

ETHOLOGICAL ASPECTS OF BIODIVERSITY WITHIN AND BETWEEN *PHYLLOSCOPUS* SPECIES: BEHAVIORAL VARIATION AMONG BIRDS FROM THE CENTRE AND PERIPHERY OF BREEDING RANGES

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Matantseva M.V., Lapshin N.V., Simonov S.A. 2015. Ethological aspects of biodiversity within and between *Phylloscopus* species: behavioral variation among birds from the centre and periphery of breeding ranges. *Acta Biol. Univ. Daugavp.*, 15 (1): 273 – 283.

In the wide sense the term ‘biodiversity’ covers all displays of the life variability, and its ethological constituent is as important in sustaining of population stability as others. We investigated the behaviour of Leaf Warblers, genus *Phylloscopus* (Boie, 1826), at northern peripheral parts of their ranges (Karelia, Russia) in comparison with the conspecifics from central parts of the ranges (published data) and found out that plasticity of territorial systems and variety of behavioural reactions along with other adaptations allow them obtain the populations even in not optimal conditions. This is relevant to relationships within and between species: (1) variety of territorial patterns of conspecifics lets them inhabit quite different sites in the vast ranges, and (2) behavioral variations among different species give them a possibility to settle at the same place. So, comparing conspecifics from central parts of ranges, Willow Warblers *Ph. trochilus acredula* (Linnaeus, 1758) and Chiffchaffs *Ph. collybita collybita* (Vieillot, 1817) in Karelia have a shorter prebreeding period, less aggressive ways of territorial borders establishing and lack of some stages of stereotype pair formation. Such reduction of territoriality is mainly caused by the limitation of time good for breeding and relatively low population densities in northern regions. Concerning interspecific variations, Willow Warblers and Chiffchaffs (common species for the region which they have been settling for evolutionary long time) form high stable territorial structures, while Wood Warblers *Ph. sibilatrix* (Bechstein, 1793) and Greenish Warblers *Ph. trochiloides viridanus* (Blyth, 1843) (settled here comparatively later) have more labile territorial structures that let them more actively move during a breeding season in search of potential reproductive partners. Besides, the behaviour of Leaf Warblers also varied depending on the level of social tension in populations, habitat structure and volume of sites suitable for nesting and foraging.

Key words: *Phylloscopus* warblers, centre and periphery of breeding ranges, territoriality, behavioral variations.

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INTRODUCTION

In the wide sense the term ‘biodiversity’ covers all displays of the life variability, and its ethological constituent is as important in sustaining of population stability as others. We investigated the behaviour of small passerine birds at northern peripheral parts of their ranges (Karelia, Russia) in comparison with the conspecifics from central parts of the ranges (published data). Our model objects are Leaf Warblers, genus *Phylloscopus* (Boie, 1826): Willow Warblers *Ph. trochilus acredula* (Linnaeus, 1758), Chiffchaffs *Ph. collybita collybita* (Vieillot, 1817), Wood Warblers *Ph. sibilatrix* (Bechstein, 1793), and Greenish Warblers *Ph. trochiloides viridanus* (Blyth, 1843). Main characteristics of the territorial behaviour of the Leaf Warblers in Karelia connect with the fact that different species live here under conditions of different ecological situations: there are differences in such parameters as the history of local population formation, remoteness from the northern borders of their ranges, number and population density in the region. Their ways and extension of migrations and wintering areas also differ as well as the terms and duration of stages of a reproductive period. An important note here is that Willow Warblers and Chiffchaffs have been inhabiting this region for evolutionary long time, whereas Wood Warblers and Greenish Warblers settled here relatively recently (Lapshin 2000, 2005, 2009, Zimin 2001). Data on Wood Warblers in North-West Russia, including Karelia, appeared only in late 19th – early 20th century (Büchner 1887, Zarudny 1910, Bianchi 1914). Greenish Warblers are known in this area since the late 1870s (Kokhanov 1987), and the first nest of the species was found in Karelia in 1974 (Lapshin 2004).

