Yellow Wagtails (Passeriformes, Motacillidae) are indicators of steppe and meadow landscapes

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Abstract - Levels of nesting site selection were identified: landscape level is related to birds' choice of landscape with yellow, pink, white, and green aspects. Ecosystem level corresponds to the detection of a water body by birds. The birds detect a station with the necessary vegetation association, where grasses and meadow halophytic associations are the basis of vegetation. The local (point) level is caused by the presence of a necessary host plant, which is a protector of birds' nests. The main signals for the selection of nesting conditions for yellow wagtails as a reflection of semiotics are (in order): landscape – habitats of predominantly yellow, less frequently pink, white and green aspects; ecosystem – proximity of a water body (river, lake, etc.); statistical – halophytic associations. The following aspects of the nesting habitats are considered: ecosystem – proximity to a water body (river, lake, etc.); statistical – halophytic vegetation and grasses on sandy loam, loamy, solonchak soils suitable for nesting holes; local (point) – presence of host plant to protect the nest. Birds select nesting habitats based on the availability of all available signals, which increases the possibility and success of colony formation. The manifestation of semiotics: yellow wagtails in the nesting habitat tend to lose their visibility and dissolve into the background of the biotope, which is a special adaptation against predator attack.

Keywords: *Motacilla flava*, habitat, landscape, vegetation, plant association, colour aspect, semiotics.

Riassunto - La biotopica come riflesso della semiotica: segnali di selezione dell'habitat di nidificazione da parte della cutrettola (Passeriformes, Motacillidae).

Sono stati identificati i livelli di selezione dei siti di nidificazione: il livello di paesaggio è legato alla scelta da parte degli uccelli di paesaggi con aspetti gialli, rosa, bianchi e verdi. Il livello ecosistemico corrisponde all'individuazione di un corpo idrico da parte degli uccelli. Il livello statistico corrisponde all'individuazione da parte degli uccelli di una stazione con la necessaria associazione di vegetazione, dove le erbe e le associazioni alofite dei prati sono la base della vegetazione. Il livello locale (puntiforme) è dovuto alla presenza di una pianta ospite necessaria, che protegge i nidi degli uccelli. I principali segnali per la selezione delle condizioni di nidificazione della cutrettola come riflesso della semiotica sono (nell'ordine): paesaggio – biotopi con aspetti prevalentemente gialli, meno frequentemente rosa, bianchi e verdi; ecosistema – vicinanza di un corpo idrico (fiume, lago, ecc.); statistica – associazioni alofile. Vengono considerati i seguenti aspetti degli habitat di nidificazione: ecosistema – vicinanza a un corpo idrico (fiume, lago, ecc.); statistiche – vegetazione alofila ed erbe su terreni sabbiosi, argillosi e solonchak adatti alle buche di nidificazione; locale (puntiforme) – presenza di una pianta ospite per proteggere il nido. Gli uccelli selezionano gli habitat di nidificazione in base alla disponibilità di tutti i segnali disponibili, il che aumenta la possibilità e il successo della formazione della colonia. La manifestazione della semiotica: le code gialle nel biotopo di nidificazione tendono a perdere la loro visibilità, dissolvendosi nello sfondo del biotopo, il che rappresenta un adattamento speciale contro l'attacco dei predatori.

Parole chiave: *Motacilla flava*, habitat, paesaggio, vegetazione, associazione di piante, aspetto cromatico, semiotica.

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INTRODUCTION

This article is devoted to the study of the problem of species differentiation of closely related species and its implementation within the framework of the semiotic concept of species. The problem of species' evolutionary relationships includes a significant range of areas of analysis. In particular, the author draws on articles by Igor Zagorodniuk and considers a triad of a) the system of niche and ecomorphological species differentiation; b) the system of reproductive isolation and its violations in the form of limited or wide hybridization, the system of prostrate and temporal species relations, including allo-, para-, and sympatry, as well as symbiotopy (Zagorodniuk, 2011) as key directions (modi). The author along with Igor Zagorodniuk considers this triad as basic, especially important when studying groups of closely related species, and therefore essential when considering the problem of evolutionary relationships.

One such group of closely related species, within which all three directions of differentiation (evolutionary relationships?) are manifested, are yellow wagtail species (*Motacilla* grex '*flava*', *Motacilla* sensu lato), which include a complex of forms of close affinity, i.e. evolutionary species at an early stage of differentiation. In this group, we can see interspecific relationships – ecomorphological and biotopic differentiation, including competition; sympatric and parapatric phenomena, including expansion of species into new territories and into each other's ranges, intraspecific hybridisation and reproductive isolation mechanisms.

Some phylogeographic and evolutionary studies have already been carried out, in particular by Alström & Ödeen (2002), Alström & Mild (2003), Alström *et al*. (2015), Pavlova *et al*. (2003). The mechanism of hybridisation and variability, and relationships and competition between closely related species have been the subject of much research (Beregovoy, 1964; Panov, 1973; Babenko, 1981; Stepanyan, 1983; Grichik, 2005; Ferlini *et al*., 2021). Species genetics of yellow wagtails has been previously studied using the example of spatial relationships of species of the Yellow Wagtail group (Artemieva, 2021). The species category is tentatively applicable to yellow wagtail forms. To avoid competition, species are detrimental when coming together, or alternatively species combine well, so there are mechanisms of divergence, which is true for the species group of yellow wagtails (Artemieva & Muravyev, 2012).

In breeding pairs of Yellow Wagtail species, the relationships are realised and unfold in a specific space – the breeding habitat. It is not so much about the range as about the habitats, and, above all, about nesting habitats, when the level of differentiation of close species in birds is particularly strong (Malchevskii, 1969, 1974; Zagorodniuk & Fesenko, 2014). The main site of events is the habitat, which acts as the main meeting place for communication and further interactions between males and females during the nesting period (Aunins *et al*., 2001; Fujioka *et al*., 2001; Batary *et al*., 2007). Stepanyan's isomorphism hypothesis does not work in yellow wagtail species (Stepanyan, 1983).

The aim of this work is to assess the selection signals (signal fields) of yellow wagtails for nesting habitats as a reflection of semiotics.

Background to the study (basic assumptions)

The basic concepts relate to conceptual, general research problems: spatial and biotopic relations of species; the general biological notion of species in a broad and narrow sense; species in a particular environment. This study focuses on the issue of closely related species.

Let us consider three principal aspects: semiotics as a form of realization of speciesness, relation of yellow wagtail species to basic colours (aspects of nesting habitats), and relation of yellow wagtail species to signal fields of habitat. The relationship of semiotics principles will be discussed in the discussion as a result of the original part of the study.

1. Definition of semiotics

The semiotic concept of speciation is based on the 'friend-or-foe' system of recognition of individuals of the same species. It is based on meaningful, iconic (in the sense of key, leading) features that are visually or verbally important for communication between individuals (Kull, 1998, 1999, 2000, 2004, 2016). Any biological species necessarily involves and is fundamentally dependent on sign processes between individuals. The individual recognition window and two-level breeding is almost sufficient as a condition for a natural species. This is due to the associativity of mating, which is not based on certain individual traits, but on the differences between individuals. It also means that the boundaries of the species are fundamentally indistinct, and the shifting of traits occurs in the case of sympatry. The biosymeotic mechanism provides the conditions and communicative constraints for the emergence and maintenance of diversity in the field of living (communicative and semiotic) systems (Kull, 2008, 2009, 2010, 2011, 2016).

The factor that separates potential partners into compatible and incompatible ones can be called the recognition window. Being an unavoidable characteristic in biparental reproduction, it creates assortativity, which leads to splitting different sets into species. The resulting categories cannot be formally defined as they are based on family similarity (Kull, 2014, 2015, 2016, 2018a, 2018b, 2020). Thus, species as a communication category is a biosemiotic system (Brier, 2000; Kull *et al*., 2003; Hoffmeyer, 2010; Kull & Torop, 2011; Kleisner & Maran, 2014).

The author draws on numerous papers on the in-depth study of the evolution of closely related species by Igor Zagorodniuk and also studies these phenomena related to the problematics of closely related species in the light of semiotics (bio- and zoosemiotics). There is a huge variety of ideas about species, but there is still no unified concept and unified criterion of species, much less the definition of species, because nature is extremely diverse (Zagorodniuk, 2020). Species as an entity evolves (Zagorodniuk, 2021a, 2021c), and somewhere conventionally above it the semiotic system of species and the semiotic model of its evolution are designated (Zagorodniuk, 2004, 2019a, 2019b).

Semiotics is only applicable to animals with complex behaviours, such as birds. Semiotic models accelerate the evolution of species, suggesting a rejection of panmixia, and promoting assortative interbreeding, which accelerates the rate of evolution. The concept of species is different for lower and higher animal species as a phenomenon – there is currently no definition of species as a whole. Semiotics accelerates speciation, especially in sympatric conditions. Semiotics exists as a phenomenon, as a stream, and as an idea (Zagorodniuk, 2021a, 2021c).

Species as a concept, in nature also undergoes evolution (Zagorodniuk, 2020), the upper stage of this process being semiotics. There is no panmixing here and behavioural mechanisms are important, differences in biotopes accumulate faster than in morphology. These do not require material changes or morphological changes. Visual changes in colouration, verbal changes (bird song, sound cues), and behaviour are important (Zagorodniuk, 2020). In addition to the idea of pluralism of the concepts of 'species'– which is indicated not only by the difference in the manifestations of 'species' in nature, but also by the difference in research tasks and taking into account the obvious ambiguity of the concepts of 'species' in relation to different systematic groups – this approach allows us to know the normality of diversity (Zagorodniuk, 2021a).

In the 2000s, the term 'vidovost' – 'speciesness' was first developed and introduced into the academic literature

(Zagorodniuk, 2004). Later, the term 'speciesness' appeared in the Western literature. The state of speciesness is a designation of the extremity, boundaries of a species as a phenomenon, a species within a community, a biota (Zagorodniuk, 2004, 2011, 2021a).

As shown earlier (Zagorodniuk, 2019a, 2019b), two concepts – monophyly and pan-mixia – add meaning to such definitions, which, however, are not universal (Zagorodniuk, 2021a, 2021b).

One of the main features of every species is the system of supporting its integrity as one of the manifestations of liminality, of finitude. More than one study in the 'biosemiotic conception of the species' cycle (Kull, 2016) is devoted to this topic. In addition to the criterion of 'familial similarity' (essentially typological), there is a system of natural integrity ('natural species criterion'), which is defined by 'individual recognition windows', i.e. the self-identification system of individuals in 'friend-or-foe' coordinates and the bisexual reproduction system. In essence, this is panmixia, which is at the heart of biosemiotics, 'the assortativity of interbreeding that is based not on certain individual traits but on the differences between individuals'. In essence, the species maintains itself from within, and the assortative interbreeding system creates a structure of non-random links of non-random relationships, so it is selective and also adaptive, which can ensure high adaptability and rapid evolution (Zagorodniuk, 2021a, 2021b). Semiotics accelerates the evolution of species.

