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Anthropogenic adaptation of reproductive biology of conditional-synanthropic birds

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The article is devoted to studying mechanisms of synanthropization and ecological segregation of birds in anthropogenic landscapes. The paper presents data on the adaptability of the anthropogenic specifics of nesting behavior of the spotted flycatcher, a conditional-synanthropic bird species. This species is generally liable synanthropization, however, it does not occur in the most urbanized parts of the cities, preferring moderately modified habitats. It is shown that anthropogenic landscape contributes to the formation of new forms of birds' behavior, which are a response to the environment. But not all of these forms are adaptive and some are peculiar ecological traps. Such peculiarities of behavior do not increase, but even decrease the reproductive success of birds, which is not always easy to establish, because as a whole the results of the synanthropic population breeding may be higher than in the wild, due to different intensity of the influence of the limiting factors of the environment.

Data on the analysis of nesting and reproductive success of wild and synanthropic populations are presented.

It is pointed out that the spotted flycatcher has specific main reproductive parameters in the anthropogenic landscape, which is the result of the reaction of birds to the features of synanthropic ecosystems and the unequal effect of the same environmental factors on them in natural and anthropogenic biocenoses. It manifests itself primarily in changing the time of the reproductive period and the widespread use of anthropogenic bases for nests fastening. There is also a higher reproductive success in the anthropogenic landscape, which we associate with more favorable microclimate and the ratio of specialized and non-specialized predators (prevalence of the latter), different than in nature.

Keywords: adaptation, birds' segregation, ecosysems, nesting, ecology, spotted flycatcher, population.

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Антропогенные адаптации репродуктивной биологии условно-синантропных птиц

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Статья посвящена исследованию механизмов синантропизации и экологической сегрегации птиц в антропогенных ландшафтах. В работе представлены данные об адаптивности антропогенной специфики гнездового поведения у серой мухоловки, условно-синантропного вида птиц. Этот вид повсеместно проявляет склонность к синантропизации, однако в наиболее урбанизированных частях городов практически не встречается, предпочитая умеренно преобразованные местообитания. Показано, что антропогенный ландшафт способствует формированию у птиц новых форм поведения, которые являются ответом на особенности среды, однако не все из этих форм адаптивны, некоторые представляют собой своеобразные экологические ловушки. Такие особенности поведения не повышают, а даже снижают репродуктивный потенциал птиц, что не всегда просто установить, поскольку в целом результаты размножения синантропной популяции могут оказаться выше, чем у дикой, за счёт иной интенсивности воздействия лимитирующих факторов среды.

Представлены данные анализа особенностей гнездования и репродуктивного успеха диких и синантропных популяций. Отмечается, что у серой мухоловки в антропогенном ландшафте существует специфика всех основных репродуктивных показателей, которая представляет собой результат реакции птиц на особенности синантропных экосистем и неравнозначного воздействия на них одних и тех же факторов среды в условиях природных и антропогенных биоценозов. Она проявляется в первую очередь в изменении сроков репродуктивного периода, а также широком использовании антропогенных оснований для закрепления гнёзд. Отмечен также более высокий репродуктивный успех в антропогенном ландшафте, что мы связываем с более благоприятным для птиц микроклиматом, и иным, чем в природе, соотношением специализированных и неспециализированных хищников (преобладанием последних).

Ключевые слова: адаптация, сегрегация птиц, биоценоз, гнездование, экология, серая мухоловка, популяция.

The questions of birds' synantropization are of great theoretical and practical signiticance, since birds are one of the most important components of urban biocenoses [1]. In anthropogenic habitats, birds usually have differences in the ecology of nesting from natural populations of the same species [1, 2, 3–6], which are usually regarded as evidence of synanthropization [7, 8]. Some of them are highly effective adaptations to habitat in anthropogenic landscape and human presence, others are non-adaptive reactions to certain features of anthropogenic landscape. The question of the adaptability and interconnection of these features often remains open, since even non-adaptive forms of nesting behavior can be accompanied by some increase in reproductive success due to unrelated factors. The reverse situation is equally common.