MATERIAL AND METHODS

In 2007 – 2014 we thoroughly investigated the territorial and reproductive behaviour of the model species at the northern periphery of their ranges. We strengthened our observations by

adding the data from the long-term research on Leaf Warblers which have been conducting in Karelia since 1973. The integrated data array on the behaviour of Leaf Warblers at the northern parts of their ranges was compared with the published data related to the central parts of these species breeding ranges.

In the northern periphery of the model species ranges the controlled plots were established in the Republic of Karelia, North-West Russia, on the base of the Biostation “Maychino” of the Institute of Biology, Karelian Research Centre, Russian Academy of Sciences. For Karelian climate it is characteristic to get quite low air temperatures in spring and summer as compared to the central parts of the species ranges, frequent returns of colds in spring and early summer, and general weather instability. At that, in Karelia relatively low temperatures in spring and summer are partly compensated by longer duration of the daylight hours, and hence, birds are able to maintain the positive energy balance (Zimin 1988).

Since the main tasks of the work were brought to the thoroughly study of bird behaviour, their realization was possible only by observations of the individually marked animals. Thereby we captured birds with mist nets and special nest traps and marked them with individual combinations of colored rings. During the work we registered and characterized all the observed aspects of bird behaviour at different stages of a reproductive period. We conducted the observations every day during the whole continuance of daylight hours and investigated the characteristics of territorial and reproductive relationships, conducted search for nests and subsequent observations to determine their fate.

We studied the bird territoriality with the point mapping method permissive to define sizes and configurations of territories marked by singing males (Odum & Kuenzler 1955). The core of this method is to determine the so-called ‘maximum-territory’ by means of mapping of a singing male’s locations continuously during 0.5 to 3 hours twice a day (in the morning and

afternoon). A bird's locations should be mapped every 5 minutes of observations or every each more or less noticeable movement of a controlled bird must be recorded as much as we get 12 points in a period of one hour. Every hour of observations the extreme points are connected to get a prominent polygon (maximum-territory), which area exceeds the area of a territory used every day. With the number of observations increasing the ultimate level of measurements will be achieved, when each subsequent one hour series leads to increase area not more than 1 %. According to the method, this level is sufficient for the complete definition of the territory and, as a rule, can be achieved for 1 – 3 days.

We modified the described method to get more accurate and detailed data. During our observations of singing males we indicated the high at which they song as far as possible to appreciate the three-dimensional positions of their territories. In order to trace the dynamic of the configuration, area and attitude of each territory during a reproductive season, we conducted the observations throughout the entire period of a controlled bird's being at a study plot. We also registered all the facts of defense of territories and mapped them.

For work with maps we used such programs as Arc View GIS 3.2 (Iverson Systems Research Institute, Inc., 1992 – 1999) and OziExplorer 3.95.4m (D & L Software Pty Ltd, 2005). Statistical analysis was carried out with the software package of SPSS 11.0.1 (SPSS Inc., 2001).

As a whole, for 8 seasons (May – September 2007 – 2014) we conducted about 9000 hours of observations of Leaf Warblers in nature and mapped about 19300 locations of these birds during the process of territory demonstration. We found and controlled 190 nests of Leaf Warblers and ringed 1149 individuals, including nestlings. In order to take into account influence of weather on bird behaviour, we recorded the weather conditions of the seasons. We also obtained the data on the ecology of Leaf Warblers in Karelia for 1973 – 2006.

RESULTS AND DISCUSSION

The territorial behaviour typical for the Leaf Warblers had been studied by many researchers (Howard 1920, May 1949, Ovchinnikova & Firsova, 1971, Ryabitsev 1993, Enemar et al. 1979, Simms 1985, Jakobsson 1988, Radesäter & Jakobsson 1989 et al.) therefore its main

