a small number of individuals with a very light ash-grey head (*M. f. leucocephala*). To assess the colour of plumage, a universal FM photometer was used, which gives a numerical indicator of blue, red, and brightness (whiteness) (Beregovoy 1970).

It can be visually observed that the whiteness index of the subspecies from the Southern Urals is higher than that of the northern subspecies *M. f. thunbergi*. With the help of a photometer, it was possible to establish that in the grey colour of the head of these subspecies, despite its different brightness, the quantitative ratio of blue and red shades is the same, which indicates that the subspecies *M. f. flava* and *M. f. thunbergi* belong to one species taxon *M. flava*. Polymorphic populations (Orenburg, Akhtuba and Ilovlya rivers) are represented by the following phenotypes: individuals with bluish-grey and light ash-grey head colouration (*M. flava*), individuals with dirty green and light pure yellow heads (*M. lutea*). All yellow-headed wagtails differ from grey-headed wagtails in their high whiteness. But in comparison with 'pure' populations (Ivdel and Baymak), they are less homogeneous: CV = 28.7–52.4%. In addition, they differ in a significantly lower index of blue tint and a greater index of red, and the reduced blue tint varies greatly: CV = 17.0–42.3%. Grey-headed wagtails (*M. f. flava*) of polymorphic populations do not differ (differences are statistically insignificant) from individuals from pure populations in brightness and in the ratio of blue and red shades. However, they contain a small number of individuals with a noticeably lighter grey head and even very light ash-grey-headed individuals (*M. f. leucocephala*). This was reflected in the whiteness variation coefficients: CV = 26.0–31.2% (Beregovoy 1970).

Thus, grey-headed wagtails (*M. f. flava*) of polymorphic populations are as heterogeneous as yellow-headed wagtails (*M. lutea*). This can only be explained by the mutual crossing of these forms (phenotypes) in a polymorphic population. If the genotype of bluish-grey-headed wagtails is represented as CCll (C is the gene that ensures the normal development of bluish-grey colour, ll determines the absence of yellow pigment in the plumage of the forehead and crown), and the genotype of the yellow-headed wagtail is ccLL (cc is a grey-colour attenuator, L determines the normal development of yellow), then from their crossing as a result of a combination of bluish-grey colour with yellow, an individual with a dark green head will be obtained (genotype CcLl). Such individuals are quite common among yellow-headed wagtails in the contact zone with grey-headed wagtails. In the second generation, a series of genotypes should be expected, of which the following are the most interesting: CCLL, CCLl, CcLL, and CcLl — all with more or less dark dirty green head, as well as Ccl and ccll — individuals with a lighter grey (whiteness index is greater than 15) and an almost white ash-grey head (whiteness index over 20). The last two phenotypes are found regularly only in mixed populations of *M. flava* and *M. lutea* (Beregovoy 1970).

Nikolai Zarudny (1891) found hybrid forms of males and females of the species *M. flava* and *M. lutea* (= *Budytes*) in Orenburg Oblast (valleys of the Ural and Chagan rivers), which were hybrids between *M. flava* (= *Budytes flava* L.) and *M. lutea* (= *Budytes campestris* Pall.). In the first generation, such hybrid individuals split into *M. l. flavissima* (= *Budytes flavifrons* Sewert.) and *M. taivana* (= *Budytes rayi* Bp.). These forms can transmit their distinctive features (yellow or green colouration of the top of the head) to hybrids of subsequent generations (Zarudny 1891).

Both of these forms live in separate nesting settlements, despite the presence of hybrids. Both forms prefer extensive meadows, treeless spaces, with abundant shallow water bodies, lush, but not too dense herbaceous vegetation. There is competition between these forms for nesting habitats. *M. lutea* (= *Budytes campestris*) rises much further north in the basin of the river Volga than is commonly believed. Sometimes the hybrids are similar to *M. taivana* (= *Budytes taivanus*). Zarudny (1891) found hybrids between *M. f. beema* (= *Budytes flava beema*) and *M. lutea* (= *Budytes campestris flavifrons*) in

the valley of the Ural River, which have intermediate characters (ash-bluish or whitish with a yellow top of the head). Hybrids were also found between *M. flava* (= *Budytes flava*) and *M. lutea* (= *Budytes campestris flavifrons*) in meadows in the valley near Station Chernorechye of Orenburg Oblast, which have similar intermediate features (ash-blue colouration of the back of the top of the head, with a green admixture, the rest of the head is yellow with a green admixture, a wide light eyebrow is developed). Thus, hybrids between *M. flava* (= *Budytes flava*) and *M. lutea* (= *Budytes campestris*) in repeated crosses may lose some intermediate characters, but in general their phenotype, and hence the genotype, remains stable (Zarudny 1891). The above data indicate that populations of the grey-headed form *M. f. flava* and yellow-headed forms of *M. lutea* in their common habitats are constantly replenished due to pheno- and genotypic cleavage, taking part in the general drift of genes in the range of the polytypic complex and should be considered as independent sympatric taxa included in the polytypic complex of *M. flava*.

Due to the exceptional similarity of morphological characters with closely related species of 'yellow' wagtails, *M. lutea* is rather difficult to isolate against the background of closely related forms. However, the accumulation of information on the biotopic separation of the nesting sites of *M. lutea* and related species of 'yellow' wagtails, stable differences in the structure of communicative signals, the size and pigmentation of eggs, sympatric distribution with other representatives of *Motacilla flava* sensu lato complex, as well as the results of analysis of mitochondrial DNA make it possible to consider this form as an independent taxon of species rank (Pavlova *et al.* 2003; Sotnikov 2006).

External characters associated with the colour of the plumage of the head of *M. lutea* males are characterized by a wide range of variation. Phenotypes with a yellow colouration of only the frontal part of the head or with a completely yellow head can be considered as separate links within the normal reaction of this trait in *M. lutea*. The presence of a certain percentage of light-headed, white-headed, and green-headed phenotypes in populations of the yellow-headed wagtail is explained, as a rule, by interspecific hybridization with *M. flava* under conditions of sympatric distribution of these species (Pavlova *et al.* 2003; Sotnikov 2006).

However, a comparison of the percentage throughout the range of normal individuals with a yellow forehead and yellow-green head colouration (60%), yellow-headed (30%), green-headed (15%), light-headed and white-headed (5%), which is maintained throughout the entire range due to balanced polymorphism, indicates the presence of a genetic mechanism of intraspecific splitting by genotypes and phenotypes based on inheritance by the type of complementarity, or double recessive epistasis (the ratio of phenotypes in this case is 9 A_B_ (yellow forehead, yellow-green colour of the head) : 3 A_cv (yellow head colouration) : 3 aaB_ (green head colouration) : 1 aavb (white or strongly lightened head colouration)).