2. Colour perception by yellow wagtails

Passerines, including yellow wagtails, have tetrachromatic vision and perceive four colours: ultraviolet, blue, green, and red (Bowmaker & Martin, 1985; Varela *et al*., 1993; Goldsmith, 2006; Vorobyev *et al*., 1998). Even within the human-visible wavelength range, they are able to detect colour differences in objects that humans do not perceive. This more precise differentiation, combined with the ability to see in the ultraviolet range, means that many species exhibit sex dichromatism which are distinguishable to birds but not to humans (Andersson, 1998; Ödeen & Hastad, 2013). The ability to perceive ultraviolet light plays a major role during the mating and courtship period. Birds fully exhibit their mating attire in ultraviolet light. In yellow wagtails, males and females of different species look similar, but they differ in the presence of areas on their feathers that reflect ultraviolet light, which the birds can clearly see. For example, during courtship, the male *Cyanistes caeruleus* (Linnaeus, 1758) displays its reflective 'crown' by raising the feathers at the back of his head (Viitala *et al*., 1995; Bright & Waas, 2002). Male *Melopsittacus undulatus* (Wilkie *et al*., 1998) has the brightest and largest UV reflective markings in their plumage. Thus, the reflection of ultraviolet light by the beak plays an important role in the communication of thrushes. Although UV components seem unimportant in interactions between territorial males, for which orange is the main factor, females respond more strongly to males with beaks that reflect ultraviolet well (Lind *et al*., 2013). The colouration of the breasts of male yellow wagtails in their mating attire is yellow, but in different shades, suggesting that they are equipped with UV markings, so that females can clearly see these differences. Although males of these species have other distinguishing features (voice as an example), so mixed pairs are not as numerous as it may seem at first glance.

An analogy in the significance of the perception of the latent wing pattern can be drawn with the limonet butterfly: their study used latent wing pattern, which is visible only in UV-light, as one of the basic taxonomic characteristics of the genus *Gonepteryx* (Nekrutenko, 1968). On this basis, it was possible to develop a taxonomic structure of the genus *Gonepteryx* and display the evolution and geography of the genus in a new light. Thus, in the ultraviolet part of the spectrum, the wing pattern becomes visible, which strongly differs in representatives of the genus *Gonepteryx* and is not visible in ordinary light: a dark marginal stripe, a dark medial line and a light central area on the upper surface of fore wings, and a contrasting dark marginal area and a light central spot on the upper surface of hind wings are clearly distinguishable. These revealed characters are reliable diagnostic markers of each taxon of the genus *Gonepteryx*, which determines the level of evolution of wing pattern of this group, as was brilliantly shown in their phylogenetic and zoogeographical studies (Nekrutenko, 1968). The technique of detecting the cryptic wing pattern visible in ultraviolet has been applied, which allowed a revision of the taxonomy and the preparation of eidological sections, including 'Discussion of categories of species and subspecies levels' (Zagorodniuk, 2019b; Artemieva, 2020).

Thus, the choice of meaningful attributes for birds may be different from that for the researcher. There is a difference in the perception of leading attributes: researchers do not see the differences between species as they are seen by the species themselves.

3. Semiotics and yellow wagtails: manifestation of signal fields in plumage colouration

So why do different species of yellow wagtails form mixed flocks and colonies? Because the species, although independent, have not lost their genetic unity. They are still capable of forming mixed nesting pairs and colonies and reproduce hybrid offspring. A common brood or a common family where different parents (mixed pair) and different offspring are born together and grow together, keep relations as relatives (individuals of the same brood, brothers and sisters), and relations in the family, the colony, and the flock during migrations and wintering.

Yellow pigments are particularly important as they reflect the UV rays of the spectrum well (xanthophylls in plants, pteridins in butterflies, and lipochromes in birds) and are therefore often used for intraspecific and interspecific communication of species (Bybee *et al*., 2012). For birds, visualization is important when selecting a nesting habitat. In light of the concept of semiotics, visualization is the recognition and interpretation of signals (signs) and the comparison of signs of the habitat and the birds in it. The verbalisation of the signs of the individuals in the habitat is the recognition and interpretation of their vocal signals and behaviour. 'Biotope flavour' of a species is the species' choice of its habitat type (appearance) and colouration (aspect). Yellow wagtails are probably good at distinguishing between yellow and UV colouration. Males in mating attire display bright yellow chest colouration to females and their mates. Moreover, the birds clearly distinguish shades of yellow, so male yellow-headed wagtails have lemon-coloured breasts, which the females of this species unmistakably choose to pair (there are no mixed nesting pairs). The plants which give the biotope its yellow aspect also have shades of yellow: gerule gives a lemon hue, and it is selected by yellow-headed wagtails, whose male breast colouration is closest to it (lemon); sweet clover and dandelion give medium yellow tint (cadmium yellow light), and it is selected by yellow and yellow-headed wagtails (their breast colouring is also most similar to that of these plants); goat's-footed wagtail of austrian and molochai selects black-headed wagtail (females have light lemon-grass breast colouring), etc. Birds are probably quite capable of perceiving the colouration and pattern of both their plumage (their appearance) and the colouration of yellow and other plant flowers (aspect) of their surrounding biotope, both under normal and UV light, as shown in birds and bees attracted to yellow flowers (Papiorek *et al.*, 2016).

The signalling fields for a group of yellow wagtail species are most pronounced in plumage colouration and pattern. Nesting habitats are focal points for the functioning of signal fields (Nagub & Wiley, 2001; Maran, 2009, 2023).

One of the key groups of birds in open landscapes are ground-nesting passerines, including species of yellow wagtails (*Motacilla flava* sensu lato) (Passeriformes, Motacillidae). The yellow wagtail *Motacilla flava flava* (Linnaeus, 1758); *Motacilla flava thunbergi* (Billberg); *Motacilla flava beema* (Sykes, 1832); blackheaded wagtail *Motacilla flava feldegg* (Michahelles, 1830); yellow-headed wagtail *Motacilla lutea* (S. G. G. Gmelin, 1774); yellow-headed wagtail *Motacilla citreola* (Pallas, 1776); mountain wagtail *Motacilla cinerea* (Tunstall, 1771 (on plains)).

The breeding ranges of yellow wagtails are expanding northwestward (Sotnikov, 2006; Artemieva & Muravyov, 2012). This is caused by climate aridization in the steppe and forest-steppe zone and the north-westward movement of plant communities suitable for this group of birds (meadow-steppe and meadow-swamp, floodplain) and food objects (insects associated with them). The nesting phenology of Yellow Wagtails is associated with a 1°C increase in temperature, which extends the distribution of meadow and meadow-steppe plant communities northward by 100-160 km (Davis, 1989; Musselman & Fox, 1991; Puhe & Ulrich, 2001; Serebryanny, 2002). Yellow Wagtails prefer hydrophytic and mesophytic biotopes for nesting in the northern parts of the range, mesophytic and xerophytic biotopes in the central areas, and xerophytic biotopes in the south. In the absence of natural habitats, birds nest in agrocenoses, wastewater treatment plants, etc. (Sotnikov, 2006; Artemieva & Muravyov, 2012; Atlas, 2022; Malovichko & Artemieva, 2023).

4. Habitats: signalling fields and behaviour implementation

The seasonal role of the habitats of Yellow Wagtail species lies in their different importance. During the nesting period (summer), they serve as the location of foraging resources (sites) and nesting birds. Birds show a particularly pronounced competition and differentiation of closely related species (plumage colouration, sound cues, choice of nesting sites, etc.). On the contrary, during the winter period such differentiation is weak or absent, and birds use a single signa ling system and move in space as a single winter aggregation.

The main site of events is the habitat, which serves as the main meeting place, communication, and further interaction between males and females during the breeding season (Aunins *et al*., 2001; Fujioka *et al*., 2001; Batary *et al*., 2007). Different behaviours are realised by the habitat: foraging, territorial, mating, breeding, seasonal migrations and migrations, etc. Habitats are focal points for the application and action of signal ing fields, which have different meanings and functions (Maran, 2017, 2020).

5. 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.

In this work, five species of the yellow wagtail group are considered: *Motacilla flava* (Linnaeus, 1758); *M. feldegg* (Michahelles, 1830); *M. lutea* (Gmelin, 1774); *M. citreola* (Pallas, 1776); *M. cinerea* (Tunstall, 1771) (Sotnikov, 2006; Artemieva & Muravyov, 2012; Artemieva, 2021). This view is one of three on the taxonomic structure of the polytypic complex of *M. flava* (*sensu lato*).

Thus, based on morphological characteristics (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 (Grant & Mackworth-Praed, 1952; Cramp, 1988; Alström & Mild, 2003; Harris~~a~~ *et al*, 2018).

2. There are five polytypic species: *M. flava* (*flava, thunbergi, beema, leucocephala, zaissanensis, plexa, macronyx, alascensis, simillima, tschutschensis, cinereocapilla, iberiae, pygmaea*), *M. feldegg* (*feldearise*), *M. lutea* (*lutea, flavissima, taivana*), *M. citreola (citreola, werae, quassatrix, calcarata, weigoldi*), and *M. cinerea* (*cinerea, melanope, robusta, schmidzi, flaviventris, clara*) (Johansen, 1946; Smith, 1950; Vaurier, 1957, 1959).

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) (Williamson, 1955; Svensson, 1963; Leisler, 1968; Sammalisto, 1968).

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, 2003) 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

The species of the group of yellow wagtails – *Motacilla flava* (Linnaeus, 1758) and *M. citreola* (Pallas, 1776) (Passeriformes, Motacillidae) subgenus *Budytes* (Cuvier, 1817) sensu lato: morphological and ecological characteristics are typical for the genus *Motacilla*; they are polymorphic species, which have a wide variability of plumage colouration traits, more than 20 species and intraspecific forms have been described so far; they inhabit extremely diverse ecological and geographical conditions and are a transpalearctic polytypic group. The studied group of yellow wagtails is represented by five species: *M. flava* (Linnaeus, 1758); *M. feldegg* (Michahelles, 1830); *M. lutea* (Gmelin, 1774); *M. citreola* (Pallas, 1776); *M. cinerea* (Tunstall, 1771) (Sotnikov, 2006; Artemieva & Muravyov, 2012; Artemieva, 2021). The nomenclature of taxa is given according to Stepanyan (2003).

Data were collected during the 2007-2022 (following the materials, field data were collected between 2011 and 2021) field seasons in the following five R1-R5 steppe landscape regions: southern European Russia, the Middle and Lower Volga region, the Southern Urals, and southern Western Siberia. Landscapes and vegetation of breeding habitats of a group of yellow wagtails were investigated. Regional data collections are from the Middle Volga Region (Ulyanovsk Region) (R1), Lower Volga Region (Volgograd and Astrakhan Regions) (R2), Southern European Russia (Rostov Region, Kalmykia) (R3), Southern Urals and North-Western Kazakhstan (Orenburg Region, Ural Region) (R4), and Southern Western Siberia (Omsk Region, Novosibirsk Region) (R5) (Fig. 1).