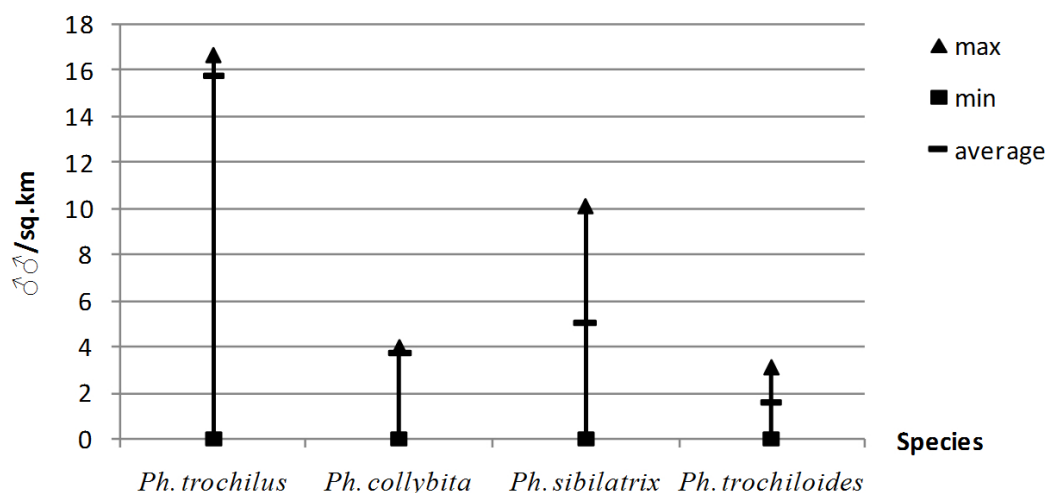


Fig. 1. Population densities of the Leaf Warblers in the study area at different stages of reproductive seasons of 2007 – 2014.

Table 1. Sizes of maximum-territories of Leaf Warblers registered in Karelia in 2007 – 2014, m²

Species	N	Median	Limits
<i>Ph. trochilus</i>	60	1032.5	378 – 10719
<i>Ph. collybita</i>	19	5870	483 – 25684
<i>Ph. sibilatrix</i>	30	1894	384 – 5987
<i>Ph. trochiloides</i>	21	3166	574 – 16120

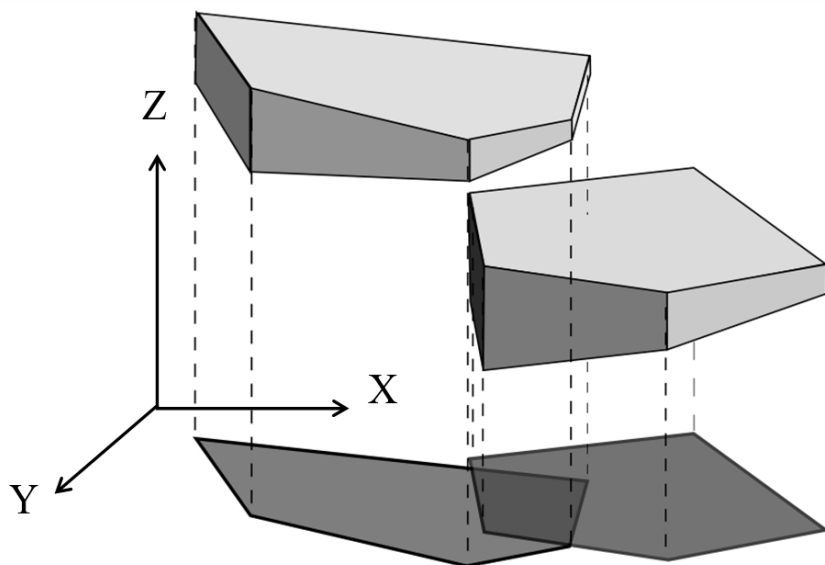


Fig. 2. The overlapping of projections of Chiffchaff territories ('maximum-territories' according to the point mapping method) and the real segregating of the territorial rooms in space: a scheme.

characteristics are well-known. However, less is known about the specifics of the territorial behaviour under different ecological conditions, which is the main focus of this paper.

Attitude, demonstration and defense of territories. Under the conditions of the study area, territories of birds of the same species were usually demarcated from each other, and males as a rule attacked other conspecific males in case of intrusion into their territories. The maximum number of such conflicts was registered for Willow Warblers and Wood Warblers. Aggressive clashes of Greenish Warblers were not observed, that may be caused by their low population densities in the study seasons (Fig. 1) and the lack of high competition for the space.

