

Nesting of the Willow Warbler (*Phylloscopus trochilus* Linnaeus, 1758) (Sylviidae, Aves) in Natural and Urban Habitats of Karelia

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Abstract—Our study was carried out within the framework of the project “Ecological and Behavioral Adaptations of Birds Typical for Natural Habitats to the Urban Environment.” The willow warbler was chosen as a model object in this investigation aimed to provide comparative analysis of the bird breeding behavior in natural and urban areas of Karelia. The breeding dates, preferred biotopes and nest sites, and the clutch characteristics and reproductive relations of the willow warblers were found to be similar in various conditions, whereas their flight distances were shorter and the alarm call intensity was higher in urban habitats than in forest ones. Possible explanations for the results obtained are given.

Keywords: willow warbler, breeding ecology, behavior, natural and urban habitats

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INTRODUCTION

For many years, anthropogenic transformation of ecosystems has been considered a key scientific problem in need of thorough study, including changes related to the very existence of animals (Gladkov, 1958; Ilichev and Fomin, 1988; Living Planet Report, 2010; etc.). The research on anthropogenically transformed ecosystems has proved to be a promising field of studies because these systems offer many possibilities for studies of various ecological and population parameters and investigation of correlations between them due to the great variety of environmental conditions formed within these ecosystems and their easy availability to researchers (Paskhalny, 2004). Birds often serve as research models in these studies (Vladyshvsky, 1975; Tsibulin, 1985; Klaustnitser, 1990; Korovin, 2004; Houck and Cody, 2000; etc.). In many of these studies, the main focus is the species composition and overall ecological characteristics of the birds within cities and other transformed habitats. Special publications contain specific descriptions of avian responses to anthropogenic influences in general (Galushin, 1982; Kozlov, 1988; Gracznik, 1982; Houck and Cody, 2000; Fernández-Juricic, 2004; Butler et al., 2010; Minor, Urban, 2010; etc.) and directly to the presence of humans and their activity in particular (Yurgenson, 1962; Vladyshevsky, 2004; Cooke, 1980; Burger and Gochfeld, 1991; Fernández-Juricic et al., 2004; Blumstein, 2005; etc.). It is evident

that the great variety of conditions encountered by birds in anthropogenically altered habitats and the variety of responses to them need to be studied further.

In our opinion, the most promising studies are those dedicated to analyzing the patterns of habitats of wild birds in artificial stations differing from typical natural habitats of these species, studies of adaptation to various forms of environmental transformation, and studies of avian responses to certain factors of anthropogenic influence. The comparative analysis of special ecological features, behavior, physiological characteristics, and other vital activities of birds in anthropogenically transformed and natural biotopes (the latter serve as a control) is important as well. Due to the fact that the first response to changes in the environment in high ranked animals such as birds is typically a change in behavior (Severtsov, 1922; Haind, 1975; McFarland, 1988; etc.), the behavioral (ecological and ethological in particular) specifics of birds inhabiting various environments has attracted our attention at this time.

This study was conducted within the framework of the project “Ecological and Behavioral Adaptations of Birds Typical for Natural Habitats and the Urban Environment” by the example of the willow warbler (*Phylloscopus trochilus* Linnaeus, 1758), which represents a common species of natural biotopes that is able to inhabit large cities at the same time (*Ptitsy gorodov Rossii*, 2012).

The aim of the present study is a comparative analysis of the characteristics of the willow warbler breeding in natural and urban areas of Karelia. It was necessary to gather data on the choice of nest sites, methods of building and placing nests, the breeding dates and their special features, the level of resistance to anthropogenic pressure, and the quality of concealment and accessibility of the nests for human and predators in every type of habitat.

MATERIALS AND METHODS

Defining the place and role of ecological and behavioral adaptations in the adaptive system of birds is possible only if based on long-term stationary research utilizing a large variety of methods. Because the main aims of this study are minimized to study of avian behavior, its implementation was possible only by observing individually identifiable specimens. Due to this factor, we caught and tagged birds with numbered aluminum and colored plastic rings in individual combinations. During the course of work, various aspects of avian behavior involving breeding were registered; we conducted a search for nests and observed them.