It is believed that the degree of nest security is of primary importance for birds in anthropogenic landscapes. One of the manifestations of this change is an increase in the height of the nest location as the gradient of synanthropization [9, 10]. Reproduction of openly-nesting birds in cities is inefficient due to the destruction of nests by humans and unspecialized predators [8, 9, 11].

All changes of those species nesting characterized by its anthropogenic specificity include peculiarities of nest placement, the time change of the reproductive period and the specific behavior in nesting time (primarily providing birds' spacing and protection from predators and humans). At the same time, anthropogenic changes in nesting behavior can be adaptive, neutral, or non-adaptive.

Purpose the aim of our work was to study the adaptability of anthropogenic specificity of nesting behavior of the spotted flycatcher (*Muscicapa striata*), having a broad norm of reaction for this aspect of biology.

The tasks of the work included comparative analysis of nesting and reproductive success and identification of nesting specifics of urban populations and their adaptability.

Material and methods

In 2000–2017 we investigated the specifics of the reproductive biology of the spotted flycatcher in natural and anthropogenic stations of Ryazan Oblast.

Studying the nest biology of flycatchers was carried out according to generally accepted methods [12]. Taking into account the height and type of nest location, the number of eggs in full egg deposition, reproductive success (% of abandoned nests of the number of eggs), the availability of nests for humans, and the causes of complete or partial death of nestlings in nests. The indicator of the nests' visibility was estimated according to the author's method, based on taking into account the method of their detection by researchers and the possibility of finding these nests by several "ordinary" people, i. e. nonspecialists in the field of ornithology, with their target search [13]. 161 nests were detected and examined.

All the received data were nominally subdivided into materials on natural biotopes (remote and suburban forests, and a forest park or a large suburban forest area) and anthropogenic stations (small intraurban parks and forest plantations, dacha communities and residential landscape). Materials for each group of stations were processed separately.

Results and discussion

The spotted flycatcher is distinguished by extreme flexibility of nesting. It can live both on trees and on human buildings, relatively in the open or in various niches of the substrate [4, 9, 10, 14]. All these bases nests are at different height and provide unequal opportunities for camouflage. The population dynamics of the species under study is characteristic of birds with a relatively low potential for synantropization. For example, the number of spotted flycatchers in cities of the Republic of Poland in the past 25 years is constantly decreasing. The same is true for most of Europe as a whole [15]. In our opinion, this may be due to the imperfection of adaptation of the species to the conditions of the anthropogenic landscape, when at low degree of its transformation there is some increase in reproductive success and in a case with high degree the conditions become unfavorable.

Nests masking and nesting height

One of the displays of changing the nesting stereotype in the anthropogenic landscape is an increase in the neight of the nest as far as the gradient of synantropization. Its effect on nesting in the anthropogenic landscape is highly contradictory. In our opinion, the direction of this influence is determined by two main factors:

1. If nests go out as the altitude of their location increases from the neight interval of easy accessibility for humans.

2. If the growth of nesting neight is accompanied by deterioration of nest masking.

According to the first of these factors, three options are possible. In the first case, nests in natural habitats are easily accessible to humans in height (i.e., it is possible to reach the nest by hand while standing on the ground; for a man of average height, this is about 2.2 m, maximum 2.5 m), and they become inaccessible in anthropogenic landscapes. In the second case nests are located much higher than the height easily accessible to humans both in natural and anthropogenic landscapes. The third case is characterized by nests below 2.5 m in both types of stations and although the nesting height in anthropogenic landscapes also increases, but it is not enough to make nests hard to reach. Obviously, only the first option can be adaptive (we mean adaptation to the anthropogenic press).

In terms of accessibility for humans, we divided all the nests into four categories [13]. Table 1 presents the data on the average altitude of nests of the spotted flycatcher in natural and anthropogenic landscapes, the degree of nests

Table 1

Nesting height of the spotted flycatcher in natural and anthropogenic stations

Parameters	Anthropogenic landscape	Natural stations
Nesting altitude, m	3.00±1.91[1] (0.4–8.5)	2.90±1.44 (0.6–7.5)
Ratio of light-, medium-, hard-to-reach and inaccessible to human nests, %	48.65/10.81/ 29.73/10.81	46.55/30.17/ 7.76/15.52
Reproductive success, %	68.0	63.8

Note:[1] – The ± sign indicates the expected variation in the values of the measured parameter.