Chiffchaffs usually defended their territories, but in 2007 two males of this species often sang close to each other and flew into the neighbor's territory quite far. Thus, their territories partly overlapped that was rather untypical for the species. Previously (in 1979 – 2006) such an overlapping of territories also periodically registered. In number of the cases, when projections of territories on the ground overlapped, the real three-dimensional positions of the territorial rooms were segregated owing to the fact that one of these males sang at the bigger high above the ground than the other male (Fig. 2). More seldom there were the situations, when the extreme posts of singing were 300 to 500 and more meters apart. These posts (as a rule, at high trees) were usually demonstrated and defended by a male (Lapshin 2000). In

such cases the territory was more a line than a polygon (Fig. 3).

Sizes of territories. Sizes of demonstrated territories in different species of Leaf Warblers registered in 2007 – 2014 are shown in Table 1. Though in every certain case a size of a territory was determined in many respects by the habitat structure and volume of sites suitable for nesting and foraging, as a whole these parameters were quite big for the model species and they were even bigger in previous years (Lapshin 1978, 2000). That exceeded sizes of these species territories measured in other parts of their ranges (May 1949, Geissbühler 1954, Simms 1985; Piotrowka & Wesołowsky 1989, Glutz von Blotzheim & Bauer 1993 et al.). Especially large territories were demonstrated by males of Chiffchaffs and Greenish Warblers.

Specifics of the territorial behaviour of Leaf Warblers which have been inhabiting the region for evolutionary long time. Willow Warblers and Chiffchaffs, as we noted above, are the species that have been breeding in Karelia for evolutionary long time and adapted to the local conditions well enough in different aspects. This concerns the adaptations of the year cycles and mates with the behaviour, including territorial

behaviour. Characterizing the main specifics of these birds' territorial behaviour, first of all we should describe the following items:

1. On average, males of Chiffchaffs and Willow Warblers appeared in the breeding areas and occupied their territories earlier than other Leaf Warblers (Fig. 4), and in most cases they stayed at these initially occupied territories for the entire duration of a reproductive period.
2. The territories of these birds were quite stable: shifts in space and size changes were minor.
3. Every year most of the local territorial Willow Warbler males successfully attracted females, although some of them stayed single due to the number prevalence of males over females (Fig. 5).

It should be noted, that the ratio of Chiffchaff single males was quite big despite the fact that birds of this species have been inhabiting the region for a long time and this is compared with the share of unmated males in species new for the region (Fig. 5). Chiffchaffs live in Karelia closer to the range borders than Willow Warblers (Lapshin 2000), in this connection the number of females is very unstable and usually low, that makes for such a great number of single males in the spring-summer populations of Chiffchaffs in this region.

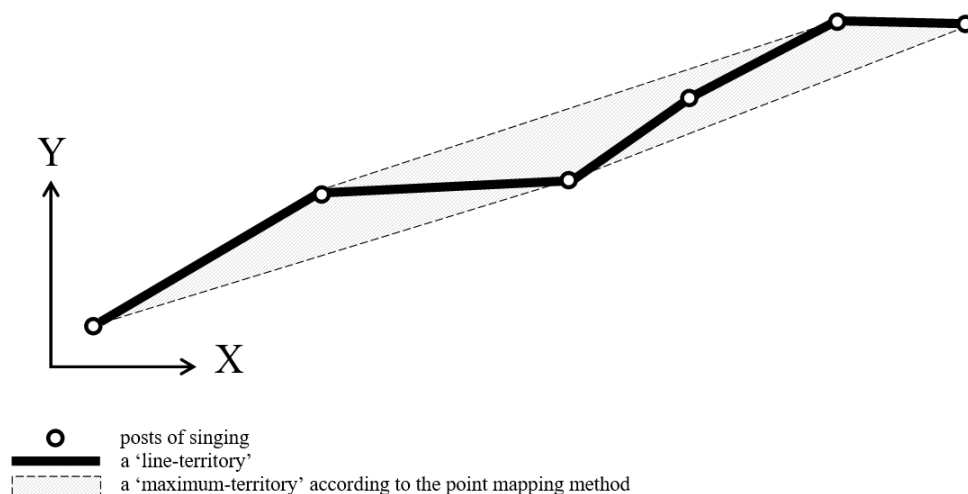


Fig. 3. The example of a 'line-territory' of a Chiffchaff male.