Materials

A total of 21 localities from the indicated five regions were surveyed: **R1**: Ulyanovsk Region, 28.08.2016, 27.05.2018, Sandy Lake, Cherdaklinsky district, flooded meadows, old fallow ground, mixed colony of yellow, yellow-headed wagtails; 25.08.2017, halophytic meadow in the floodplain of the Malaya Tereshka River, Radischevsky District; 18.05.2018, env.of Radischevo village, Radischevsky District, flooded saline meadows in the floodplain of the Tereshka River, mixed colony of

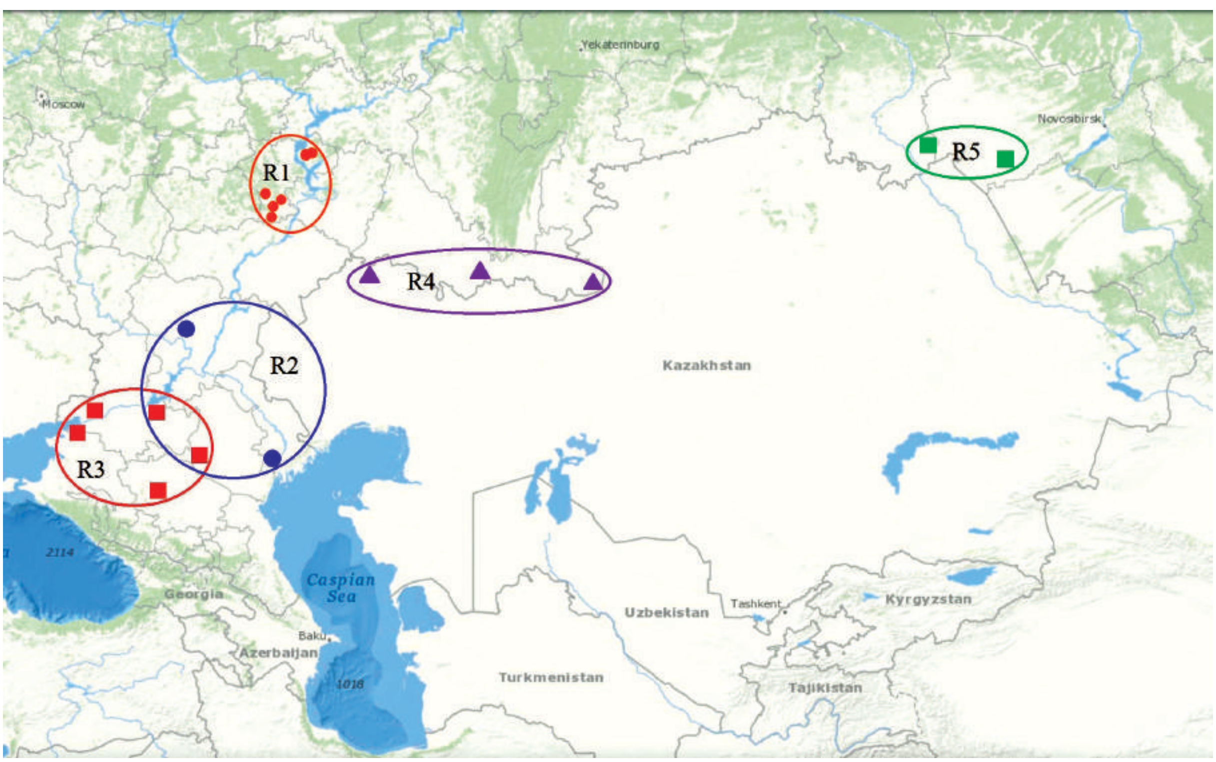

Fig. 1 - Map of the regions studied: R1-R5 (base map taken by Ferlini & Artemyeva, 2020) / Mappa delle regioni studiate: R1-R5 (mappa di base tratta da Ferlini & Artemyeva, 2020).

R1 - Middle Volga region / Regione del Medio Volga

R2 - Lower Volga region / Regione del Basso Volga

R3 - South of the European part of Russia / A sud della parte europea della Russia

R4 - Southern Urals and North-Western Kazakhstan / Urali meridionali e Kazakistan nord-occidentale

R5 - South of Western Siberia / A sud della Siberia occidentale yellow and yellow-headed wagtails; 20.05.2018, pond near Solovchikha village, Radischevsky District, colony of yellow wagtails; 11.06.2018, env. of Radischevo village, Radischevsky District, Tereshka River floodplain, flooded halophytic solonaceous meadow, yellow and yellow-headed wagtails colony; 10.06.2020, 10.06.2020, Oktyabrsky pond, Radishchevsky District, halophytic meadow, colony of yellow, yellow-headed and yellow wagtails; 14.06.2020, Oktyabrsky pond, Radishchevsky District, halophytic meadow, colony of yellow and yellow-headed wagtails. **R2**: Volgograd Region, 2.05.2011; Astrakhan Region, 10-12.05.2011, Ilmeno-Bugrovskiy Reserve, Ikryaninskiy District, halophytic meadows, solonchaks, yellow wagtail nesting habitat. **R3**: Rostov Region, 3.06.2011, env. of Volgodonsk, halophytic meadow, yellow wagtail nesting habitat; Rostov Region,14-16.06.2012, env. of of Kagalnik, Azovsky district; 4-9.06.2011, 3-5.05.2013, Mishkinskaya floodplain, Aksai district, black-headed wagtails colony. Republic of Kalmykia, 28.03.2021, env. of Elista, halophytic meadows, solonchaks, yellow wagtail nesting habitat; Stavropol Region, 2.06.2018, Izobilnenskii District, yellow and black-headed wagtail colony. **R4**: Orenburg Region, Uralsk Region, 11.06.2021, Sazan settlement, Belyaevsky District, steppe station 'Orenburg Tarpania', yellow wagtail nesting habitat and colony; 11.06.2021, steppe station 'Orenburg Tarpania', nesting habitat of yellow wagtails colony; 11.06.2021, steppe station 'Orenburg Tarpania', foraging habitat of yellow wagtails; Orenburg Region, 25.04.2020, Svetlinsky Nature Reserve, foraging and nesting habitat of yellow wagtails; 28.04.2015, Uralsk Region, steppe, saline marsh, nesting habitat of yellow wagtails. **R5**: Omsk Region, 28.07.2020, Okoneshnikovsky, Cherlaksky districts, Reserve 'Stepnoy', salt lake Porshnevoe, nesting habitat of yellow wagtails. Novosibirsk Region, 30.07.2020, Barabinskiy, Chanovskiy Rayons, 'Kirzinskiy' Reserve, Chany salt lake, nesting habitat of yellow wagtails.

In the nesting habitats of yellow wagtail colonies, the vegetation and plant species composition of nest points (composition of grasses and forbs, plants giving yellow, white and pink aspects of the habitat, dominant species, background species, plant species protecting birds' nests, plants used by birds for nest construction) were studied. Plant identification was carried out according to summaries by Blagoveshchensky (1984), Mayewsky (2006). Bird nests were identified according to Mikheev (1996). Russian and Latin names of birds were given according to compilations by Stepanyan (2003) and Koblik *et al*. (2006).

Photographs of Yellow Wagtail species in natural habitats were taken. Examples of male and female Yellow Wagtail species are shown in Fig. 2.

A bank of photographs of nesting habitats of a group of yellow wagtail species was created including 2088 specimens; 1349 individuals of 5 yellow wagtail species were counted, 98 colonies were observed, and 47 nests were recorded.

The habitat photos are divided into groups by study area. The data are summarised in Tables 1-3. Habitat types of Yellow Wagtail species and vegetation aspects of their breeding habitats are highlighted. The authors accept in the null hypothesis that yellow wagtail species most often prefer habitats with yellow aspect. A total of 3 main habitat aspects were identified: yellow, pink, and white for five yellow wagtail species. Combinatorics of 100 options were used, of which 64 combinations out of 100 possible (100-36 = 64) were filled. Habitat selectivity by yellow wagtail species was observed; not all variants were populated by all yellow wagtail species. We chose to use the habitat assignment coefficient (F_{ij}) as a measure. All species of yellow wagtails were determined based on the authors' long-term experience and genetic testing of bird samples, eggs, feathers, identification of their nests, etc. (Artemieva & Muravyov, 2012; Artemieva *et al*., 2016a, 2016b; Ferlini & Artemyeva, 2020; Artemieva, 2021).

A table was compiled to match the number of occurrences (frequency of occurrence) of yellow wagtails selecting a particular habitat type with a particular colour aspect (Tab. 1).

The coefficient of relative occurrence (correspondence) of species to biotope was determined according to the formula (Naglov & Zagorodniuk, 2006):

$$F_{ij} = (n_{ij} \times N - n_i \times N_j) / (n_{ij} \times N + n_i \times N_j - 2n_{ij} \times N_j),$$

Where n_{ij} is the number of individuals of the i-th species in the j-th sample (biotope) of volume N_j, n_i is the number of individuals of that species in all collections of total volume N.

A correlation coefficient for alternative traits, the tetrachoric relationship index ra (Lartseva & Muksinov, 1985) was determined. Alternative traits were determined: x (+–) – yellow aspect, y (+–) – yellow colouring. Alternative groups: p_1 (+ +), p_2 (+–), p_3 (– +), p_4 (—). A tetrachoric indicator r_a between the yellow aspect of the habitat and yellow colouration of birds was determined (Tab. 5).

The relationship of alternative traits was studied: the yellow aspect of the vegetation of the nesting habitat (the first character), a different aspect and the yellow colour of the plumage of birds (the second character), a different colour. The bird population of the studied habitat was conditionally divided into four groups: p_1, individuals with both traits (+ +); p_2 – individuals having the first trait, but not having the second trait (+ –); p_3 – individuals that do not have the first trait, but have the second trait (– +); p_4 – individuals lacking both traits (– –).

The relationship between alternative traits was studied: yellow aspect of the nesting habitat vegetation (first trait), other aspect and yellow colouration of birds' plumage (second trait), and other colouration. The bird populations of the habitats studied were conditionally divided into four groups: p_1 – individuals with both traits (+ +); p_2 – individuals with the first trait but no second trait (+ –); p_3 – individuals without the first trait but with the second trait (– +); p_4 – individuals without both traits (– –).

The tetrachoric link index (r_a) was calculated using the formula (r_a):

$$r_a = \frac{(p_1 \cdot p_4) - (p_2 \cdot p_3)}{\sqrt{(p_1+p_2) \cdot (p_3+p_4) \cdot (p_1+p_3) \cdot (p_2+p_4)}}$$

Statistical processing of the data was carried out in Excel 2007.