All possible intermediate genotypes and phenotypes also fit well within the proposed model (working hypothesis). The proposed model seems to be quite adequate for the sympatric species of this group. In natural populations of *M. lutea*, over the entire area of the geographic range, the splitting of heterozygous phenotypes with a yellow-green head colouration constantly occurs, which maintains a constant ratio of frequencies of the other three main homozygous phenotypes, as well as all possible intermediate heterozygotes. At the same time, the reverse process of formation of heterozygotes from all possible mixed crosses of homozygotes contained in populations occurs.

This model of inheritance of head plumage traits in *M. lutea* is also supported by the facts of nesting of this species in joint settlements in the territory of the range with closely related sympatric species — *M. flava* and *M. citreola*, with the obligatory maintenance of the species originality (species-specific traits) of each of the three species forms on the basis of their ecological isolation due to different daily activity, different food supply, different biotopic confinement, biochemical indicators of eggshell colour and pattern, different sound communication signals, peculiarities of the structure of nests, etc.

The genetic mechanisms of sympatric speciation and the formation of spatial groups of populations of 'yellow' wagtails include gene interaction, or double recessive epistasis, possible changes in the number of chromosomes in the karyotype (polyploidy), and possible intraspecific and interspecific hybridization (Pavlova *et al.* 2003; Sotnikov 2006).

The existence of hybridization of the yellow-headed wagtail with other species of this complex, namely *M. flava* and *M. feldegg*, is a widespread and proven phenomenon (Zarudny 1891; Beregovoy 1970), and it is the most important limiting factor in the distribution and abundance of the model species. The accumulation of information on the biotopic dissociation of nesting sites of yellow-headed wagtails and related species of 'yellow' wagtails, stable differences in the structure of communicative signals, the size and pigmentation of eggs, sympatric distribution with other representatives of *M. flava* sensu lato complex, as well as the results of analysis of mitochondrial DNA make it possible to consider this form as an independent species (Pavlova *et al.* 2003; Sotnikov 2006).

Species of 'yellow' wagtails with similar ecology and a common developmental history have a similar structure of genotypic and phenotypic variation in the colour of the plumage of the head, but the range of variation of these characters for stenobiontic species (for example, *M. lutea*) is less than that for eurybiontic species (for example, *M. flava*).

Thus, factors of ecological and geographical isolation play a leading role in the formation of the characteristic phenotypic appearance of *M. lutea* populations throughout the range. Currently, there is an active process of isolation of two species forms *M. flava* and *M. lutea* under conditions of wide sympatry within the framework of a single polytypic complex.

Intraspecific hybridization

Intraspecific hybridization of subspecies of each of the considered species of the group of 'yellow' wagtails leads to constantly occurring genotypic and phenotypic splitting, which support intraspecific polymorphism of populations, replenishing the composition of phenotypes and genotypes, keeping their ratio at a certain level. This process has its own characteristics within the boundaries of the ranges of each species, maintaining the homeostasis of population groups of these sympatric species and the genetic integrity of each of them.

Interspecies hybridization

Interspecific hybridization is typical only for three of the considered species of the group of 'yellow' wagtails: *M. flava*, *M. lutea*, and *M. feldegg*. Moreover, only *M. flava* forms hybrids with the listed species. Hybrids between *M. lutea* and *M. feldegg* have never been recorded by researchers, which indicates the species independence of both *M. lutea* and *M. feldegg*, which have more limited and isolated ranges. *M. flava*, in comparison with them, has a much wider range that covers almost the entire Palaearctic and forms a series of vicarious species from Western Europe to Primorye. It is likely that the modern polytypic complex of *M. flava* (in the narrow sense, a series of species and subspecies of only *M. flava*), probably formed as a polyploid group (we mean by a polyploid group species prone to interbreed with a multiple increase in the number of chromosomes) in the historical time based on the original hybrids between *M. lutea* and *M. feldegg*, which are no longer possible at present, since their genetic systems are finally formed, closed and closed for re-hybridization. The proposed model of sympatric speciation in the group of 'yellow' wagtails is in good agreement with the results of the analysis of mitochondrial DNA of these species and allows to explain the structure and content of clusters of the obtained dendrogram of the genetic similarity of species (Pavlova *et al.* 2003).

The presence of *M. flava* subspecies in the same clusters with *M. lutea* or *M. feldegg* may indicate their hybrid origin based on the original genomes of *M. lutea* or *M. feldegg* species. There are three well-separated clusters of hybrid forms of *M. flava*: *M. f. macronyx*, *M. f. plexa*, *M. f. tschutschensis*, *M. f. simillima* (based on the original genomes of *M. taivana* and *M. flava*); *M. f. beema*, *M. f. flava*, *M. thunbergi* (based on the original genomes of *M. lutea* and *M. flava*); and *M. f. zaissanensis*, *M. f. leucocephala*, *M. feldegg feldegg*, *M. feldegg melanogrisea* (based on the original genomes of

M. feldegg and *M. flava*). At the same time, the species *M. citreola* and *M. cinerea* do not form hybrids either with each other or with any of the above species of the group. In terms of the degree of genetic similarity, the most distant taxon from the rest is *M. cinerea*, while *M. citreola* is much closer in its genesis to the rest of the species of the group. Both of these taxa form separate clusters in the general microevolutionary pattern of the group under consideration, which indicates their early separation from the common branch of the ancestors of 'yellow' wagtails.

In this work, it is proved that during 7–9 years of observations of the populations of 'yellow' wagtails, it was possible to establish that the compared taxa *M. flava* and *M. lutea* differ little genetically, while individuals from the left bank (eastern) (Cherdakly) occupy a separate position in the dendrogram and show spatial differences from the right bank (western) (Radishchevo) population groups (Fig. 7). The dendrogram (Fig. 6) shows the formation of two clusters of samples: a hybrid group consisting of individuals of the left-bank (eastern) *M. flava*, left-bank (eastern) *M. lutea*, and left-bank (eastern) light-headed hybrids *M. f. beema* × *M. lutea*, as well as the clean line of the left-bank (eastern) *M. lutea*. Within the hybrid group, the light-headed hybrids *M. f. beema* × *M. lutea*, which are related to both *M. lutea* and *M. flava*, are clearly separated. Some of the *M. lutea* individuals are mestizo and therefore entered the cluster of the hybrid group, while the *M. lutea* individuals, which make up the cluster of the pure line, represent a more stable group. *M. flava* is also a mestizo and is found in a hybrid group cluster (Fig. 6).