Thus, spatial territorial structures of populations in Chiffchaffs and Willow Warblers are quite stable during a season. Such stable structure forms generally as early as the very beginning of a reproductive period. Relatively early arrival to the breeding areas allows these birds rather peacefully distribute territories among conspecific males in the beginning of a season and breed at them in case of attraction of females.

Along with it, Willow Warblers and Chiffchaffs in Karelia have the brief first stage of a prebreeding period (before arrival of females) in relation to the limitation of time suitable for reproduction. The establishment of territorial

borders is rather peaceful, and some stages of the stereotyped behaviour (particularly the stages of companionship and courtship feeding) are lacking, as compared to more southern parts of ranges (May 1949, Ovchinnikova & Firsova 1971, Ovchinnikova 1973). Apparently, more peaceful character of territorial relationships among birds in North-West Europe is linked to the lower population densities than at the other parts of the species ranges. This, in its turn, is due to less pronounced fragmentation and disconnection of habitats suitable for breeding. For instance, in the Prepolar Ural, where habitats are fragmented and Leaf Warblers form dense populations, conspecific males attack each other more often (Ryabithev 1993).

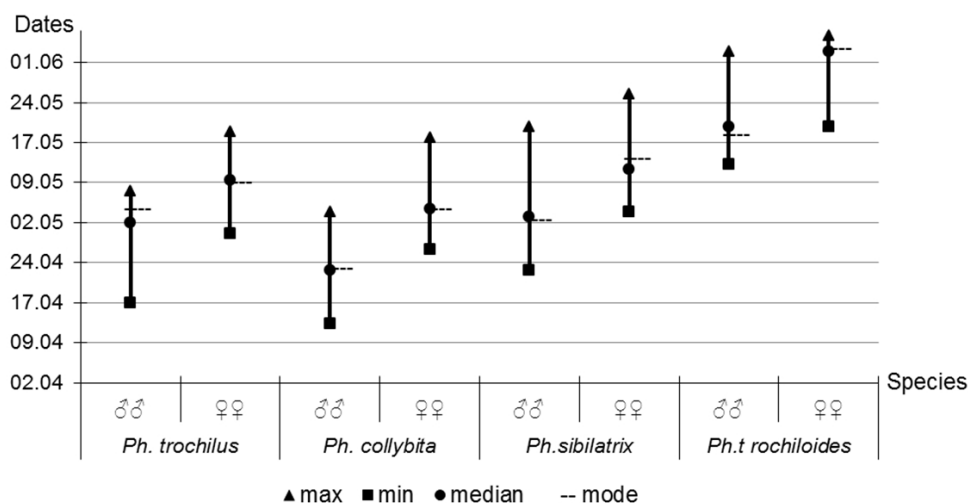
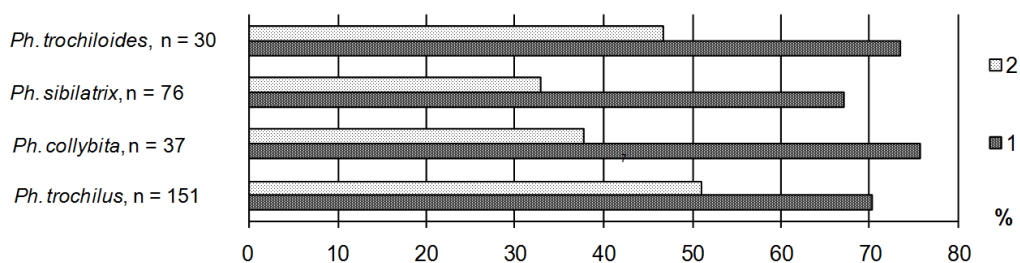


Fig. 4. Terms of arrival of Leaf Warblers to the breeding areas in 1973 – 2014.