During the research on the choice of nest sites, we described the biotopes, nesting microstations, and immediate surroundings of every nest and conducted analysis of the patterns of placement and fixation on the substrate. The exposition of entrances, the level of disguising of the nest (within the microrelief and vegetation), the reliability of fixation of the structure on the substrate, and other parameters were recorded. The level of disguise and accessibility of nests was measured by the following parameters: (1) the depth of the nest's location within the canopy (the distance between the outer border of the canopy where the nest is located and the nest); (2) the index of the nest's concealment by its surroundings (this index characterizes how well the nest is concealed by vegetation, microrelief, etc., and is visible from a distance; the index is evaluated visually, a surface area 2 m in radius with the nest as its center is assumed as 100%); (3) the index of nest accessibility to humans and predators (on an increasing scale from 0 to 5, from complete inability to reach the nest to its full accessibility).

The intensity of vocal signals of alarm around the nest was chosen as a parameter that characterizes the resistance of birds to the presence of humans. All displays of distress that accompanied an observer approaching the nest were recorded and evaluated as one of the following conditional activity levels: 1, absence of audible signs of distress; 2, presence of rare alarm signals; 3, regular alarm signals at the observer's approach; 4, very active distress.

During statistical analysis of the data acquired, we tested the distribution using the Kolmogorov–Smirnov test and the F -test for checking the equality

of variances. For data with a normal distribution in two independent datasets and equal variances, an independent two-sample t -test was used to compare the mean values of a parameter. Its nonparametric analog, the Mann–Whitney U -test, was used if necessary. Relations and correlations between the values were evaluated using Spearman's rank correlation, which is independent of the distribution and is weakly sensitive to exclusion of samples. Statistical hypotheses were tested at a 5% significance level. Statistical analysis was conducted using Microsoft Excel, SPSS, and StatGraphics.

The willow warbler was studied in the urban environment in 2012–2013 in Petrozavodsk; in natural environments, it was studied in 2007–2009 in the forests of Priladozhie. Controlled areas within the borders of the urban environment were marked in locations with various features: in the park zone, in the zone of multistorey apartment blocks in the city center, in a recreational zone actively visited by people, and in a private building zone and gardens on the city periphery. The studied areas within the natural habitats included a lane of wide mixed forests massif that is rarely visited by humans and on the southeast coastline of Lake Ladoga in the Olonetskii district of Karelia. A detailed description of the controlled biotopes in this region is given in one of our previous publications (Matantseva and Simonov, 2012).

Data on the 56 nests found and observed during the listed seasons is presented in this study.

RESULTS AND DISCUSSION

Choice of the Nest Sites

Data acquired during long-term study of biotopic distribution of the willow warbler in Karelia have been cited in numerous publications (Zimin et al., 1976, 1993; Sazonov, 1997; Lapshin, 2001); we will not go into great detail on this subject. Our data, collected in 2007–2013, are shown in Figs. 1 and 2. It must be noted that local breeding density of the willow warbler within the green belts of a city can be high, which is possibly connected to both the concentration of birds in areas within the borders of a highly mosaic environment suitable for inhabiting and the higher accessibility of food sources within the urban landscape.

The willow warbler prefers bright microstations, which is the reason this species is rare in spruce forests and is dominant in bright pine and deciduous forests of Priladozhie (Spearman's rank correlation positive for breeding density and the presence of pine and birch in the upper forest layers: $r = 0.241$, $p = 0.034$ and $r = 0.264$, $p = 0.022$, respectively). The willow warbler inhabits stations surrounding forest fringes, which are the brightest areas in the forest, more readily; this confirms the data on the attraction of this species to light (Gotzman, 1965; Jablonsky, 1969; Ptushenko, 1954; Martynov, 1973; etc.). Such preference for the fringe

habitats can be noted in the city as well. At the same time, the birds avoided continuous forest massifs and homogenous park vegetation. Usually the birds nested at the fringes of the green belts, choosing microstations with a pronounced shrub layer, under the canopy of which the nests were well concealed. Under these conditions, the nesting locations of the willow warbler ranged from highly urbanized territories in the courtyards of multistorey apartment blocks to the remaining areas of forest biotopes in locations rarely visited by humans.

The patterns of nesting placement of the willow warbler are shown in Tables 1 and 2. Most frequently this species nests on the ground and less frequently (typically in wet places) on the hummocks and roots of fallen trees. In 2012, also in a wet area, a nest was found placed in a willow tree at 0.5 m height. The diversity of nest placements in the urban environment (Shannon index of 2.80) did not exceed that in continuous forest massifs (2.55); the comparison of the Shannon index values by *t*-test gave $t = 0.02$, $t_{table} = 2.00$, $p > 0.05$.