Individuals from the left-bank (eastern) sample of populations (Cherdakly) and the right-bank (western) sample of populations (Radishchevo) of the taxon *M. flava* are well distinguished on the dendrogram of phylogenetic relationships (Fig. 7), showing spatial differences between the two groups of samples.

Hybrid light-headed *M. f. beema* × *M. lutea* from the left-bank (eastern) sample (Cherdakly) are closer to *M. flava* from the right-bank (western) groups of population (Radishchevo) and to *M. lutea* than to *M. flava* from the left-bank (eastern) group of populations (Cherdakly).

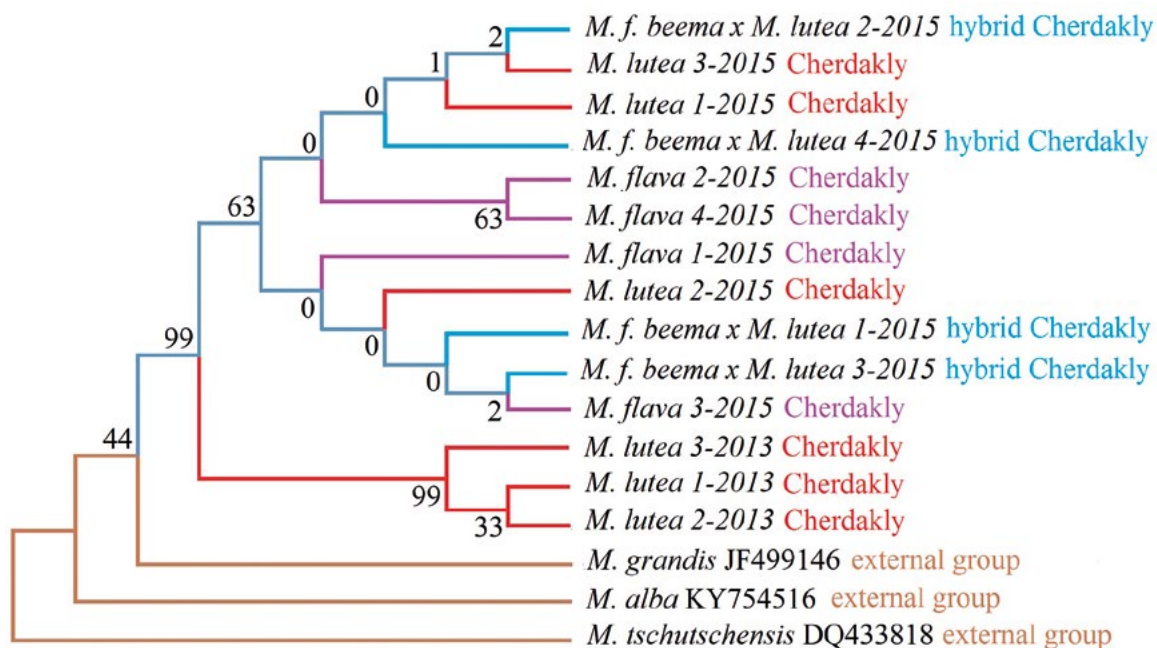


Fig. 6. Dendrogram of the genetic similarity of individuals from samples of 'yellow' wagtails (2013–2015) for cytochrome c-oxidase I. The numbers indicate genetic distances between individuals in samples (the greater is the distance, the greater are genetic differences between the objects).

Рис. 6. Дендрограма генетичної схожості особин з вибірок «жовтих» плисок (2013–2015 рр.) за цитохромом с-оксидази І. Цифри позначають генетичні дистанції між особинами у вибірках (чим більше величина дистанції, тим вище генетичні відмінності між об'єктами).