Fig. 2 - Species of yellow wagtails* in the field. / Specie di cutrettola gialla* in campo. A) male / maschio *M. flava* (Ulyanovsk oblast / regione, env. of / villaggio di Barataevkavillage, 27.04.2012); B) female / femmina *M. flava* (near / vicino Nizhny Novgorod, Artemovskie meadows / prati, 9.05.2012); C) male / maschio *M. fedegg* (Rostov oblast / regione, env. of / villaggio di Kagalnik, bank of / riva di Azov, 19.06.2012); D) female/femmina *M. fedegg* (Rostov oblast / regione, settlement of / insediamento di Kagalnik, bank of / riva di Azov, 19.06.2012); E) male / maschio *M. lutea* (Ulyanovsk oblast / regione, Cherdakly village / villaggio, Sandy lake / lago Peschanoye, 5.07.2013); F) female / femmina *M. lutea* (Ulyanovsk oblast / regione, Cherdakly village / villaggio, Sandy lake / lago, 22.05.2012); G) male / maschio *M. citreola*; H) female / femmina *M. citreola* (near / vicino Nizhny Novgorod, Artemovskie meadows / prati, 9.05.2012); I) female / femmina *M. cinerea* (Kemerovo oblast / regione, env. of / villaggio di Kemerovo, 3.07.2007, photo / foto A. Belyankin); J) female/femmina *M. cinerea* (Ulyanovsk oblast / regione, Novoulyanovsk, 27.12.2008, photo / foto V. Kiryashin). (Photo: / Foto: Elena Artemieva).

* These taxa are given as an independent species according to the concept: there are five polytypic species (Introduction). The nomenclature of taxa is given according to Stepanian (2003). / Questi taxa sono indicati come specie indipendenti secondo il concetto: ci sono cinque specie politipiche (Introduzione). La nomenclatura dei taxa è riportata secondo Stepanian (2003).

Tab. 1 - Distribution of frequency of occurrence of yellow wagtail species in different habitat types. / Distribuzione della frequenza di presenza delle specie di cutrettola in diversi tipi di habitat.

Species	Habitats, vegetation aspect									
	Steppe yellow/other	Meadow yellow/other	Coastal yellow/other	Marsh yellow/other	Mountain yellow/other	Forest yellow/other	Floodplain yellow/other	Forest belts yellow/other	Old deposits yellow/other	Agrocenoses yellow/other
Motacilla flava	65/42	93/65	46/39	46/32	-	-	58/21	3/12	79/24	88/54
Motacilla feldegg	75/38	87/26	28/32	5/13	-	-	42/39	-	-	76/47
Motacilla lutea	58/23	96/48	34/27	1/3	-	-	37/34	-	85/17	9/14
Motacilla citreola	-	36/12	27/19	68/31	-	-	25/20	-	28/14	3/21
Motacilla cinerea	-	3/2	1/3	-	5/1	3/2	2/1	-	-	-
TotalΣ	Σ	Σ	Σ	Σ	Σ 5/1	Σ 3/2	Σ	Σ	Σ	Σ
1312/776	198/103	315/153	136/120	120/79			164/115	3/12	192/55	176/136
6							5			

RESULTS

Plant associations of nesting stations were identified for the studied regions (north to south, west to east). Already reported in the methods.

1. Nesting habitats of a group of yellow wagtail species
1.1. General characteristics of nesting habitats

The nesting habitats of Yellow Wagtail species are generally meadow and meadow-steppe and steppe plant communities.

The species composition of the vegetation of the breeding habitats of yellow wagtails species in the studied regions were analysed. In Table 2, we present the results of determining plants typical for nesting sites of the group of yellow wagtails. For each region in nesting habitats, dominant plant species forming the main components of nesting habitats were identified: cereals (grasses); background plant species (motley grass); plant species giving a certain aspect (yellow, pink, white) to nesting habitats.

1.2. Preferred plant communities

Yellow Wagtail species prefer open landscapes, steppe, grassland, and meadow-steppe communities for nesting. The habitat types of Yellow Wagtail species can be grouped into the following groups: natural (steppes, meadows, marshes, coastal areas, open ungrown floodplains) and anthropogenic (agrocenoses, old fallow lands). As exceptions, birds may be found in forest belts (for yellow wagtail) and mountain-forest habitats (only for mountain wagtail) (Tab. 1). As a rule, yellow wagtail species avoid enclosed and densely overgrown habitats (forests, scrub, etc.). The basic habitats for their nesting sites are various types of grassland (floodplain, floodplain, halophytic, solonetzic) and steppe (meadow-steppe). Therefore, we pay special attention to these habitat types.

1.2.1. Preferred plant compositions in meadows

The main groups of plants in the nesting habitat are:

a) grasses: *Elytrigia repens* (L.) Nevski, *Dactylis glomerata* L., *Bromopsis inermis* (Leys.) Holub., *Cleistogenes squarrosa* (Trin.) Keng;

b) host plant: *Stemmacantha serratuloides* (Georgi) Dittrix, *Inula helenium* L, *Senecio schvetzovii* Korsh, *Cirsium arvense* (L.) Scop., *Carduus acanthoides* L., *Artemisia absinthium* L., *Rumex confertus* Willd;

c) plants with yellow aspect: *Inula helenium* L., *Senecio schvetzovii* Korsh, *Melilotus officinalis* (L.) Lam, *Barbarea vulgaris* W. T. Aiton, *Chamaecytisus ruthenicus* (Fisch. ex Wol.) Klask., *Galium verum*(L.), *Verbascum orientale* (L.) All., *Verbascum lychnitis* L.

1.2.2. Preferred plant compositions in steppe (grassland-steppe)

The main plant groups of the nesting habitat are:

a) grasses: *Koeleria sclerophylla* P. A. Smirn., *Bromopsis inermis* (Leyss.) Holub, *Poa bulbosa* L., *Poa trivialis* L., *Agropyron desertorum* (Fisch. ex Link) Schult. & Spach., *Phleum phleoides* (L.) H. Karst;

b) protective plant (host plant): *Glycyrrhiza echinata* L., *Althaea officinalis* L., *Limonium gmelinii* (Willd.) Kuntze, *Rumex crispus* L.;

c) plants giving yellow aspect: *Scorzonera austriaca* Willd., *Euphorbia seguieriana* Neck., *Senecio grandidentatus* Ledeb, *Senecio jacobaea* L., *Crepis tectorum* L., *Tulipa scythica* Klokov et Zoz, *Crinitaria villosa* (L.), *Tanacetum vulgare* L.

1.2.3. Common features of nesting habitats

In general, yellow wagtails prefer certain types of habitats for nesting: open floodplains, steppes, meadows, meadow-steppes, etc. Yellow Wagtail species form nesting colonies in floodplain landscapes of lakes and ponds

Tab. 2 - Species composition of meadow, meadow-steppe and steppe plant communities in the breeding habitats of Yellow Wagtail species. / Composizione delle specie delle comunità vegetali di prato, prato-steppa e steppa negli habitat riproduttivi delle specie di cutrettola gialla.

Region	**Cereals, grass meadows**	**Motleygrass**	**Yellow aspect**	**Pink aspect**	**White aspect**
Middle Volga (R1)	*Festuca pratensis* Huds., *Elytrigia repens* (L.) Nevski, *Dactylis glomerata* L., *Bromopsis inermis* (Leys.) Holub., *Cleistogenes squarrosa* (Trin.) Keng.	*Artemisia absinthium*L., *Rumex confertus* Willd., *Lathyrus tuberosus* L., *Astragalus austriacus* Jacq., *Salvia nemorosa pseudosylvestris* (Stapf) Bornm.	*Inula helenium* L., *Senecio schvetzovii* Korsh., *Melilotus officinalis* (L.) Lam., *Barbarea vulgaris* W. T. Aiton, *Taraxacum officinale* Wigg., *Rorippa palustris* (L.) Bess., *Erucastrum armoracioides* (Czern. ex Turcz.) Cruchet, *Hieracium pilosella* L., *Brassica napus* L., *Chamaecytisus ruthenicus* (Fisch. exWol.) Klask., *Galium verum* (L.), *Verbascum orientale* (L.) All., *Verbascum lychnitis* L., *Brassica napus* L., *Iris pseudacorus* L.	*Stemmacantha serratuloides* (Georgi) Bobrov, *Cirsium arvense* (L.) Scop., *Carduus acanthoides* L.	*Melilotus albus* Medik., *Sinapis alba* L.
Lower Volga (R2)	*Anisantha tectorum* (L.) Nevski, *Festuca cretacea* T. I. Popov & Proscor., *Juncus articulatus* L., *Crypsis schoenoides* (L.) Lam., *Poa bulbosa* L., *Agropyron desertorum* (Fisch. Ex Link) Schult., *Eremopyrum orientale* (L.) Jaub. & Spach.	*Bassia sedoides* (Pall.) Asch., *Cirsium incanum* (S.G. Gmel.) Fisch., *Corispermum marschallii* Stev., *Vicia tenuifolia* Roth, *Artemisia nitrosa* Weberex Stechm., *Salvia pratensis* L., *Fritillaria meleagroides* Patrin ex Schult. F., *Atraphaxis spinosa* L., *Clausia aprica* (Stephan ex Willd.) Trotzky, *Papaver rhoeas* L., *Pedicularis dasyantha* Hadac, *Artemisia santonica* L., *Fritillaria meleagroides* Patrin ex Schult. & Schult. F., *Iris humilis* Georgi, *Iris tenuifolia* Pall., *Iris scariosa* Willd. Ex Link.	*Tanacetum kittaryanum* (C. A. Mey.) Tzvelev, *Tulipa biebersteiniana* Schult & Schult. F., *Euphorbia semivillosa* (Prokh.) Krylov, *Sisymbrium loeselii* L., *Tulipa biebersteiniana* Schult. & Schult. F., *Astragalus wolgensis* Bunge, *Tragopogon pratensis* L., *Senecio jacobaea* L., *Linaria genistifolia* (L.) Mill.		*Tulipa biflora* Pall., *Matricaria chamomilla* L., *Astragalus lactiflorus* Ledeb., *Myosoton aquaticum* (L.) Moench, *Valeriana tuberosa* L., *Tulipa biflora* Pall.
South of the European part of Russia (R3)	*Anisantha tectorum* (L.) Nevski, *Cleistogenes squarrosa* (Trin.) Keng., *Poa pratensis* L., *Poa trivialis* L., *Poa angustifolia* L., *Bromopsis inermis* (Leyss.) Holub, *Carex hirta* L.,	*Glycyrrhiza echinata*L., *Althaea officinalis* L., *Crambe tataria* Sebeok, *Goniolimon elatum* (Fisch. ExSpreng.) Boiss., *Limonium gmelinii* (Willd.) Kuntze, *Achilleam icrantha* Willd., *Gratiola officinalis* L., *Plantago lanceolata* L.,	*Scorzonera austriaca* Willd., *Euphorbia seguieriana* Neck., *Hieracium pilosella* L., *Tragopogon podolicus* (DC.) S. A. Nikitin, *Senecio vernalis* Waldst. et Kit., *Senecio congestus* (R. Br.) DC,		