No distinct patterns were found during the analysis of the orientation of nest entrances according to cardinal directions (Fig. 3). In particular, it would have been a logical assumption that on the coastline of Lake Ladoga, where breezes are common, birds would place their nests “away from the wind,” with entrances facing south or north. However, many nests, even those on the very shore several dozen meters away from the water, had entrances facing west, i.e., in the direction of the wind blowing from the lake (including nests placed on the slopes of boulders parallel to the shore). In most cases, both in the city and in the forest, it was evident that the orientation of the nest was determined by its immediate surroundings, e.g., exposition of the slope or roughness of the substrate.

Breeding Dates

During the years of study, more than 75% of the willow warblers begin laying clutches in the last ten days of May to the first ten days of June in both Priladozhie and Petrozavodsk (Fig. 4). These dates are common for the beginning of breeding of the willow warbler in this region (Lapshin, 2001). The earliest clutch (May 18) was noted in Priladozhie. The nest building usually began in the middle of May. Significantly stretched breeding dates and the presence of late clutches are mostly associated with repeated nesting after destruction of the nest, clutch or nestlings; and to a lesser degree, with later arrival of a portion of birds. This species was never registered to have two broods per season (Lapshin, 2001).

Characteristics of the Clutches

During the seasons studied, the willow warbler clutches in Priladozhie consisted of 6.15 ± 0.12 ($n = 34$)

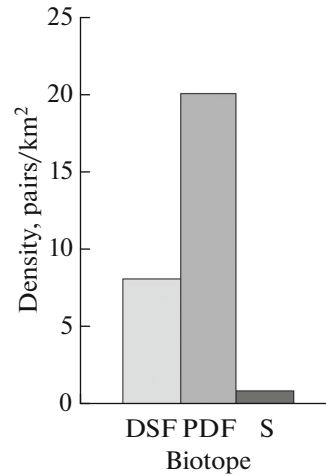


Fig. 1. Biotopic distribution and breeding density of the willow warbler in Priladozhie. DSF, deciduous and spruce forests; PDF, pine and deciduous forests; S, spruce forests.

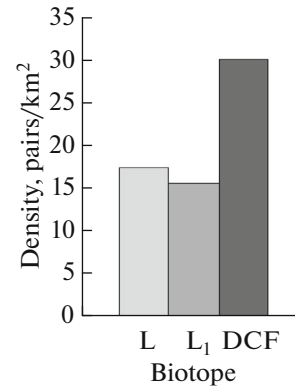


Fig. 2. Biotopic distribution and breeding density of the willow warbler in Petrozavodsk. L, lane of tree and shrub vegetation with pronounced herbaceous layer in an industrial city area; L₁, lane of tree and shrub vegetation with pronounced herbaceous layer in a residential city area; DCF, deciduous and coniferous forest on the city periphery.

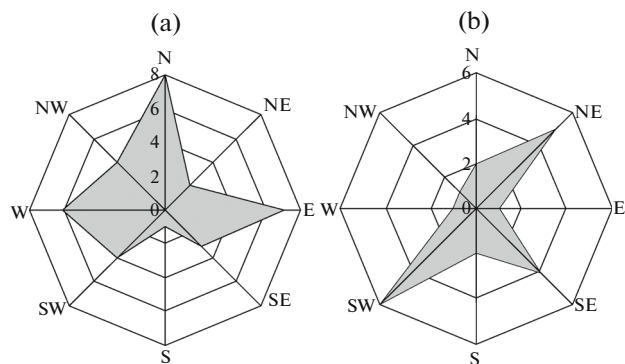


Fig. 3. Proportion of nests with various entrance orientations, % (*n* is listed): (a) Priladozhie; (b) Petrozavodsk.

Table 1. Locations and patterns of nest placement of the willow warbler in Priladozhie

Substrate	Placement within the substrate	Disguising method	<i>n</i>
On the ground	In the roughness of the substrate	Among the brushwood branches or roots and/or under the leaf litter	4
		In thick subshrub and/or herbaceous layer vegetation and/or in moss	7
	On an even, flat surface		9
	On a slope (partially submerged into the slope)	Under a spruce branch or in the cover of a branch of a leaf tree	2
			1
	In a thick herbaceous and/or subshrub layer vegetation	1	
A wall of a drainage ditch/trench		Within a moss layer + in thick herbaceous and/or subshrub layer vegetation + can be covered by a spruce branch	1
Moss-covered hummock (usually moss and blueberry, former root part; less frequently, moss-covered trunk of a fallen tree)			7
	On the top of a hummock, under a layer of moss, completely submerged into the hummock like in a hole	A moss “cover,” completely shielding the nest	1
A fallen tree with roots torn out of the ground	In the ground part of a fallen tree, inside a niche above the ground	Among the roots of a fallen tree	1