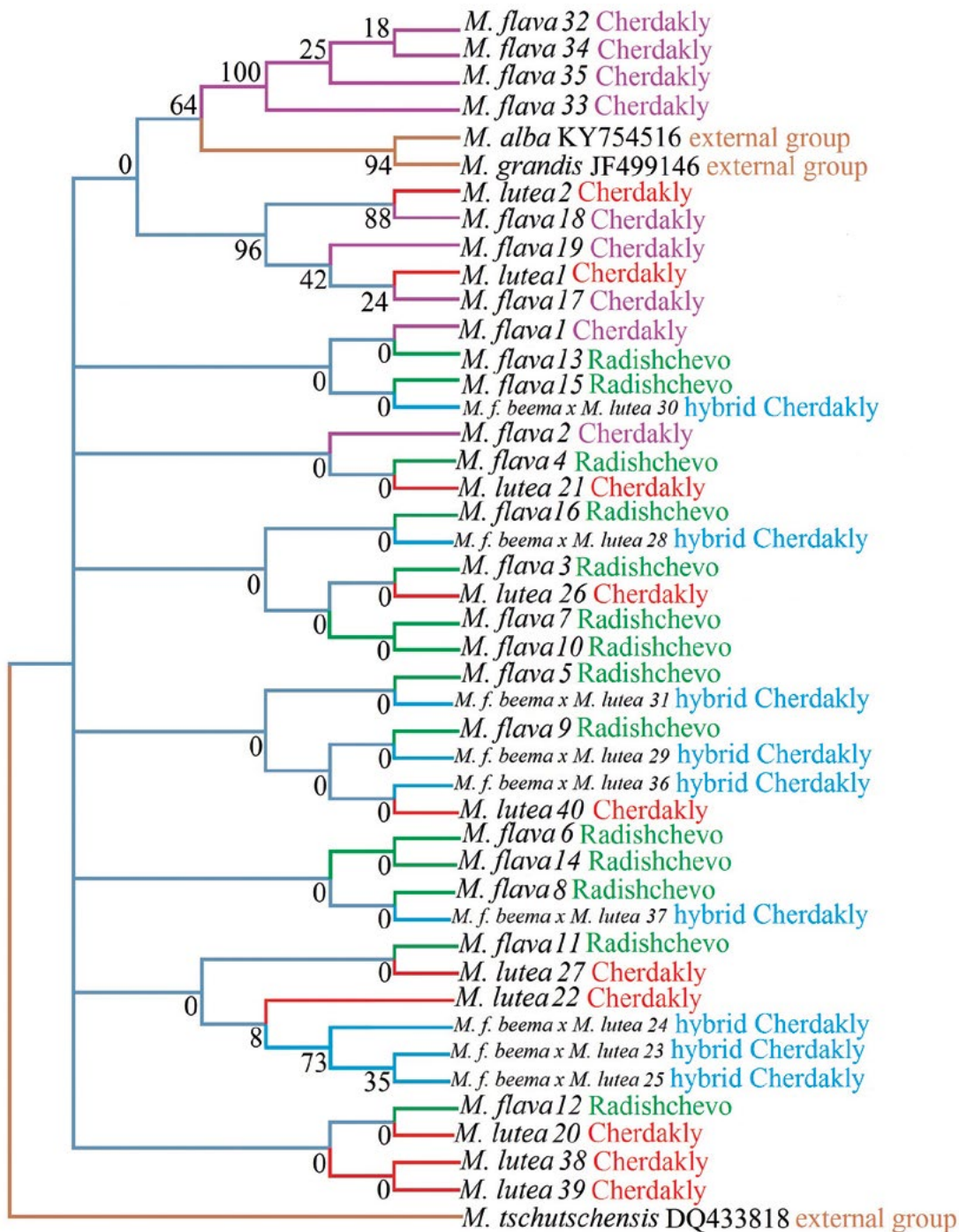


Fig. 7. Dendrogram of the genetic similarity of individuals from samples of 'yellow' wagtails (2013–2019) for cytochrome c-oxidase I. The numbers indicate genetic distances between individuals in the samples (the greater is the distance, the greater are genetic differences between the objects).

Рис. 7. Дендрограма генетичної схожості особин з вибірок «жовтих» пликос (2013–2019 рр.) за цитохромом с-оксидази І. Цифри позначають генетичні дистанції між особинами у вибірках (чим більша величина дистанції, тим вищі генетичні відмінності між об'єктами).

In relation to the yellow-headed wagtail *M. lutea*, hybrid light-headed individuals *M. f. beema* × *M. lutea* show much greater genetic similarity with it (with a predominance of *M. lutea* characters) than with *M. flava*. At the same time, light-headed individuals *M. f. beema* × *M. lutea* more

often fall into common branches with *M. flava* individuals from the western group of populations (Radishchevo) than from the eastern one (Cherdakly). Light-headed hybrids are genetically closer to the yellow-headed wagtail *M. lutea* than to the western yellow wagtail *M. flava*.

At present, in the contact zone between closely related forms of 'yellow' wagtails, a system of their spatial and reproductive interaction with each other has been formed under conditions of wide sympatry. This interaction is manifested in the existence and maintenance in the population samples of three components of their genetic system: the genotypes *M. flava*, *M. lutea*, and the light-headed hybrid form *M. f. beema* × *M. lutea*. Particular attention should be paid to the isolation of light-headed hybrids into a separate cluster and separate branches of the combined clusters associated with the right-bank (western) group of *M. flava* populations (Fig. 7).

Thus, three points of view on the taxonomic structure of the polytypic complex of 'yellow' wagtails (see above) exist, which were previously built mainly on the basis of morphological characters (primarily morphometric parameters and colouration of the plumage of males during breeding season, etc.), now significantly supplemented by molecular genetic and bioecological studies (Pavlova *et al.* 2003; Sotnikov 2006; Artemieva *et al.* 2016a–b).

One of the concepts is that all 'yellow' wagtails, except for the yellow-headed and the mountain wagtail, are subspecies of *M. flava*, as a polytypic species has the right to exist (Alström & Mild 2003; Alström *et al.* 2015; Harris *et al.* 2018, others).

The second concept is that there are five polytypic species: *M. flava* (*flava*, *thunbergi*, *beema*, *leucocephala*, *zaissanensis*, *plexa*, *macronyx*, *alascensis*, *simillima*, *tschutschensis*, *cinereocapilla*, *iberiae*, *pygmaea*), *M. feldegg* (*feldegg*, *melanogrisea*), *M. lutea* (*lutea*, *flavissima*, *taivana*), *M. citreola* (*citreola*, *werae*, *quassatrix*, *calcarata*, *weigoldi*), and *M. cinerea* (*cinerea*, *melanope*, *robusta*, *schmidzi*, *flaviventris*, *clara*) (Artobolevsky 1924; Dement'ev 1937; Beregovoy 1970). *M. flava* and *M. lutea* are considered independent species (Zarudny 1891; Dement'ev 1941; Zavyalov *et al.* 2009). This concept has the right to exist and is proved in many works (Artemieva & Muravyov 2012; Ferlini & Artemyeva 2020; Ferlini *et al.* 2021; and others).

The third concept is that there are five polytypic species and three monotypic species of 'yellow' wagtails: *M. flava* (twelve subspecies); *M. feldegg* (two subspecies); *M. lutea* (two subspecies); *M. citreola* (four subspecies) and *M. werae*; *M. taivana*; *M. macronyx* (monotypic species); *M. cinerea* (six subspecies). This concept also emphasizes the reality of the species taxa *M. flava* and *M. lutea*.

The work by Harris *et al.* 'Discordance between genomic divergence and phenotypic variation in a rapidly evolving avian genus (*Motacilla*)' (2018), upon detailed consideration and comparison of the results, does not contradict the author's data, since in this case the problem is considered from different points of view. On the one hand, from the standpoint of molecular biology with specificity of their research methods, and on the other hand — from the standpoint of a population bioecologist who has its own research methods. One may well complement the other. Each of the existing concepts of taxonomic relations of species within the polytypic complex '*M. flava*' is not final and irrevocable, in the light of modern data, it is more adequate to accept a compromise option, in which there are no rigid boundaries between taxa, both species and subspecies rank, which is a direct consequence of the existing real process of hybridization and based on its speciation in 'online mode' under sympatric conditions. This process, observed in the populations of the complex '*M. flava*,' is characteristic of young and rapidly differentiating groups. We observe this already existing process of differentiation. At present, the taxa *M. flava* and *M. lutea* demonstrate almost complete genetic identity, but at the same time they have systems of their own individual morphological characters that distinguish them well from each other (shown above).

The new data obtained significantly supplement the understanding of the intraspecific interaction of three forms: *M. flava*, *M. lutea*, and the light-headed hybrid form *M. f. beema* × *M. lutea*. The hybrid form *M. f. beema* × *M. lutea* only emphasizes the uniqueness of both *M. flava* and *M. lutea*. Moreover, light-headed hybrids are a kind of a 'bridge' between them, while having their own specific

stable traits at different levels: morphological, behavioural, and molecular-genetic as confirmation of the genetic interaction existing in natural populations between the two species, which is an interspecies mechanism for maintaining their structure.