Region	Cereals, grass meadows	Motleygrass	Yellow aspect	Pink aspect	White aspect
South of the European part of Russia (R3)	*Juncus atratus* Krock., *Eremopyrum orientale* (L.) Jaub & Spach.	*Artemisia austriaca* Jacq., *Artemisia armeniaca Lam.*, *Artemisia absinthium* L., *Phragmites australis* (Cav.) Trin. ex Steud., *Lathyrus tuberosus* L., *Salvia tesquicola* Klokov et Pobed., *Scutellaria dubia* Taliev & Sirj., *Rumex crispus* L., *Achillea setacea* Waldst. & Kit., *Artemisia arenaria* H. C. Fu, *Bassia laniflora* (S. G. Gmelin) A. J. Scott, *Amaranthus blitoides* S. Watson, *Filago arvensis* L., *Lepidiumper foliatum* L., *Petrosimonia brachiata* (Pall.) Bunge, *Trifolium arvense* L., *Centaurea diffusa* Lam., *Artemisia santonica* L., *Ceratocarpus arenarius* L., *Agriophyllum pungens* (Vahl) Link ex A. Dietr., *Eryngium campestre* L., *Artemisia absinthium* L., *Dianthus leptopetalus* Willd.	*Senecio jacobaea* L., *Crinitaria villosa* (L.) Grossh., *Neslia paniculata* (L.) Desv., *Tanacetum vulgare* L., *Tanacetum akinfiewii* (F. N. Alex.) Tzvelev, *Crepis tectorum* L., *Potentilla argentea* L., *Iris pseudacorus* L.		
Southern Urals and Northwestern Kazakhstan (R4)	*Bromopsis inermis* (Leys.) Holub.	*Ceratoides papposa* Botsch. et Ikonn., *Salicornia europaea* L., *Chenopodium* sp.		*Tulipa patens* C. Agardh ex Schult. & Schult. F., *Aster tripolium* (L.) Greuter	
South of Western Siberia (R5)	*Koeleria sclerophylla* P. A. Smirn., *Bromopsis inermis* (Leys.) Holub., *Phleum phleoides* (L.) H. Karst., *Poa trivialis* L.	*Artemisia austriaca* Jacq., *Filago arvensis* L., *Phragmites australis* (Cav.) Trin. &Steud., *Artemisia absinthium* L., *Asparagus pallasii* Miscz., *Iris halophila* Pall., *Fritillaria meleagroides* Patrin ex Schult. & Schult. F.	*Tanacetum vulgare* L., *Odonta rrhenatortuosa* (Waldst. & Kit. ex Willd.) C. A. Mey., *Gagea fedtschenkoana* Pascher.	*Tulipa patens* C. Agardh ex Schult. & Schult. F.	*Allium tulipifolium* Ledeb.

and depend quite strongly on the cyclicity of water bodies (water levels etc.), as well as on soil type (Artemieva & Kalinina, 2019; Artemieva *et al*., 2020).

We considered a series of features characterising the biotopes, in particular, in addition to plants, data on soil types were included in the analysis.

The data on the vegetation features of nesting habitats of yellow wagtails in the study regions are presented in Table 3.

The main habitat features of Yellow Wagtail species are as follows.

Grass-grass and grass-forest habitats are primarily inhabited by yellow wagtails. They are most preferred for nesting by Yellow Wagtails because of their protective properties in relation to the nest. Tall, vigorous plants also serve as decoys for birds. Mass flowering plants of *Inula helenium* L., *Senecio schvetzovii* Korsh., *Melilotus officinalis* (L.), *Tulipa scythica* Klokov et Zoz, *Tanacetum vulgare* L., *Brassica napus* L., *Helianthus annuus*, and others create a yellow aspect (main colour background) of the nesting habitat against which yellow wagtails easily hide from predators. At the base of the stalks of the

Stemmacantha serratuloides and the above species, the females build their nests in the pit. Peristock-grass-grass and fescue-grass stands were less common and selected by Yellow Wagtails when sites in the first group were scarce. Other plant associations are usually used as foraging sites, where birds feed and collect insects for feeding their chicks. The dominant species in the vegetation associations of yellow wagtails nesting sites are the *Inula helenium* L. and *Senecio schvetzovii* Korsh.

Yellow Wagtails prefer cereal-herbaceous, cereal-grass, cereal-sphagnum and cereal-tamarisk associations in steppes of Volgograd, Rostov, and Astrakhan Regions. Yellow Wagtails prefer cereal-grass, cereal-tulip, cereal-wormwood, and cereal-pigeon associations in the halo-

Tab. 3 - Peculiarities of landscape and vegetation of breeding habitats of yellow wagtail colonies during the breeding season by regions. / Caratteristiche del paesaggio e della vegetazione degli habitat riproduttivi delle colonie di cutrettola durante il periodo riproduttivo per regione.

Locality: region, habitat during the nesting period / aspect during the nesting period	**Soil type**	**Station, plant association**	**Dominant species**	**Perch plants**	**Nest-protecting plant species (hostplant)**
MiddleVolga (R1): Floodplain meadows, water meadows, sunflower fallow lands / yellow	sandy, loamy	cereal and sunflower	*Helianthus annuus*, *Barbarea vulgaris*, *Melilotus officinalis*	*Melilotus officinalis, M. albus, Rumex confertus*	*Helianthus annuus* (dry stems) *Carduus acanthoides*, *Cirsium arvense*
Halophytic meadows / yellow	clayey	cereal and elecampane	*Inula helenium, Senecio schvetzovii*	*Inula helenium*	*Inula helenium, Senecio schvetzovii*
Flood solonetzic meadows /pink	sandy, loamy, solonetsous chernozems, solod	cereal-leuzean	*Stemmacantha serratuloides*	*Stemmacantha serratuloides*	*Stemmacantha serratuloides*
Floodplain meadows / yellow	loamy	cereal and elecampane	*Brassica napus*, *Sinapisalba*	*Melilotus officinalis, Artemisia absinthium, Rumex confertus*	*Melilotus officinalis*
Floodplain meadows, halophytic meadows / yellow	loamy	cereal-cross	*Senecio schvetzovii, Inula helenium*	*Senecio schvetzovii, Verbascum lychnitis*	*Verbascum lychnitis, V. orientale*
Halophytic solonetsous meadows / pink	sandy, loamy, solonetsous chernozems, solod	cereal-leuzean	*Stemmacantha serratuloides*	*Stemmacantha serratuloides*	*Stemmacantha serratuloides*
Halophytic meadows/ yellow	loamy	cereal and elecampane	*Inula helenium*	*Inula helenium*	*Inula helenium*
Halophytic meadows / yellow	loamy	cereal and elecampane	*Inula helenium*	*Inula helenium*	*Inula helenium*
Lower Volga (R2): Floodplain halophytic meadows / yellow, white	sandy, loamy	cereal-tulip	*Tulipa biflora, Tulipa biebersteiniana*	*Cirsium incanum, Artemisia nitrosa, Phragmites australis*	*Cirsium incanum, Tanacetum kittaryanum, Phragmites australis*
Flood plain meadows, halophyte meadows, solonchaks / yellow	sandy, loamy, saline	grass-forb	*Agropyron desertorum, Eremopyrum orientale, Poa bulbosa*	*Senecio jacobaea, Sisymbrium loeselii*	*Euphorbia semivillosa*
South of the European part of Russia (R3): Azov coast, halophytic meadows / white	loamy	cereal-cermeic	*Cleistogenes squarrosa, Limonium gmelinii*	*Althaea officinalis, Rumex crispus*	*Limonium gmelinii*
Floodplain Halophytic meadows / yellow	sandy, loamy	cereal-licorice, cereal-cross	*Poa angustifolia, Euphorbia seguieriana, Scorzonera austriaca*	*Glycyrrhiza echinata*	*Glycyrrhiza echinata*
Halophyte meadows, solonchaks/yellow	loamy, saline	grass-forb	*Eremopyrum orientale, Cleistogenes squarrosa*	*Tanacetum akinfiewii*	*Euphorbia seguieriana*

Locality: region, habitat during the nesting period / aspect during the nesting period	Soil type	Station, plant association	Dominant species	Perch plants	Nest-protecting plant species (hostplant)
Southern Uralsand Northwestern Kazakhstan (R4): Floodplain meadows, halophytic meadows, salt marshes / yellow	downed southern chernozems, solonetzes and solonchaks	grass-forb, cereal-tulip	*Tulipa scythica, Crinitaria villosa*	*Phragmites australis*	*Crinitaria villosa, Phragmites australis*
Floodplain meadows, halophytic meadows, salt marshes / yellow	downed southern chernozems, solonetzes and solonchaks	grass-forb, cereal-tulip	*Tulipa scythica, Crinitaria villosa*	*Phragmites australis*	*Crinitaria villosa, Phragmites australis*
Floodplain meadows, halophytic meadows, salt marshes / yellow	downed southern chernozems, solonetzes and solonchaks	grass-forb, cereal-tulip	*Tulipa scythica, Crinitaria villosa*	*Phragmites australis*	*Crinitaria villosa, Phragmites australis*
Floodplain meadows, Halophytic meadows, saltmarshes / pink	sandy, loamy, solonchaks	cereal-tulip	*Tulipa patens*	*Phragmites australis*	*Phragmites australis*
South of Western Siberia (R5): Floodplain meadows, halophytic meadows, salt marshes / yellow	sandy, loamy, solonchaks	cereal-tansy	*Tanacetum vulgare*	*Tanacetum vulgare, Phragmites australis*	*Tanacetum vulgare*
Floodplain meadows, Halophytic meadows, saltmarshes / pink, yellow	sandy, loamy, solonchaks	cereal-tulip, cereal-wormwood	*Tulipa patens*, *Artemisia absinthium*	*Artemisia absinthium, Phragmites australis*	*Artemisia absinthium*

phytic steppes of the Southern Urals and southern Western Siberia (Orenburg, Omsk and Novosibirsk oblasts). The most preferred species of grasses in the breeding habitats of yellow wagtails are: *Elytrigia repens* (L.) Nevski, *Dactylis glomerata* L., *Bromopsis inermis* (Leys.) Holub., *Cleistogenes squarrosa* (Trin.) Keng. A. Smirn., *Poa trivialis* L., *Poa angustifolia* L., *Poa bulbosa* L. Dried stems of cereals are used by females for nest building as a base for nest walls. Dried stems of mixed grasses are used as additional building material. Soaked fine grass roots form the basis of the lining of the nest tray. Therefore yellow wagtails prefer cereals of different variations as nesting sites.