Table 2

Features of reproductive success in easily discernible and disguised nests of the spotted flycatcher in natural and anthropogenic stations

Parameters	Natural stations		Anthropogenic stations	
	Easily discernible nests	Other nests	Easily discernible nests	Other nests
Fraction, %	25.2	74.8	12.8	87.2
Height, m	2.6±1.0 (1.2–5.0)	3.0±1.6 (0.6–7.5)	3.3±2.0 (1.7–8.5)	3.0±1.9 (0.4–6.5)
Reproductive success, %	48.1	68.7	59.6	70.8
Reproductive successin unravaged nests, %	88.6	85.8	71.8	94.6
Clutch of eggs size, specimen	4.5±1.1	4.5±1.1	4.7±0.7	4.8±0.6
Fraction of ravaged nests, %	46.7	21.3	60.0	20.6

availability and reproductive success (abstracting in this case from the fact that changes of the latter may be a consequence of other factors).

The second factor is the connection between nesting neight and degree of masking that can be illustrated by the ratio of easily visible and other nests, the nature of the connection between visibility and availability of nests and the difference of reproductive success in easily visible and other nests.

We consider nests' visibility as a "relatively subjective" parameter. As visibility of nests for different people can be opposite, we believe it is correct to assess the visibility of nests not mechanically, due to the presence of obstacles between the nest and the observer, but on the basis of the possibilities and methods of their detection by the man [13].

A comparative analysis of data on natural and anthropogenic habitats showed that in the first one the distribution of nests by categories of visibility and accessibility for a person had more often some link with parameters of reproductive success than in the second one (Table 2).

The dynamics of the same parameter, for example, reproductive success depending on the neight of the nest, in natural and residential settings can vary right up to the opposite.

As the anthropogenic impact pressure increases, the proportion of well camouflaged nests increases (by almost 13%). In this case, it seems that camouflage is different from that in nature. If in natural habitats the average neight of easily visible nests is lower than well camouflaged, then in the anthropogenic landscape the inverse ratio of altitudes is observed. Thus, less visibility for a person is achieved not by increasing the height of their location, but by camouflage peculiarities. In both natural and anthropogenic landscapes, the most noticeable nests are primarily ruined. Among unravaged nests in anthropogenic habitats, reproductive success is also higher in well-camouflaged ones, perhaps because of their better protection not only from predators, but also from climatic factors. In natural forests, these parameters are almost identical, with a slight advantage of easily visible nests. Probably, the specific character of the urban microclimate proves to be sufficient for shifting the selection from an open location (in our opinion, it provides better ventilation and drying out after rains) to a more closed one. The pressure of predators in both types of stations is aimed at selecting the most disguised nests. In general, reproductive success, that is more obvious with visible nests, increases in both categories of nests when transferring from natural stations to anthropogenic ones.

It is obvious that in nature birds are able to take into account the relative intensity of different threatening factors for their offspring. And as to confront each of them a specific method of nesting is necessary, birds try to choose the best placement of the nest. Therefore, in general, those nesting methods, which are accompanied by an increased risk of death of the offspring, are less common, although there is a possibility of individual success in such nests. Polymorphism of the population in general is probably maintained by the ratios of various risk factors in different habitats and even at different areas of the same structure habitats. In the anthropogenic landscape birds' ability to assess the risk of each type of nesting is much smaller, so this ratio is more like random.