1 – males with territories; 2 – mated males at these territories
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Fig. 5. Ratio of males of different statuses from the number of all the males tried to occupy territories in the study area in 2007 – 2014.

Specifics of the territorial behaviour of Leaf Warblers settled in the region of investigations relatively recently. Wood Warblers and Greenish Warblers, as we noted above, settled in Karelia as a breeding area relatively recently, and their adaptations to local conditions are not considered as well developed. Besides that, this region is located at the northern periphery of the species ranges, and specifics of North also influence on biology of these birds. The main characteristics of the territorial behaviour of Wood Warblers and Greenish Warblers in Karelia are listed below.

1. Wood Warbler and Greenish Warbler males keep high degree of mobility during a season. So, Wood Warbler males more often change places of singing during a reproductive period than

other Leaf Warbler males (Fig. 6). According to the data of long-term observations in Karelia, as was partly reported earlier (Lapshin 2005), polyterritoriality is very typical for Wood Warblers, when unmated males move between territories in limits of tens and hundreds meters and even farther.

The degree of mobility of Greenish Warblers is rather high as well. But, in contrast to Wood Warbler males, they usually occupy large territories and move freely within their borders (Fig. 7). Probably, high mobility of Wood Warbler males promotes them to meet females under the conditions of their relatively low and unstable number that is typical for a periphery of a species range. Actually, an encounter with a female is a really seldom event in such

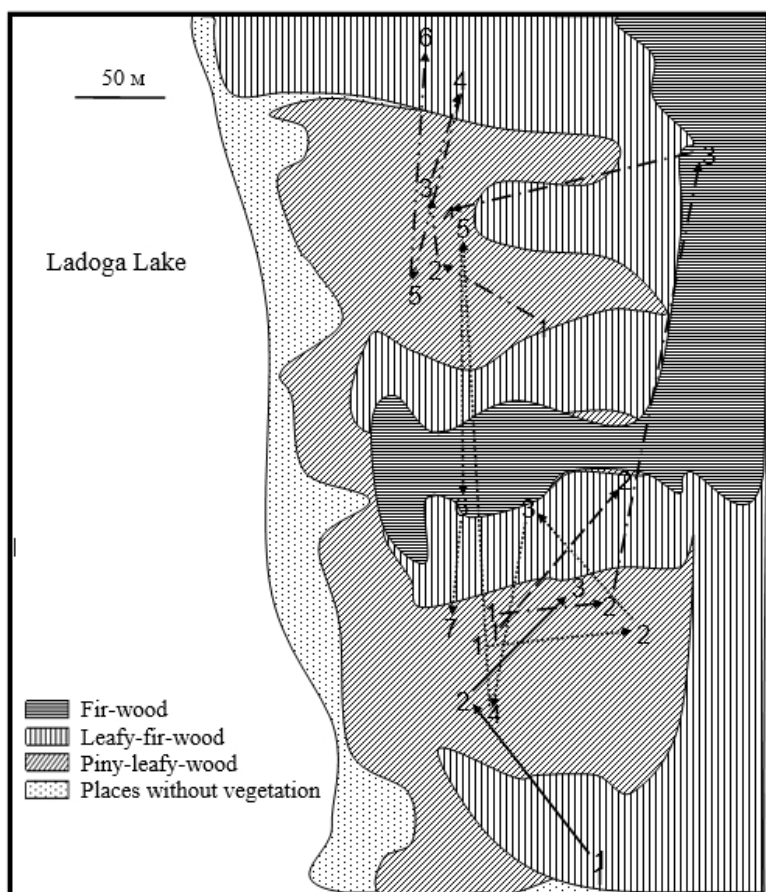


Fig. 6. Change of places of singing (1, 2, etc.) during a season in Wood Warblers. Examples for some different controlled males are indicated by the lines of different types (2007 – 2014).

conditions, and the great number of Greenish Warbler males is indicative of that (Fig. 5).

2. Most of the territories of Wood Warblers are very unstable: they noticeably shift in space during a season (Fig. 6) and significantly vary in sizes (Table 1). The territory borders of Greenish Warblers are also quite movable. It is hard to define the preferable places of singing according to which we can determine the territory borders for birds of this species. These borders are as if 'degraded'.