In steppe conditions, Yellow Wagtails prefer to nest in halophytic habitats– meadows, which are developed around steppe water bodies. Loamy and sandy loam soils are the most suitable substrate for digging a nest hole, as these types of soil are quite malleable. Halophytic meadows in floodplains of lakes and rivers in steppes become isolates (refugia) for colonies of yellow wagtails. Halophytic meadows are exploited by Yellow Wagtail species provided they are not flooded during the breeding season. For Yellow Wagtails, the development and existence cycle of salt lakes and soil composition (as for many soil-associated animals) are of primary importance in the formation of colonies in steppes, which determine the development of necessary plant associations (Artemieva & Grudinin, 2021; Artemieva, 2022). Yellow Wagtails during the breeding season tend to prefer nesting biotopes with a well-defined yellow aspect, which has cryptic importance. Other options may be nesting biotopes with pink or white aspect, with green aspect being pure grassland.

2. Distribution of Yellow Wagtail species by breeding habitats

Consider the distribution of the five species of yellow wagtails across the ten habitat types (Tab. 1).

The results of the calculation of the coefficient of relative confinement (F_{ij}) of the Yellow Wagtail group to habitats are presented in Table 4. In particular, minimum and maximum habitat preference (avoidance) indices were determined for the studied yellow wagtail species. For 10 main habitat types, the preferences of birds of the same habitat type were determined, differing by aspects of vegetation in the nesting period: yellow and others. Thus *M. flava* prefers forest belts and agrocenoses with yellow aspect (1.00 and 0.27), *M. feldegg* prefers steppes with yellow aspect and agrocenoses (0.31 and 0.41), *M. lutea* prefers fallow lands (0.45), *M. citreola* prefers bog meadows (0.77), and *M. cinerea* prefers mountain foresthabitats (1.00). When the same habitats with different aspects are combined, their preference for yellow wagtail species remains in the same proportion.

Yellow Wagtail species prefer open landscapes for nesting including meadows, steppes, open floodplains, and in the event of their ploughing and destruction they prefer agrocenoses and old fallows. The group of yellow wagtails species shows weak biotopical confinement, but on the contrary, shows evident avoidance of most habitats, which can be explained by destruction of original indigenous ecosystems and biotopes (meadows and steppes, including intrazonal habitats): birds cannot nest wherever they could, but only wherever it is possible. The indices show that in most cases there is high avoidance of particular habitats, rather than high timing. Thus, for the most part, birds select nesting habitats by an exclusion method: a habitat where it is impossible to form a colony is excluded.

All species of yellow wagtails, except for the mountain wagtail, are capable of forming colonies, and choose only those habitats that have all levels of signals – signal fields (attributes), which include the main components of the nesting habitat: open landscapes with yellow, pink, and white aspects, the presence of a water body, the presence of certain plant composition with dominant and background species, grasses, and protecting nest plants. In contrast, the mountain wagtail clearly demonstrates attachment to its habitat as it nests isolated singly or in several pairs in chalky forested or gully-shaped habitats. However, all species of yellow wagtails differ with respect to humidity. For *M. flava* the highest values (0.12-0.14) are in meadows and fallow land; for *M. feldegg* 0.31-0.41 in steppes and agrocenoses; for *M. lutea* 0.19-0.20 for meadows and fallow land. Only *M. citreola* and *M. cinerea* show high affinity to meadow-marsh habitats (0.58-0.77) and mountain-steppe, mountain-forest habitats (1.00). In percentages the Yellow Wagtail chooses steppe biotopes – 14%, meadow – 22%, coastal – 12%, marsh – 10%, floodplain – 13%, forest belts – 1%, fallows – 12%, agrocenoses – 15%. Floodplain, coastal biotopes and forest belts are chosen by birds as feeding habitats, where in shallow waters, along the water's edge and in thickets they catch insects and mollusks. All other habitats are potentially suitable for nesting (Table 4).

Tab. 4 - Coefficient of relative attribution of Yellow Wagtails to habitats. / Coefficiente di assegnazione del biotopo relativo per la cutrettola gialla.

Habitat	*flava*	*feldegg*	*lutea*	*citreola*	*cinerea*	sum		*flava*	*feldegg*	*lutea*	*citreola*	*cinerea*
steppe yellow	65	75	58	0	0	198		-0.09	0.31	0.15	-1.00	-1.00
steppe others	42	38	23	0	0	103		0.09	0.29	-0.03	-1.00	-1.00
meadow yellow	93	87	96	36	3	315		-0.16	0.09	0.18	-0.14	0.07
meadowothers	65	26	48	12	2	153		0.12	-0.22	0.20	-0.33	0.09
coastal yellow	46	28	34	27	1	136		-0.06	-0.11	0.05	0.18	-0.20
coastalothers	39	32	27	19	3	120		-0.09	0.06	-0.02	0.05	0.39
marsh yellow	46	5	1	68	0	120		0.03	-0.76	-0.95	0.77	-1.00
marsh others	32	13	3	31	0	79		0.08	-0.24	-0.77	0.58	-1.00
mountain yellow	0	0	0	0	5	5		-1.00	-1.00	-1.00	-1.00	1.00
mountainothers	0	0	0	0	1	1		-1.00	-1.00	-1.00	-1.00	1.00
forest yellow	0	0	0	0	3	3		-1.00	-1.00	-1.00	-1.00	1.00
forest others	0	0	0	0	2	2		-1.00	-1.00	-1.00	-1.00	1.00
floodplain yellow	58	42	37	25	2	164		-0.03	0.03	-0.02	0.03	0.05
floodplain others	21	39	34	20	1	115		-0.44	0.23	0.16	0.11	-0.12
forest belts yellow	3	0	0	0	0	3		1.00	-1.00	-1.00	-1.00	-1.00
forest belts others	12	0	0	0	0	12		1.00	-1.00	-1.00	-1.00	-1.00
deposits yellow	79	0	85	28	0	192		0.09	-1.00	0.45	0.00	-1.00
deposits others	24	0	17	14	0	55		0.14	-1.00	0.19	0.33	-1.00
agrocenoses yellow	88	76	9	3	0	176		0.27	0.41	-0.73	-0.82	-1.00
agrocenoses others	54	47	14	21	0	136		0.06	0.24	-0.45	0.03	-1.00
Habitat	*flava*	*feldegg*	*lutea*	*citreola*	*cinerea*			*flava*	*feldegg*	*lutea*	*citreola*	*cinerea*
steppe	107	113	81	0	0			-0.03	0.02	-0.22	-1.00	-1.00
meadow	158	113	144	48	5			-0.07	-0.29	-0.13	-0.67	-0.96
coastal	85	60	61	46	4			-0.08	-0.31	-0.30	-0.45	-0.95
marsh	78	18	4	99	0			0.05	-0.71	-0.93	0.26	-1.00
mountain	0	0	0	0	6			-1.00	-1.00	-1.00	-1,00	1.00
forest	0	0	0	0	5			-1.00	-1.00	-1.00	-1.00	1.00
floodplain	79	81	71	45	3			-0.19	-0.17	-0.26	-0,50	-0.96
forest belts	15	0	0	0	0			1.00	-1.00	-1.00	-1.00	-1.00
deposits	103	0	102	42	0			0.10	-1.00	0.10	-0.48	-1.00
agrocenoses	142	123	23	24	0			0.18	0.06	-0.76	-0.75	-1.00

A more detailed examination reveals that *M. flava* prefers dry meadows, *M. feldegg prefers* mesophilic halophytic meadows, *M. lutea prefers* mesophilic flood meadows, and *M. citreola* prefers wet and damp meadows and marshy meadows. At the same time, wagtails are capable of forming mixed colonies in which each species will territorially occupy areas of the mesorelief (mesolandscape) most comfortable for it in terms of moisture (Fig. 3). The exception is the mountain wagtail *M. cinerea*, which chooses areas with rugged topography, most often different variants of mountainous landscapes; in locations with flat landscapes, it chooses chalk outcrops, ravines with high walls and niches in them, precipices, etc.

In ploughed steppes and grasslands, yellow wagtails are forced to nest in agrocenoses (*M. flava*, *M. feldegg*). *M. flava* most often nests in grasslands, old fallow land, and agrocenoses. *M. feldegg* prefers meadows and steppes for nesting, moving to agrocenoses when they are ploughed. *M. lutea* chooses meadows and old fallows for nesting, and steppes in case of sufficient moisture. *M. citreola* is the most water-loving species, often nesting in damp and wet meadows and marshes. *M. cinerea* is originally a mountain species, choosing deep ravine systems with chalk outcrops, steep high walls and niches for nesting in plains, and does not avoid floodplain forest areas along mountain rivers and streams and rivers with steep banks.

In relation to selection of habitats with yellow aspect for nesting by birds, it can be concluded in general that the colour aspect of the habitat is not in this case the only leading signal (attribute), but only in combination with all other levels of signals (attributes). Thus, *M. flava* has the maximum indicator (0.27) for agrocenoses; *M. feldegg* (0.31-0.41) for steppes and agrocenoses; *M. lutea* (0.45) for fallows. Only *M. citreola* and *M. cinerea* show high affinity to habitats with a yellow aspect, 0.77 and 1.00, respectively.

The resulting tetrachoric relationship of alternative traits ($r_a = +0.536$) also indicates a positive, but not strong effect of the yellow aspect of the vegetation of nesting habitats on the occupancy of yellow-coloured birds (yellow wagtails): as the number (area) of habitats with yellow aspect increases, the number (density) of yellow wagtails in them increases (Tables 5, 6).

Table 6 shows that Yellow Wagtails nest in habitats with different colour aspects, in proportion: 68.1% with Yellow, 19.1% with Pink, and 12.8% with White aspects. Bird densities are highest in biotopes with yellow aspect (mean 12.33 ind./he), slightly lower in habitats with pink aspect (mean 10.26 ind./he), and significantly lower in habitats with white aspect (mean 5.51 ind./he). Yellow Wagtails form colonies in habitats with different colour aspects in the proportion: 73.5% with yellow, 18.4% with pink, and 8.2% with white aspects (Table 6).

In addition to the three main aspects of nesting habitats discussed above, biotopes with a green aspect (pure herbaceous grasses without herbs), which are also used for nest building, are of considerable importance. They can account for up to 13% of the nesting habitats. All other habitats may account for up to 10%. Thus the percentage of nesting habitat selection is (in decreasing order of preference) as follows: yellow – 34%; white – 26%; pink – 17%; green – 13%; others – 10%.