Table 2. Locations and patterns of nest placement of the willow warbler in Petrozavodsk

Substrate	Placement within the substrate	Disguising method	<i>n</i>
On the ground	On a slope (partially submerged into slope)	In thick herbaceous and/or subshrub layer vegetation and under leaf litter	2
			10
	On an even, flat surface		3
	In the roughness of the substrate	In thick herbaceous vegetation and in the brushwood	1
A wall of a drainage ditch/trench	On a slope (partially submerged into slope)		1
		Among the roots of deadwood or among the roots and under leaf litter	1
On a steep side	On the side of an ameliorative canal		2
	On the extreme border of a rock		1
In a willow tree	In the stem rosette	Disguised by leaves and branches of the substrate plant	1

eggs, on average; clutches in Petrozavodsk consisted of 6.32 ± 0.19 ($n = 22$) eggs, on average. The minimum clutch size was 4 eggs (completed late clutch), and the maximum size was 8 eggs. Similar data were obtained in other regions of northwestern Russia (Bozhko, 1958; Paevsky, 1991; Lapshin, 2001). The coloration of the willow warbler eggs in various areas studied corresponded to that typical for the species within the limits of individual variations (Ptushenko, 1954; Simms, 1985; Snow and Perrins, 1998).

Concealment and Accessibility of the Nests

No statistically significant differences in the level of concealment of the willow warbler nests in the forests and in the city was found for the chosen parameters (Mann–Whitney *U*-test: $p > 0.05$ for all parameters). It is acceptable that the absence of unambiguous answers for the formulated questions may be determined by an insufficient dataset size for every parameter. At present, according to the data obtained, the main nest building parameters for the willow warbler

were found to be highly stereotypical and constant under varying conditions.

Resistance to Anthropogenic Pressure

The behavior of the willow warblers during the nesting period is in general secretive and aimed at concealing the nest's location. However, when nestlings are ready to fly out of the nest, birds can openly display visual demonstrations of distress. This occurred at all studied areas. Usually, in case of the visual demonstrations of distress, increased vocal activity was also observed, which began immediately after the birds spotted the observer, even if he was still far away from the nest.

During this study, a higher level of vocal distress signal demonstrations was observed for the city willow warblers as compared to the forest (Mann–Whitney U -test: $W_{33,45} = 588.5$; $p = 0.026$). The birds nesting in locations frequently visited by humans manifest distress more openly than the birds that inhabit areas that are hard for humans to access. This can possibly be associated with the fact that humans usually do not pay attention to quiet distress signals of the willow warbler and do not search for the nests based on them. Because of this, secretive behavior around the nest in a noisy city is not a protective mechanism for warbler's nestlings from humans, and other possible nest predators in the cities apparently do not rely on their hearing as much as on vision and smell. As opposed to this, in the forest, the bird's distress is more noticeable, and predators can react to it. Because of this, birds in the forest behave more cautiously. There is no need for this in the city, and against the background of the birds being more actively distressed by the environment, they can be more "disturbed" permanently. It must be noted that at the moment this is only a hypothesis in need of further study.

Another parameter for evaluating the avian resistance to anthropogenic pressure is the *distance to which the bird flies off from the nest at the sight of the approaching observer*. Analysis of the data confirmed our hypothesis that the city birds allow the human closer than the forest ones (Mann–Whitney U -test: $W_{24,36} = 636.5$; $p = 0.006$). Apparently, this is associated with higher tolerance of the city birds to humans due to their constant presence and the fact that they usually do not pose any threat to the nest.

Reproductive Relations

Typically, the willow warblers form a socially monogamous pair, but polygyny is also not excluded for this species (Lapshin, 1975, 1983; Paevsky, 1991; Haartman, 1969; Neergaard and Arvidson, 1995; etc.). Using the method of molecular genetic analysis in Karelia allowed a high level of "concealed" polygyny for this bird species, which leads to extra-pair offspring (Lapshin et al., 2007, 2013), to be revealed.