Dynamics of the composition of breeding pairs in the samples of 'yellow' wagtails

The area of spatial and reproductive interaction of species is marked by the presence of light-headed hybrids of two initial species — the western yellow wagtail *M. flava* and the yellow-headed wagtail *M. lutea*. In this work, it is shown that over the course of nine years of observation of the ratio of nesting pairs in population samples in the contact zone of the two species, there is a gradual decrease in the number of nesting pairs of yellow-headed wagtails and an increase in the number of nesting pairs of western yellow wagtails. At the same time, the number of mixed breeding pairs of yellow white-eared and yellow-headed wagtails increases. Descendants (males) from mixed nesting pairs have a strongly bleached, whitish ('grey-haired') head colour. The number of breeding pairs of hybrid wagtails also increases annually (Table 1).

Table 1. Dynamics of the composition of breeding pairs in samples of 'yellow' wagtails in the Middle Volga region

Таблиця 1. Динаміка складу гніздових пар у вибірках «жовтих» плисок з регіону Середнього Поволжя

Date (years)	Number of nesting pairs of <i>M. flava</i>	Number of nesting pairs of <i>M. lutea</i>	Number of mixed nesting pairs of <i>M. f. beema</i> × <i>M. lutea</i>	Number of nesting pairs of light-headed hybrids
2012	35%	65%	5%	1%
2015	75%	25%	30%	20%
2018	95%	5%	65%	54%
2019	99%	1%	85%	70%
2020	99.9%	0.1%	99%	95%

The area of overlapping ranges of the western yellow wagtail *M. flava* and the yellow-headed wagtail *M. lutea* was revealed in the studied territory of the Volga region, which corresponds to the eastern outpost of the zone of interaction of the species *M. flava* and *M. lutea* in the area of their co-occurrence (Fig. 8). The hybridization zone is supported by populations of the yellow-headed wagtail *M. lutea*, which receive a constant influx of individuals from adjacent territories (Samara and Orenburg oblasts, Russia and Kazakhstan).

The mapping of geographic ranges showed that three species of 'yellow' wagtails form an extensive zone of sympatry in the Volga region: the western yellow wagtail *M. flava*, the yellow-headed wagtail *M. lutea*, and the citrine wagtail *M. citreola* (Fig. 9). The border shows the area of spatial and reproductive interaction of these species in the study area — the area of sympatry between subspecies and specific forms of *M. f. flava*, *M. f. beema*, and *M. lutea*. The marker of the border of the zone of spatial and reproductive sympatric relationships of species is the appearance and accumulation of hybrids from mixed nesting pairs — yellow, yellow white-eared, and yellow-headed wagtails in samples of light-headed ('grey-headed') individuals.

Light-headed hybrids — markers of interactions between species

The revealed pattern of spatial and reproductive relationships between *M. flava* and *M. lutea* indicates the existence of western (right-bank) and eastern (left-bank) groups of populations of these species. In areas of sympatry (overlapping ranges) populations are found, samples from which show a fairly high percentage of mixed nesting pairs (Fig. 10). It can be seen that the maximum number of mixed nesting pairs (*flava-lutea*, *beema-lutea*) was found in samples from the left bank (up to 70–74%). The minimum number of such pairs was noted in populations from the right bank (up to 5–8%). A wedge (the frequency gradient of mixed pairs in space) is quite clearly traced in the west–east direction. The reproductive relationships of the forms in the zone of spatial contact are characterized as zones of intergradation with unlimited hybridization between the contacting forms *flava-lutea* and *beema-lutea*, which leads to the appearance of light-headed hybrids *M. f. beema* × *M. lutea* and which are peculiar markers of these relations (Fig. 11).

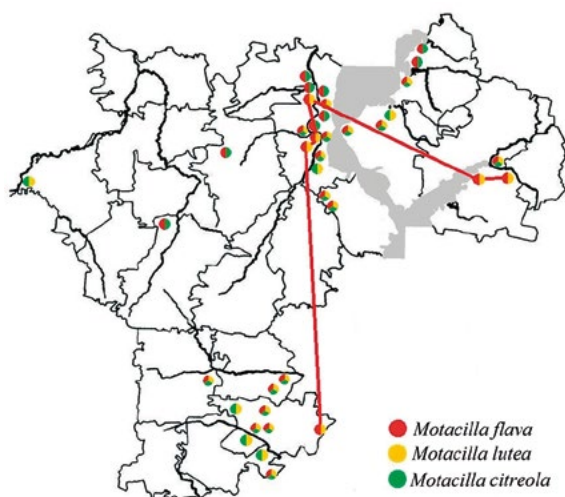


Fig. 8. Genetic structure of populations of species of 'yellow' wagtails and the border of the area of sympatry of *M. flava* and *M. lutea* in the Middle Volga region.

Рис. 8. Генетична структура популяцій видів «жовтих» плисок і межа області симпатрії у *M. flava*, *M. lutea* на території Середнього Поволжя.

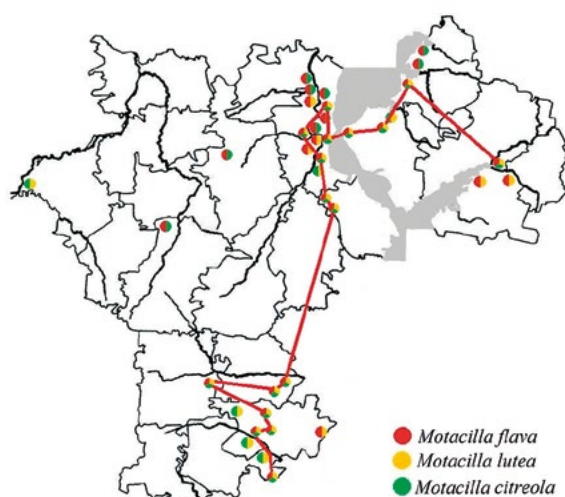


Fig. 9. Genetic structure of populations and the boundary of the area of sympatry of *M. f. beema* × *M. lutea* in the Middle Volga region.

Рис. 9. Генетична структура популяцій і межа області симпатрії у гібридів *M. f. beema* × *M. lutea* на території Середнього Поволжя.