DISCUSSION

Yellow Wagtail colony formation strategy and dynamics

The subspecies concept considers all species of yellow wagtails to be forms of one species, *Motacilla flava* (Alström & Ödeen, 2002; Alström *et al*., 2015). It has previously been shown that the presence of the breast plumage pattern, a 'necklace' in females of *M. lutea*, is a common ancient feature of all species of yellow wagtails, which is evident in fledglings and young individuals in their first winter attire and which plays a kind of 'sign' for the organisation of individuals into flocks on nomadic migration and then into large flocks on seasonal migrations (Artemieva, 2021). In individuals in mating attire, the same trait retains its role as an identifying 'sign', a signal (external manifestation of an individual barcode of an individual) in communication between males and the formation of breeding pairs (Panov, 1973, 1989, 1993; Artemieva, 2021).

The formation strategy and mixed colony dynamics of the three species of yellow wagtails is based on the different attitudes of the species towards the water body, which tends to be the initial reference point for the future nesting colony as a foraging habitat for birds. *M. citreola* builds nests close to the shoreline (the most water-loving species). Dry land is occupied by nests of *M. flava* (the most dry-loving species). Mesophilic areas are occupied by nests of *M. lutea* (Fig. 3). The topography of the colony shows the dynamics and order of occupancy of the nesting territory by birds. Yellow-headed Wagtails were the first to start settlement and development of the area. Yellow-headed Wagtails follow them in mass settlement. Three to four years after the colony of yellow wagtails flourishes, the first individuals of yellow wagtails appear and this subsequently causes the yellow wagtail colony to fade as a result of hybridisation.

It has previously been shown that males *M. f. beema* and *M. f. flava* wagtails arrive almost a week earlier than male *M. lutea* yellow wagtails and often form mixed breeding pairs with female *M. lutea* yellow wagtails, thereby causing an increasing degree of hybridization in the colony year by year. As a result of genetic cleavages, hybrid light-headed individuals (*M. f. beema* × *M. lutea*) emerge and accumulate in the colony (Artemieva, 2021).

Saxicola rubetra (Linnaeus, 1758) is an accompanying species of the Yellow Wagtail colonies, nesting in meadows adjacent to the lake at the edge of the colonies, which is important as it vigilantly guards its breeding grounds and warns other birds with a loud 'chirp' of approaching predators. A colony of Yellow Wagtails are accompanied by *Emberiza calandra* (Linnaeus, 1758), *Saxicola rubicola* (Linnaeus, 1766), *Locustella naevia* (Boddaert, 1783), *Luscinia svecica* (Linnaeus, 1758), *Alauda arvensis* (Linnaeus, 1758), and *Oenanthe oenanthe* (Linnaeus, 1758) and are basic background species of meadow and steppe floodplain habitats.

Yellow Wagtails have an 'ecological memory' and do not abandon their nesting sites even after they have been ploughed away. The colonies are able to maintain historical nesting points (Fig. 3).

Tab. 5 - Distribution of alternative traits (yellow aspect, yellow colouration) in groups of birds. / Distribuzione dei caratteri alternativi (aspetto giallo, colorazione gialla) nei gruppi di uccelli.

Bird groups	Yellow habitats	318 (p_1) – yellow colouration	94 (p_2) – non-yellow colouration	$p_1 + p_2 = 412$
Bird groups	Non-yellow habitats	79 (p_3) – yellow colouration	258 (p_4) – non-yellow colouration	$p_3 + p_4 = 337$
Σ sums of groups by columns		$p_1 + p_3 = 397$	$p_2 + p_4 = 352$	Σ sums of groups by rows
P	0.05	0.05	0.05	0.05
$r_a = +0.536$				

Tab. 6 - Distribution of yellow wagtails in nesting habitats with different vegetation aspects. / Distribuzione della cutrettola negli habitat di nidificazione con diversi aspetti della vegetazione.

Habitat aspects	yellow			pink			white		
Species	Number of nests	Density (ind./he)	Number of colonies	Number of nests	Density (ind./he)	Number of colonies	Number of nests	Density (ind./he)	Number of colonies
Motacilla flava	9	9.83±0.036	23	5	4.01±0.110	7	1	2.04±0.140	3
Motacilla feldegg	5	14.67±0.032	12	1	8.51±0.021	6	2	12.00±0.024	2
Motacilla lutea	13	30.00±0.012	18	2	28.00±0.021	4	1	10.00±0.012	1
Motacilla citreola	3	5.07±0.210	17	1	0.52±0.140	1	1	2.06±0.220	1
Motacilla cinerea	2	1.43±0.230	2	-	-	-	1	1.43±0.230	1
Total: 6	Σ 32	Average 12.33±0.104	Σ 72	Σ 9	Average 10.26±0.073	Σ 18	Σ 6	Average 5.51±0.125	Σ 8
p	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05

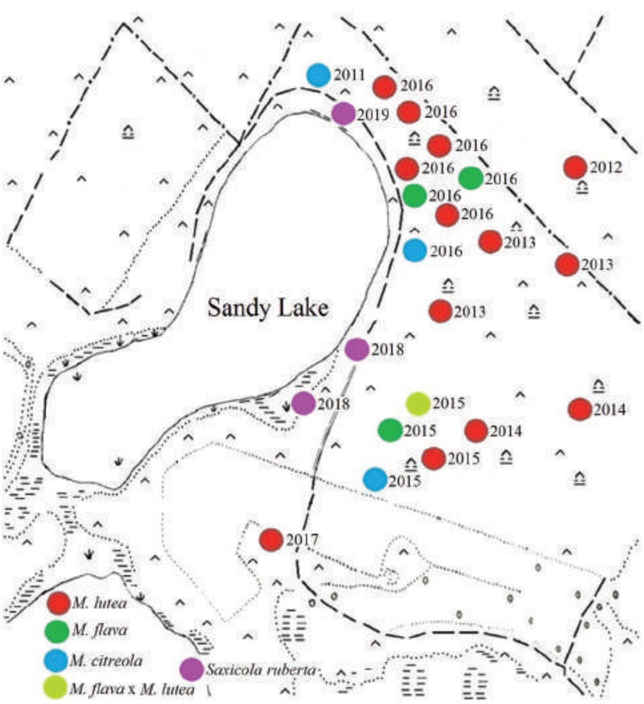

Fig. 3 - Topography of a mixed colony of yellow wagtails at Sandy Lake (Cherdakly, Ulyanovsk Region). The dynamics of the colony's occupancy of the nesting area by year (nest finds) is shown. Coloured poissons indicate bird species. / Topografia di una colonia mista di cutrettole al lago Sabbioso (Cherdakly, regione di Ulyanovsk). È mostrata la dinamica dell' occupazione dell' area di nidificazione da parte della colonia per anno (ritrovamenti di nidi). I pallini colorati indicano le specie di uccelli.

Levels of nesting habitat selection signals by yellow wagtails

Yellow Wagtails select nesting habitats from a bird's eye view by flying over landscapes. They settle in landscapes that look attractive to them from their flight height (yellow, pink, white, green) during the nesting period, due to the mass flowering of the dominant plants (*Brassica napus* L., *Barbarea vulgaris* W. T. Aiton, *Senecio schvetzovii* Korsh., *Scorzonera austriaca* Willd., *Taraxacum officinale*, etc.) in spring and summer (late April - May, June, early July). Different wagtail species select biotopes with different dominants (e. g. *M. flava* with *Barbarea vulgaris* W. T. Aiton, *M. feldegg* with *Euphorbia seguieriana* Neck., etc.). The composition of plant associations usually depends on the specific locality, landscape, and natural zone (climate).

Landscape level of nesting site selection signal is associated with birds' choice of open landscapes with yellow, pink, and white aspects (Figs. 4, 5).

The ecosystem level of the nesting site selection signal is related to the detection of a water body (foraging biotope) by birds, even a minor one. The historical points of joint nesting settlements are related to the history of the lake, pond, floodplain, and their perennial cycles (Fig. 6).

The status level of the nesting site selection signal corresponds to the discovery of a locality with the necessary vegetation association for nesting by birds, where grasses and meadow halophytic associations are the basis of vegetation (Figs. 7, 8).

Fig. 4 - Most preferred aspects of breeding habitats for yellow wagtails during the breeding season: yellow/ Aspetti preferiti dell'habitat riproduttivo della cutrettola gialla durante il periodo riproduttivo: giallo. A) *Tulipa scythica* for / per *M. f. beema* (Orenburg region / regione, 'Orenburgskaya Tarpania' station / stazione, 19.04.2020, photo: / foto: D. Grudinin); B) *Inula helenium, Senecio schvetzovii* for / per *M. flava, M. lutea, M. citreola* (Ulyanovsk oblast / regione, Oktyabrsky pond / stagno, 28.07.2011); C) *Senecio congestus, Euphorbia seguieriana* for / per *M. fedegg* (Rostov region / regione, Mishkinskaya floodplain / pianura alluvionale, Aksai river / fiume, 5.06.2011); D) *Euphorbia seguieriana* for / per *M. fedegg* (Rostov region / regione, Mishkinskaya floodplain / pianura alluvionale, Aksai river / fiume, 7.06.2011); E) *Taraxacum officinale* for / per *M. cinerea* (Ulyanovsk region / regione, Attsa river / fiume, 22.05.2011); F) *Erucastrum armoracioides* for /per *M. cinerea* (Ulyanovsk region / regione, Tushna village / villaggio, 1.07.2008); G-H) *Barbarea vulgaris* for / per *M. flava, M. lutea, M. citreola* (Ulyanovsk region / regione, Cherdakly village / villaggio, Sandy Lake / lago, 28.06.2018). (Photo: / Foto: Elena Artemieva).

Fig. 5 - The most preferred aspects of nesting habitats of yellow wagtails during the breeding season: yellow, pink, white. / Aspetti preferiti dell'habitat riproduttivo della cutrettola gialla durante la stagione riproduttiva: giallo, rosa, bianco. A) *Hieracium pilosella* for / per *M. citreola* (Ulyanovsk oblast / regione, Cherdakly village / villaggio, Sandy lake, 5.06.2016); B) *Rorippa palustris* for / per *M. citreola* (Ulyanovsk oblast / regione, Arbuzovka village / villaggio, floodplain of the Sviyaga river / pianura alluvionale del fiume Sviyaga, 3.06.2007); C) *Helianthus annuus* for / per *M. flava* (Lazure hills / colline, Radishevsky district / distretto, Ulyanovsk oblast / regione, 29.07.2011); D) *Inula helenium* for / per *M. lutea* (Ulyanovsk oblast / regione, Oktyabrsky pond / stagno, 28.07.2011); E) *Senecio congestus* for / per *M. fedegg* (Rostov oblast / regione, Mishkinskaya floodplain / pianura alluvionale, Aksai river / fiume, 3.05.2013); F) *Linum usitatissimum* for / per *M. fedegg* (Rostov oblast / regione, 4.06.2011); G-H) *Stemmacantha serratuloides* for / per *M. flava, M. citreola* (Ulyanovsk region / regione, floodplain of the Tepeshka river / pianura alluvionale del fiume Tepeshka, 11.06.2018); I) *Taraxacum officinale* for / per *M. citreola* (Ulyanovsk region / regione, Cherdakly village / villaggio, Sandy lake / lago, 21. 05.2016);J) *Allium cepa* for / per *M. flava* (Stavropol region / regione, 2.06.2018, photo: / foto: L. Malovichko). (Photo: / Foto: Elena Artemieva).