Duration of the reproductive period

In regard to the causes of this phenomenon, researchers have no common opinion. It is well known that the urban climats is warmer than

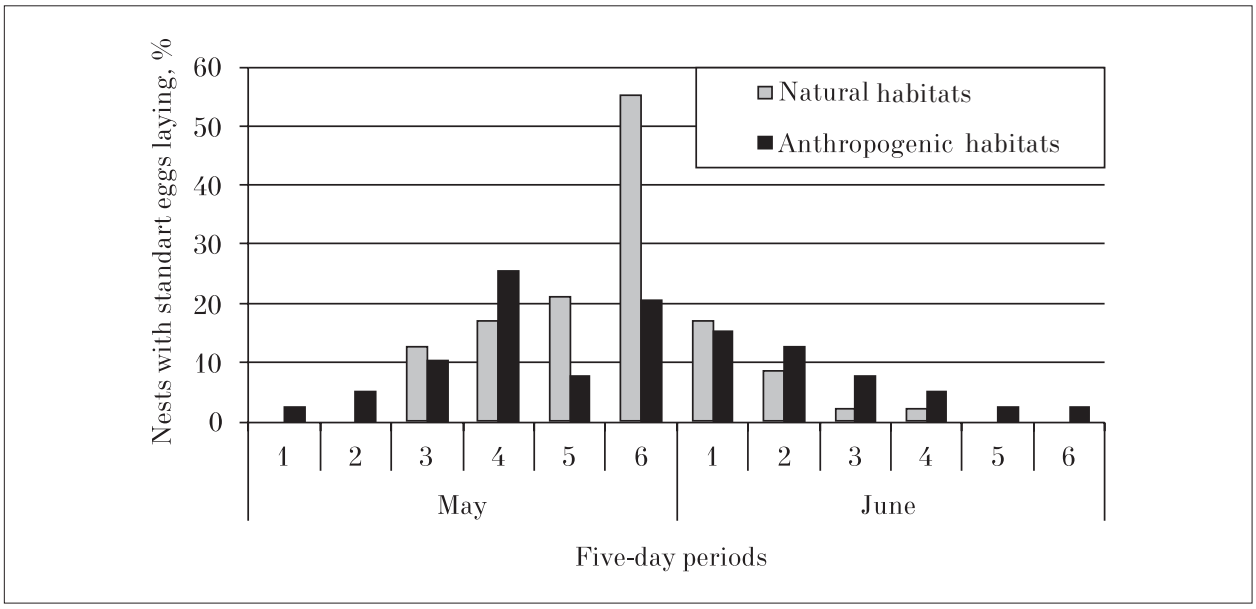

Fig. Dynamics of reproductive period of the spotted flycatcher in natural and anthropogenic stations

Table 3

Dynamics of the success of reproduction (juvenile from laid eggs, %) of the spotted flycatcher depending on the time of egg laying (2010–2017)

Egg laying time	Natural stations	Anthropogenic stations
2 first five-day periods	100.0	84.8
Nests with laying, started during the period of mass egg laying	57.8	65.2
3 last five-day periods	18.8	28.6

that of zonal landscapes. At the same time, there are data that an increase in average temperatures of only 1–2 degrees is accompanied by significant rearrangements in the population structure of the fauna, not to mention phenology. It was noted that on non-urbanized territories the date of various phenological phenomena, including those related to birds, over the last century (warming by different estimates and for different regions by 0.5–2.0 degrees) shifted by 2–17 days [16]. Taking into account that the temperature in Ryazan's residential areas may be 2–5 degrees higher than that in the suburbs, depending on the strength of the wind, it is obvious that the climate of urban areas is close to the characteristic one for zonal landscapes in the more southern regions. Therefore, an earlier start of nesting in cities can be explained by a climatic factor. It can also contribute to the features of resource availability, artificial lighting, "heated" shelters for overnight stops and nesting, as well as the presence of microclimatic mosaic (warming and protection from the wind of the wall space of buildings of the southern exposition).