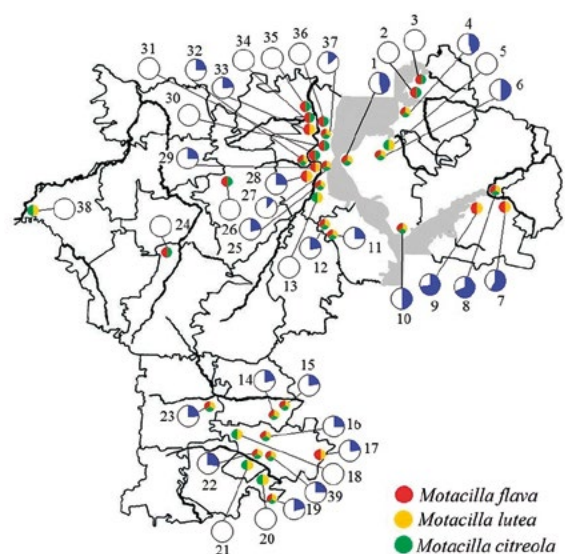


Fig. 10. Share of mixed nesting pairs (*flava-lutea*, *beema-lutea*) in the area of sympatry of 'yellow' wagtails in the Middle Volga region (shaded).

Рис. 10. Частка змішаних гніздових пар (*flava-lutea*, *beema-lutea*) в області симпатрії у «жовтих» плисок в Середньому Поволжі (заштрихована).

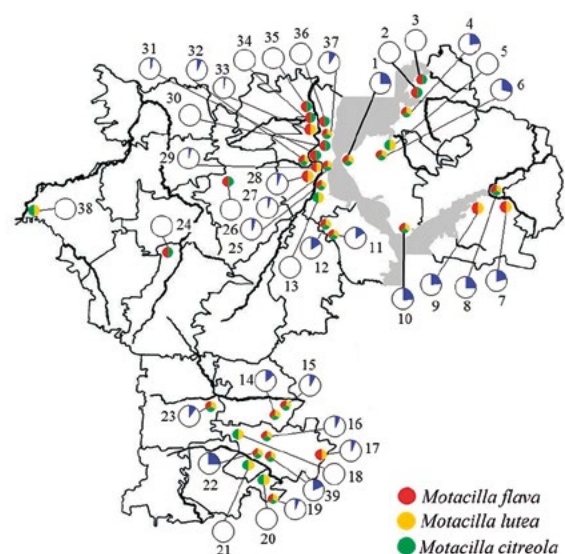


Fig. 11. Share of hybrids of *M. f. beema* × *M. lutea* in the area of sympatry of 'yellow' wagtails in the Middle Volga region under conditions of co-occurrence of species (shaded).

Рис. 11. Частка гібридів *M. f. beema* × *M. lutea* в області симпатрії у «жовтих» плисок в Середньому Поволжі в умовах співіснування видів (заштрихована).

Spatial and reproductive relationships in the contact zone

The high variability of various characters, as well as the wide range of variants of reproductive relationships of individual forms (including the phenomena of intergradation, the presence of zones of interspecific hybridization under conditions of wide sympatry) make it possible to consider the group of species of 'yellow' wagtails as an evolutionarily young group. As a result of the study of phenotypic structure of samples from the western (right-bank) and eastern (left-bank) populations, ideas about

the spatial and reproductive relationships between *M. flava* and *M. lutea* in the area of their sympatry (Volga region) were obtained — the share of hybrids *M. f. beema* × *M. lutea* in the area of sympatry (Fig. 11).

It can be seen that the maximum share of hybrids in the samples was found among ‘yellow’ wagtails of the left bank (up to 17–25%), which are represented by mixed pairs of western yellow and yellow-headed wagtails. The minimum share of hybrids was noted in samples of ‘yellow’ wagtails from the right bank (up to 10%). The wedge (the frequency gradient of the hybrids in space) is well traced in the west–east direction. Samples of ‘yellow’ wagtails from the right bank differ in the share of hybrid individuals from those of the left bank. The appearance of light-headed (‘grey-headed’) individuals is associated with the spatial and reproductive relationships of the species *M. flava* and *M. lutea* inhabiting the studied region. Samples of ‘yellow’ wagtails from the right bank have a minimum content of light-headed individuals — up to 0.2–0.8%, while in samples of ‘yellow’ wagtails from the left bank their share reaches 2.5–5%. A wedge (frequency gradient) of light-headed individuals is clearly traced in space in the west–east direction.

Clinal pattern of variation of the western yellow wagtail

Specifics in phenotype frequency distribution in *M. flava* samples in the studied territory of the Volga region were revealed. The clinal pattern of variation of the western (right-bank) and eastern (left-bank) samples of the western yellow wagtail *M. flava* in the area of spatial and reproductive relationships of species is due to the share of genotypes and phenotypes of individuals that correspond to subspecies taxa of *M. flava* (Fig. 12). In populations of the western yellow wagtail, the genotypes and phenotypes of *M. f. flava* varies from 75% to 100% in the northern part of the right bank, while in the southern part of the right bank their frequency reaches 60–70%. The share of the genotypes and phenotypes of *M. f. beema* ranges from 75% to 95%. Three groups of populations of the western yellow wagtail are well distinguished also in terms of the share of rarer genotypes and phenotypes, which correspond to the subspecies *M. f. thunbergi* (up to 10% in left-bank populations) and hybrids *M. f. beema* × *M. lutea* (up to 5% in left-bank populations). In right-bank populations, the share of these subspecies is extremely small and does not exceed 0.2–0.8%.

Clinal pattern of variation of the yellow-headed wagtail

Specifics in phenotype frequency distribution in *M. lutea* samples in the studied territory of the Volga region were revealed. The clinal pattern of variation of the western (right-bank) and eastern (left-bank) samples of the western yellow wagtail *M. flava* in the area of spatial and reproductive relationships of species is due to the share of genotypes and phenotypes of individuals that correspond to hybrids of the yellow-headed wagtail *M. lutea* with subspecies of the western yellow wagtail *M. flava* (Fig. 13).

The composition of samples of the yellow-headed wagtail from the right bank and the left bank differs well in the share of genotypes and phenotypes of individuals, which correspond to purebreds and hybrids of *M. lutea* with different subspecies of the western yellow wagtail *M. flava*. Samples of the yellow-headed wagtail *M. lutea* from the right bank are characterized by maximum frequencies of individuals of purebred *M. lutea* (up to 90–100%). In samples of the yellow-headed wagtail from the left bank, hybrid individuals predominate: *lutea*–*flava* hybrids up to 50% and *lutea*–*beema* hybrids up to 45%. In northern right-bank samples of *M. lutea*, the frequencies of hybrid individuals of *lutea*–*flava* and *lutea*–*beema* do not exceed 15%; in southern populations of *M. lutea*, the frequencies of hybrid individuals of *lutea*–*flava* do not exceed 15%, and those of *lutea*–*beema* are under 10%.