Fig. 6 - Reservoirs with developed colonies of yellow wagtails in halophyte meadows. / Corpi idrici con colonie sviluppate di code gialle in prati alofili. a) wetmeadows in the floodplain of the Sviyaga river for / prati umidi nella pianura alluvionale del fiume Sviyaga per *M. flava, M. citreola* (Kashinka village / villaggio, Tsilninsky district / distretto, Ulyanovsk region / regione, 10.05.2008); b) Oktyabrsky pond for / stagno Oktyabrsky per *M. flava, M. lutea*, *M. citreola* (Radishchevsky district / distretto, Ulyanovsk region / regione, 26.07.2011); c) Sandy lake for / lago Sabbioso per *M. flava, M. lutea, M. citreola* (Cherdakly village / villaggio, Ulyanovsk region / regione, 5.06.2016); d) wetmeadows in the floodplain of the Sviyaga river for / prati umidi nella pianura alluvionale del fiume Sviyaga per *M. flava, M. citreola* (village of Barataevka, environment of Ulyanovsk / villaggio di Barataevka, dintorni di Ulyanovsk, 29.04.2012); e) flooded Artemovsky meadows for / prati allagati di Artemovsky per *M. citreola* (environment of / distretto di Nizhny Novgorod, 4.05.2012); f) Sandy lake for / lago Sabbioso per *M. flava, M. lutea, M. citreola* (Cherdakly village / villaggio, Ulyanovsk region/ regione, 19.05.2012); g) Azov coast for / riva di Azov per *M. fedegg* (Kagalnik village / villaggio, Azov district / distretto, Rostov region/ regione, 16.06.2012); h) pond in the Sun Eagles valley for / stagno nella valle di Sunny Eagle per *M. flava, M. lutea* (Solovchikha village / villaggio, Radishevsky district / distretto, Ulyanovsk region/ regione, 25.06.2015). (Photo: / Foto: Elena Artemieva).

Fig. 7 - Plant associations for nesting yellow wagtails (nest entrance). / Associazioni vegetali per la nidificazione della cutrettola (ingresso del nido). a) forbs with *Barbarea vulgaris*, meadows in the floodplain of the Sviyaga river for / foraggi con *Barbarea vulgaris*, prati nella pianura alluvionale del fiume Sviyaga per *M. flava* (Barataevka village / villaggio, Ulyanovsk surroundings/dintorni, 3.07.2011); b) rump grassland, water Artemovsky meadows for / prati di groppa, prati d'acqua Artemovsky per *M. citreola* (near / vicino Nizhny Novgorod, 6.05.2012); c) forbs with *Senecio schvetzovii*, meadows in the floodplain of the Oktyabrsky pond for / prati con *Senecio schvetzovii*, prati nella piana alluvionale dello stagno Oktyabrsky per *M. lutea* (Radishchevsky district / distretto, Ulyanovsk region / regione, 28.07.2011); d) grassland, water Artemovsky meadows for / praterie, prati d'acqua Artemovsky per *M. citreola* (environment / ambiente Nizhny Novgorod, 09.05.2012); e) grassland on an old sunflower fallow in the floodplain of Sandy lake for / praterie su un vecchio maggese di girasole nella pianura alluvionale del lago Sandy per *M. lutea* (Cherdakly village / villaggio, Ulyanovsk region / regione, 20.05.2012); f) grassland, halophytic meadows in the floodplain of the Aksai river for / prateria, prati alofili nella pianura alluvionale del fiume Aksai per *M. fedegg* (Mishkinskaya floodplain / pianura alluvionale, Rostov region / regione, 09.06.2011). / (Photo: / Foto: Elena Artemieva).

Fig. 8 - Plant associations for nesting yellow wagtails (nest entrance). / Associazioni vegetali per la nidificazione della cutrettola (ingresso del nido). a) *Cleistogenes squarrosa* and / e *Limonium gmelinii*, halophyte meadows for / prati alofili per *M. fedegg* (Kagalnik village / villaggio, Azov district / distretto, Rostov region / regione, 16.06.2012); b) grassland, water meadows in the floodplain of the Malaya Tereshka river for / praterie, prati d'acqua nella pianura alluvionale del fiume Malaya Tereshka per *M. flava* (Radishchevsky district / distretto, Ulyanovsk region / regione, 11.05.2015); c) grasslands in the floodplain of Sandy lake for / praterie nella pianura alluvionale del lago Sandy per *M. flava* (Cherdakly district / distretto, Ulyanovsk region / regione, 8.06.2015); d) grassland on an old sunflower fallow in the floodplain of Sandy lake for / praterie su un vecchio maggese di girasole nella pianura alluvionale del lago Sandy per *M. lutea* (Cherdakly village / villaggio, Ulyanovsk region / regione, 19.06.2016); e) grassland, halophytic meadows in the floodplain of the Tereshka river for / prateria, prati alofili nella pianura alluvionale del fiume Tereshka per *M. flava* (Radishchevsky district / distretto, Ulyanovsk region / regione, 11.06.2018); f) grassland with *Stemmacantha serratuloides*, halophytic meadows in the floodplain of the Tereshka river for / prateria con *Stemmacantha serratuloides*, prati alofili nella pianura alluvionale del fiume Tereshka per *M. flava* (Radishchevsky district / distretto, Ulyanovsk region / regione, 11.06.2018); g) grassland with forbs, halophyte meadows in the floodplain of the Tereshka river for / prateria con forbie, prati alofili nella piana alluvionale del fiume Tereshka per *M. flava* (Radishchevsky district / distretto, Ulyanovsk region / regione, 11.06.2018); h) grassland with *Festuca pratensis*, *Stipa pennata*, and *Inula helenium*in the floodplain of the Oktyabrsky pond for / prateria con *Festuca pratensis*, *Stipa pennata* e *Inula helenium* nella piana alluvionale dello stagno Oktyabrsky per *M. flava* (Radishchevsky district / distretto, Ulyanovsk region / regione, 14.06.2020). (Photo: / Foto: Elena Artemieva).

Fig. 9 - Plants (host plant), which are the protectors of bird nests. / Piante (piante ospiti) protettrici dei nidi di uccelli. a) *Carduus acanthoides* for / per *M. lutea* (Cherdakly village / villaggio, Ulyanovsk region / regione, 20.05.2012); b) *Verbascum lychnitis* for / per *M. flava* (Barataevka village / villaggio, Ulyanovsk environment / ambiente, 8.07.2011); c) *Senecio schvetzovii* for / per *M. lutea* (Oktyabrsky pond / stagno, Radishchevsky district / distretto, Ulyanovsk region / regione, 28.07.2011); d) *Glycyrrhiza echinata* for / per *M. fedegg* (Mishkinskaya floodplain / pianura alluvionale, Rostov region / regione, 8.06.2011); e) *Artemisia absinthium* for / per *M. flava* (Barataevka village / villaggio, Ulyanovsk surroundings / dintorni, 3.07.2011); f) *Glycyrrhiza echinata* for / per *M. fedegg* (Mishkinskaya surroundings/dintorni, Rostov region / regione, 6.06.2011); g) *Helianthus annuus* for / per *M. lutea* (Cherdakly village / villaggio, Ulyanovsk region / regione, 19.06.2016); h) *Verbascum lychnitis* for / per *M. lutea* (Cherdakly village / villaggio, Ulyanovsk region / regione, 23.05.2015); i) *Stemmacantha serratuloides* for / per *M. flava* (Radishchevsky district / distretto, Ulyanovsk region / regione, 11.06.2018); j) *Inula helenium* for / per *M. lutea* (Oktyabrsky pond / stagno, Radishevsky district / distretto, Ulyanovsk region / regione, 5.08.2014). (Photo: / Foto: Elena Artemieva).

The local (point) level of the nesting site selection signal is due to the presence of a necessary host plant which protects birds' nests (e.g. *Glycyrrhiza echinata* L., *Stemmacantha serratuloides*, *Senecio schvetzovii* Korsh., *Inula helenium* L., *Helianthus annuus*on the old fallow ground, etc.) (Fig. 9). When nesting in grassland, birds often use the dry stems of tall plants that have survived since autumn and are prominent among the lower grasses (*Artemisia, Cicorium*, etc.).

Birds, being in the nesting biotope, tend to lose their visibility in order to dissolve into the background of the habitat in the surrounding landscape, which can probably be considered as a special protective adaptation against attacks by predators. Thus, the habitat, then voice and behaviour (Panov, 1973, 1989, 1993) become the leading attributes of Turk's search for their mates (estimation of the window of recognition 'friend-or-foe'). Not only is colouring important for birds (Kistyakovsky, 1967), but also the pattern of plumage plumage has a signifi cant meaning (signs, signposts) for males and females during mating season, when communicating in a flock and nesting colony, etc. Female yellow wagtails have small spots of different configurations on their throat (neck-chest) in the form of a 'necklace'. Their presence has a lot to do with the behaviour of birds; they play a role in different outfits of birds in different sexes and species of yellow wagtails. This trait plays the role of a peculiar barcode of an individual when communicating between the sexes (Artemieva, 2021). This can serve as an example of a sign in the semiotic 'friend-or-foe' species identification system for yellow wagtails.

CONCLUSIONS

The main signals for the selection of nesting conditions for yellow wagtails as a reflection of semiotics are (in descending order of scale): landscape – habitats of predominantly yellow, pink, white, and green aspects; ecosystem – proximity of a water body (river, lake, etc.); statistical – vegetation association (halophytic vegetation, cereals, sandy loam, loamy and solonchak soils malleable for nesting holes. The following are the most important aspects of nesting habitats: ecosystem – proximity of water body (river, lake, etc.); statistical – plant association (halophytic vegetation and grasses) on sandy loam, loamy, saline soils suitable for nest hole; local (point) – presence of host plant or host plant on nesting area to protect nesting habitat. Nesting habitats are selected based on the availability of all available signals (traits), which increases the possibility and success of colony formation.

Yellow Wagtails are indicators of the conservation of steppe and meadow landscapes and halophytic habitats in floodplains of rivers and lakes, especially relict halophytic plant meadow and meadow-steppe cenoses in floodplains of saline saucer lakes in steppe regions (Artemyeva & Muravyov, 2012; Sundev & Leahy, 2019). As a result of global climate change, there is a tendency for fragmentation and reduction of steppe and grassland ecosystems and drying up of steppe lakes (Chibilyov, 2002), which in turn may lead to thedisappearance of natural habitats of yellow wagtails.

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