Figure presents the start time of the spotted flycatcher's laying in natural and anthropogenic landscapes. Beginning of egg laying in synanthropic populations is two five-day periods earlier than in natural ones, and lasts also for two five-day periods longer. The peak of laying falls on the fourth five-day period of May, then, after some decline in the fifth five-day period, on the sixth five-day period of this month. Probably, the second peak is associated with additional laying instead of the dead. In nature the peak of egg laying falls on the last five days of May (more than 55% of nests). Thus, in a case of one normal laying a season (two successful reproductial cycles were observed only once), the reproductive period in anthropogenic stations turns out to be substantially longer (two decades more), and the time of the laying start is more uniform. This cannot be explained by a large number of repeated laying instead of dead nests, since the loss of nests in the anthropogenic landscape is like thatin the natural landscape. On the other hand, the uniform distribution of nests by reproduction time is more favorable for the population in terms of avoiding dangerous weather factors,

which can largely determine the reproductive success of spotted flycatchers [14, 17].

Analysis of the data obtained reveals two main regularities:

1. The duration of the reproductive period of the spotted flycatcher in the anthropogenic habitats is greater than in the natural ones. This is due to the earlier beginning of reproduction and its late finish.

A longer breeding period in anthropogenic habitats is determined by the more frequent devastation of nests, and, accordingly, by numerous attempts of re-nesting [2, 9]. In our opinion, this is not so at least in regard to Ryazan. In small parks and residential landscapes, reproductive success was close to that in suburban forests and large marginal parks, and it was significantly higher in undamaged nests. Therefore, repeated laying is more common in the latter, i.e. the inverse of the regularity described in the literature is observed. However, even so, the duration of the reproductive period in anthropogenic habitats is longer.

2. Besides the differences in time of the beginning and end of nesting in natural and anthropogenic habitats, the frequency distribution within this interval reveals some marked specifics. The diagram of the beginning of the laying in the man-made habitats is more gentle, which reflects a more even distribution of the started laying for five-day periods. The specifics of the dynamics of the beginning of nesting (as well as the distribution of clutches in the number of eggs, nests altitude, etc.) in anthropogenic habitats may be associated with a different quality of individuals in the population of nesting birds [9]. In our opinion, the specifics of the anthropogenic stations themselves is of paramount importance. Mutual differences of small parks, wastelands and different types of residential landscapes are much more significant than those for natural stations. Therefore, the parameters of nesting biology at each site are also different, and when data are combined for all anthropogenic habitats, the impression is generally very variable. The analysis of the data for each micro tract separately is extremely difficult because of the small number of nesting individuals.

The question arises whether the change in the timing of reproduction should be considered the adaptation of birds to the anthropogenic landscape. From previous publications it is known that the contribution of early broods to the reproduction of the population is much higher than the late ones. Besides, adult birds with a longer reproductive cycle are characterized by increased mortality in the post-reproductive period [6, 18–21]. Therefore, the prolongation of the reproductive period towards its end probably does not contribute to the reproductive success of the population as a whole. This is especially important for such birds as the spotted flycatcher, which is characterized by complex forage behavior, which can only be mastered by the young ones for a long time, during which they stay close to their parents [3]. According to our observations, the share of ovules and dead embryos is large in late nests [13]. Non-hatching of chicks from half or more eggs in late laying is quite common for all species studied by us. The reproductive success of the spotted flycatcher in nests, where egg laying began during the last three five-day periods (n = 7), was only 25.9%, while on average 64.5%. Early clutches (n = 5), postponed in the first two five-day periods of the reproductive period, were 100% successful.

In natural habitats, the reproductive success naturally decreases from the beginning to the end of the reproductive period. Within the city the dynamics of birds' reproductive success depending on the start of layingis similar to the natural one.

Conclusions

The obtained data show that the spotted flycatcher in the anthropogenic landscape has specific main reproductive parameters, which is the result of the reaction of birds to the peculiarities of synanthropic ecosystems and the unequal impact of the same environmental factors on them in natural and anthropogenic ecosystems. A similar phenomenon was previously found in all birds studied in this respect, even having no associations with elements of the anthropogenic landscape. In the case of the spotted flycatcher, this is manifested primarily in the change in the timing of the reproductive period, as well as in the widespread use of anthropogenic bases to fasten nests. There is also a higher reproductive success in the anthropogenic landscape, which we associate with a microclimate more favorable for birds, and the ratio of specialized and non-specialized predators (prevalence of the latter), different than in nature.

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