Breeding strategy in the zone of reproductive contact of species

It was previously shown that the genome of *M. citreola* is associated with both the *M. lutea* genome and the *M. flava* genome (Artemieva *et al.* 2016a–b). In previous publications, it was shown that in populations of ‘yellow’ wagtails in areas of sympatry, there is hybridization between subspecies of the

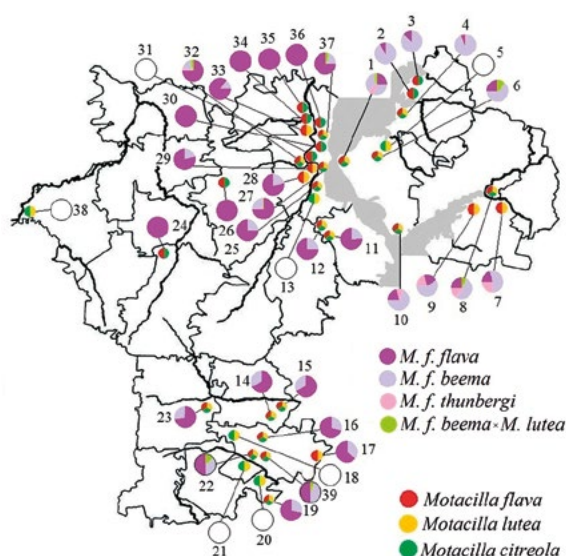


Fig. 12. Subspecific structure of populations of the western yellow wagtail *M. flava* in the area of sympatry of 'yellow' wagtails in the Middle Volga region.

Рис. 12. Підвидова структура популяцій жовтої пливки *Motacilla flava* в області симпатрії у «жовтих» пливках в Середньому Поволжі.

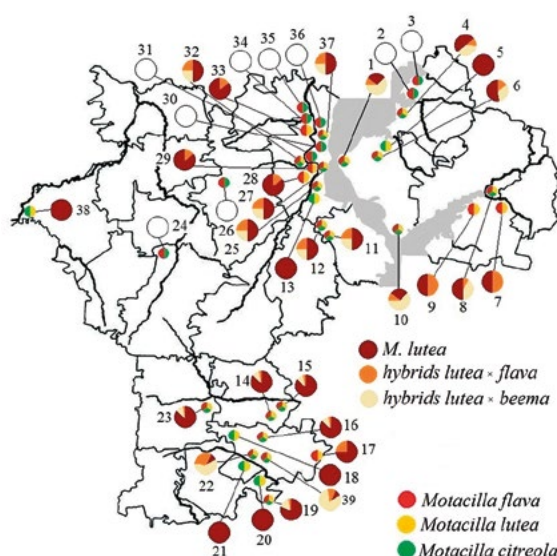


Fig. 13. Hybrid structure of populations of the yellow-headed wagtail *M. lutea* in the area of sympatry of 'yellow' wagtails in the Middle Volga region.

Рис. 13. Гібридна структура популяцій жовтолобої пливки *Motacilla lutea* в області симпатрії у «жовтих» пливках в Середньому Поволжі.

western yellow wagtail (*M. f. flava* and *M. f. thunbergi* (Billberg, 1828)) and subspecies of the yellow-headed wagtail (*M. c. citreola* and *M. c. werae* (Buturlin, 1907)) in the territory of the European part of Russia. In order to identify the distinctive features of these hybrids, a system of signs of colouration and plumage pattern and a system of morphometric characters were developed, as well as ranges of their variation and variants of the state of characters were identified (Artemieva *et al.* 2016a–b). Earlier it was shown that populations of 'yellow' wagtails are genetically heterogeneous, which is due to the genetic diversity of individuals; these processes underlie the divergence of natural populations and their groups (Artemieva *et al.* 2016a–b).

In this work, it is shown that the spatial and reproductive relationships between the species *M. flava* and *M. lutea* in the area of their contact and overlapping ranges lead to hybridization, to the emergence of a light-headed hybrid form *M. f. beema* × *M. lutea*, which, as a result of further evolution, can become an independent species with its own systems of traits (morphological, ecological, genetic, geographic, and behavioural). In this work, we have identified areas of spatial and reproductive relationships between species of 'yellow' wagtails in areas of overlap of their geographic ranges in the Volga region (European part of Russia) — the yellow white-eared wagtail *M. f. beema* and the yellow-headed wagtail *M. lutea*, which are characterized by the presence of light-headed hybrid individuals in the populations with characteristic features of the colouration of the plumage of the head, the colour and pattern of the eggshell, as well as the features of the structure of the nests and behavioural characters.

Dark egg morphs (with a thick, dark brown-chocolate pattern) of all yellow wagtail species show the presence of *M. lutea* genes. Genetically, species cannot exist without each other, so they nest together, forming areas of sympatric speciation. Genomes of *M. lutea* females unite populations of species of 'yellow' wagtails in areas of overlapping ranges, in which they live together. Hybrid, heterozygous, intermediate forms gradually create the basis for the formation of subspecies, and then specific forms. Their splitting maintains the genetic system of populations at a certain level, helping to preserve both species — *M. f. beema* and *M. lutea*. The presence of a sign of breast plumage pattern — a 'necklace' in *M. lutea* females — is a common ancient feature of all species of the group of

'yellow' wagtails, manifested in fledglings and juveniles in the first winter plumage, which plays the role of some kind of 'sign' in the organization of individuals in flocks during migrations, then in large flocks during seasonal migrations. In the plumage of breeding individuals, this trait retains its role as an identification 'sign' (an external manifestation of an individual's individual barcode) in communication between sexes and in the formation of breeding pairs.

The topography of the area of co-occurrence of 'yellow' wagtail species includes three levels in relation to the water body, which, as a rule, is the initial reference point for the habitation of bird populations (feeding biotope): external — occupied by nests of *M. citreola* (the most moisture-loving species), internal — occupied by nests of *M. flava* (the most dry-loving species), between them are nests of *M. lutea* (mesophilic species) forming a kind of interlayer — an intermediate, or transitional level. Western yellow wagtails *M. flava* strengthen the rear of the colony, occupying the highest upland areas — at the maximum distance from the water body. Citrine wagtails control the outer border of the colony, occupying the lowest and wettest areas — at the minimum distance from the water body. Yellow-headed wagtails nest in the intermediate zone, occupying mesophilic areas. At the same time, a certain sequence of species in the development of a nesting biotope is observed: initially, *M. citreola* populates, then *M. flava* populates, then *M. lutea* appears, and the populations reach their heyday.