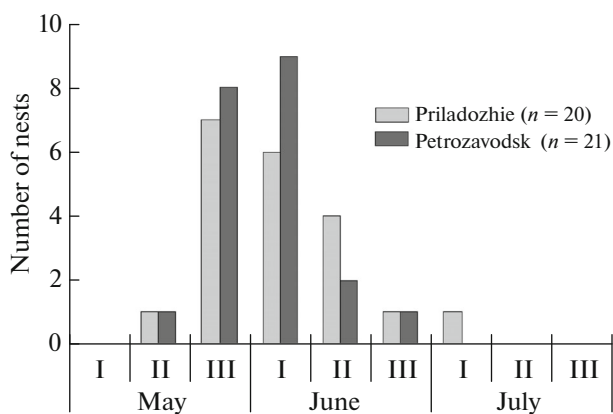


Fig. 4. Dates of the beginning of nesting (dates of the first egg being laid).

Open polygamy, when one male formed pairs with two females at the same time, was registered twice in Priladozhie and once in Petrozavodsk during the years of study. In all three cases, polygamy was observed under a high local density of the bird population. In the forest, the birds gathered in the most preferred microstations (in which nesting was registered annually); in the cities, birds gathered in a relatively isolated green zone surrounded by industrial and residential development areas.

Breeding Success and the Causes of Nest Destruction

Breeding success of the willow warbler was high during the seasons studied: 73.3% in Priladozhie and 83.1% in Petrozavodsk (calculated as the ratio of the number of nestlings that flew off the nest to the number of eggs laid). Causes of offspring death, the major one being predation by various animals, are shown in Table 3. The common viper is one of the main nest predators in Priladozhie. The hooded crow and small mustelids preyed on the nests as well. Dogs destroyed one nest in the forest area visited by humans. Certain clutches were lost due to the eggshells being damaged by snails and slugs. A portion of the nests was abandoned after a cuckoo laid an egg in them. In the city the nests can be preyed on by hooded crows, cats, dogs, and rodents.

CONCLUSIONS

As a result of the present study, we found the nesting periods, preferred stations, locations and patterns of placement of the nests, features of the clutches, and specifics of reproductive relations of the willow warbler in spring to be similar in the forest and in the city, which is apparently determined by strict species-specific stereotypes. At the same time, parameters that characterize the resistance of birds to anthropogenic pressure were found to be significantly different for

Table 3. Causes of death of the willow warbler offspring during the seasons studied

Causes of death	Priladozhie		Petrozavodsk	
	<i>n</i>	%	<i>n</i>	%
Number of controlled eggs	191		142	
Unfertilized eggs and embryonic death	7	3.7	2	1.4
Abandoned after cuckoo egg was laid in the nest	8	4.2	0	0
Abandoned after slug crawled on the clutch	7	3.7	0	0
Nest preyed upon by predators	11	5.8	0	0
Total	33	17.3	2	1.4
Number of controlled nestlings	158		140	
Hatchling with retarded development	1	0.6	0	0
Nest preyed upon by predators	17	10.8	15	10.7
Abandoned after the attack of ants on the nest	0	0	7	5.0
Total	18	11.4	22	15.7
Total number of offspring	191		142	
Unfertilized eggs and embryonic death	7	3.7	2	1.4
Abandoned after cuckoo egg was laid in the nest	8	4.2	0	0
Abandoned after slug crawled on the clutch	7	3.7	0	0
Hatchling with retarded development	1	0.5	0	0
Nest preyed upon by predators	28	14.7	15	10.6
Abandoned after the attack of ants on the nest	0	0	7	4.9
Total	51	26.7	24	16.9

different types of habitats. The distance of a bird's distress reaction and flight off the nest was observed to be smaller and the intensity of the vocal alarm signals was higher in the city than in the forest, which is associated with specific environmental conditions of different habitats of the willow warbler and adaptations to them. In the city, warblers demonstrate more tolerance towards humans and allow them to get closer to their nests than in the forest. It is evident that this tolerance is necessary for birds that inhabit urban territories with a constant human presence, which is usually harmless. The lability in avian behavior that allows them to acquire such tolerance, in turn, ensures their ability to breed even in the cities. However, the behavior of forest willow warblers is more secretive and careful than that of the city birds, which is evidently aimed at preservation of nests in situations where stressed behavior can attract predators.

Thus, the willow warbler is a species capable of inhabiting both natural and highly urbanized environments, preserving certain nesting stereotypes but showing great lability in the choice of habitat with varying anthropogenic pressure and altering their behavior depending on the current environmental conditions. In conclusion, it must be noted that, during construction of urban green belts that correspond to the main requirements for highly reliable

nesting sites of this bird species, the willow warbler is expected to inhabit them even in a highly urbanized environment.

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