Subsequently, under possible negative impacts of anthropogenic or weather factors, the population of *M. lutea* begins to thin out and be replaced by *M. flava*, the males of which form mixed pairs with females of *M. lutea*. Male yellow white-eared wagtails *M. f. beema* and western yellow wagtails *M. f. flava* arrive almost a week earlier than male yellow-headed wagtails *M. lutea* and therefore capture female yellow-headed wagtails, as well as with a shortage of *M. lutea* males they form mixed pairs thus causing an increase in the degree of hybridization in populations from year to year. As a result of genetic splitting, hybrid light-headed individuals (*M. f. beema* × *M. lutea*) appear and accumulate in populations. Hybrid individuals from mixed pairs gradually accumulating for several years create conditions for maintaining the adaptive strategy and genetic system of the population in areas of spatial and reproductive relationships that are resistant to environmental influences.

Adaptive nesting strategies of 'yellow' wagtail species include: atypical cases of tray lining associated with the presence of mixed pairs — with the presence of down and feathers, without horsehair. The revealed atypical cases of nest tray lining are associated with the presence of mixed nesting pairs: female yellow-headed wagtails *M. lutea* build nests characteristic of their species. The nesting strategy during an unstable extreme breeding season is due to the presence of a second clutch (instead of the lost one); the clutches are strongly stretched in time. The difference in daily activity between *M. flava*, *M. lutea*, and their hybrids is also one of the adaptive strategies in conditions of populations living in the area of spatial and reproductive contact.

Conclusions

As a result of the study of the interaction between *M. flava* and *M. lutea* species in the contact zone of their geographic ranges, the following was revealed.

The concept of a system of characters of the light-headed hybrid *M. f. beema* × *M. lutea*, which marks the hybridization zone of the model species *M. flava* and *M. lutea*, has been proposed. The population characteristics of this system have been determined and the possibility of their use in population and evolutionary studies of a group of species of 'yellow' wagtails has been shown.

As a result of spatial and reproductive interaction between species in populations, a light-headed hybrid *M. f. beema* × *M. lutea* is formed, which integrates the characters of the two original species and has its own, peculiar traits, which can mark the boundaries between the western (left-bank) and eastern (right-bank) groups of populations and the boundaries of their distribution. Accordingly, differences appear and divergence of these groups of populations occurs, which may reflect the processes of sympatric speciation. Spatial relationships between the model species has been clarified. According to the differences in phenotype frequencies in samples of the model species, hybrid zones were revealed in the study area under conditions of wide sympatry.

The identified processes of spatial and reproductive interaction of species are characterized by ongoing divergence of their populations to the west and east, to the isolation of hybrid populations with the presence of the light-headed form *M. f. beema* × *M. lutea*, which is the result of microevolutionary transformations. The revealed tendencies in the variation of groups of characters throughout the geographic range of the model species have a clinal character and may indicate the directions of microevolution of species. The identified hybrid zones within the boundaries of species ranges have a central position (Spear 1987; Yesou 1991; Rohwer *et al.* 2001; Vili *et al.* 2009). The result of the spatio-temporal divergence of groups of populations (western and eastern) are *M. flava*, *M. lutea*, and their hybrid light-headed form *M. f. beema* × *M. lutea*, which may later become an independent species.

The occupation of new habitats by 'yellow' wagtail species is associated with the advance of key plant communities and food objects of this group of birds to the northwest, which, in turn, is caused by climate aridization in the steppe and forest-steppe (Ferlini & Artemyeva 2020). Temperature thresholds for the nesting period of 'yellow' wagtails are associated with an increase in spring and summer temperatures in steppe and forest-steppe regions, which, in turn, is due to global warming: each increase by 1°C promotes the distribution of plant communities 100–160 km north (Devis 1989; Musselman & Fox 1991; Puhe & Ulrich 2001). Hybrid light-headed *M. f. beema* × *M. lutea* may well be the starting point for further evolution and formation of a new species on a hybridogenic basis, which will actually replace the morphologically similar white-headed wagtail *M. f. leucocephala* (to become its sibling species) and contribute to the expansion of range boundaries of the original species *M. flava* and *M. lutea* and occupation of new territories.

Thus, in populations of *M. flava* and *M. lutea*, there are spatial and reproductive relationships between these species forms, which are marked by the appearance of light-headed hybrids (*M. f. beema* × *M. lutea*) in the studied territory of the Volga region. In the contact zone between *M. flava* and *M. lutea*, unlimited hybridization of these species occurs, which is provoked by differences in the phenology of arrival of *M. f. beema* and *M. f. flava*, arriving earlier than *M. lutea* males and therefore having the ability to mate with *M. lutea* females, as well as when *M. lutea* males are deficient in the contact zone of the two species forming mixed pairs. A hypothesis was proposed and substantiated: hybridization can be a mechanism for increasing reproductive isolation (inactivation of individuals with errors in identifying their own species) and contribute to the further divergence of hybrids from the two original paternal forms.

In this case, there is an isolation of light-headed hybrid forms with a characteristic manifestation of various groups of characters: morphological — colouration of the plumage of the head, colouration and pattern of the eggshell; ecological — features of nest structure; behavioural — features of daily activity (twilight activity of hybrids); genetic — distinguishing light-headed hybrids from the original species (*M. flava* and *M. lutea*). This phenomenon can act as a mechanism to maintain the integrity of 'yellow' wagtail species, both the western yellow wagtail *M. flava* and the yellow-headed wagtail *M. lutea* due to the constantly occurring interspecific hybridization in areas of wide sympatry within a single polytypic complex. These studies should be continued with an emphasis on the development of a species identification system during the formation of nesting pairs, the study of the fine ecology of species and their hybrids, the nesting behaviour of species in the zone of hybridization, and other issues.

Acknowledgments

The author sincerely thanks Andrey Mishchenko, Ulyanovsk State Pedagogical University and Technocentre 'Quantorium' for carrying out molecular genetic analysis of the material, assistance in choosing and justifying methods and obtaining genetic trees; Olexander Peklo for providing the Catalogue of the Oological Collection of the National Museum of Natural History NAS of Ukraine and Tatyana Kezhevatoва for the provided photo of yellow wagtail hybrids. Special thanks to Igor Zagorodniuk, leading researcher of the National Museum of Natural History NAS of Ukraine for important comments on the manuscript. This study was supported by a regional grant from the Russian Foundation for Basic Research, project No. 18-44-730002/19.

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