3. The number of Wood Warblers and Greenish Warblers significantly vary from year to year (Lapshin 2001) and this is especially typical for females (these number fluctuations are much bigger than in other relative species whereas Wood Warblers and Greenish Warblers live here close to the very edge of their species ranges) (Lapshin et al. 2013). In this connection in some years a lot of males, even seized territories, remain unmated (Fig. 5).

Thus, there are certain characteristics of the territorial behaviour of Wood Warblers and Greenish Warblers, which promote high plasticity of their territorial structure. This may be the evidence of 'insufficient readiness' of these birds to the conditions relatively new to them. Nevertheless, it is more probable, that such behavioural features help birds to cope with new factors, including conditions of new regions.

CONCLUSIONS

According to the results of this study, we can formulate the next conclusions:

1. The territorial behaviour of the model species has a quite high degree of plasticity.
2. The Leaf Warblers occupied the northern parts of the current species ranges relatively recently form more labile territorial structures of their populations than the Leaf Warblers that had been inhabiting in this region for evolutionary

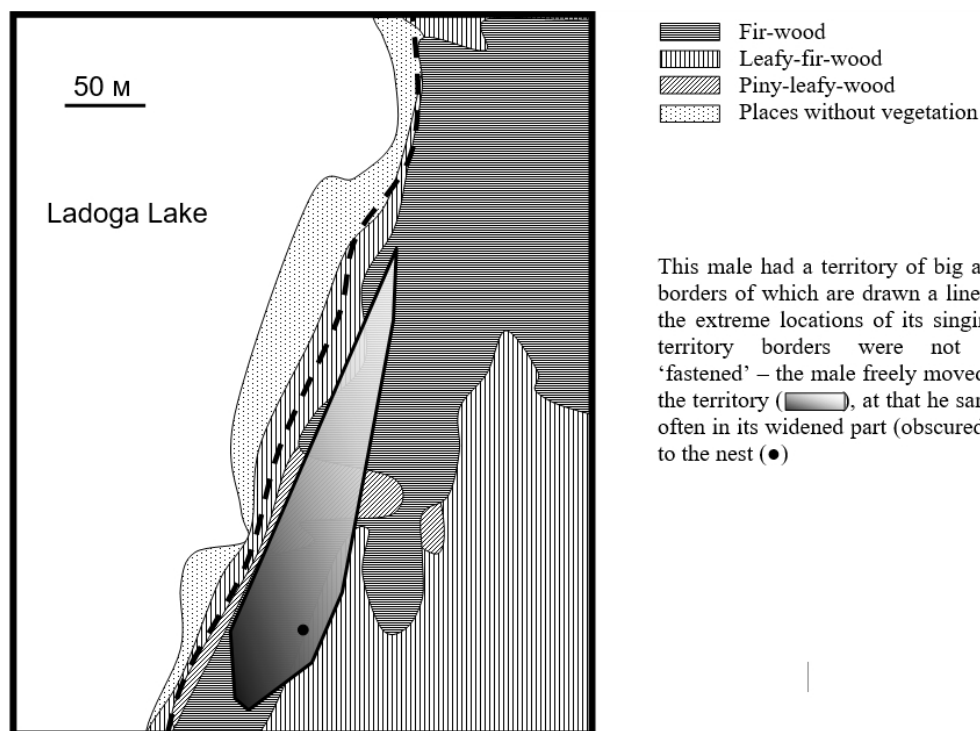


Fig. 7. The example of a Greenish Warbler male's territory.

long time.

3. Diversity of the behavioural options is an important prerequisite of bird adaptations to changing environmental conditions and settlement in new habitats.

Indeed, the obtained data are indicative of a high plasticity of the model objects. They react to every change of environmental conditions (the level of social tension in populations and population density, habitat structure and volume of suitable places, remoteness of range borders and the degree of adaptiveness to the certain conditions) and change their behaviour correspondingly.

We may conclude, that the plasticity of territorial systems and variety of behavioural reactions in Leaf Warblers along with other adaptations allow maintenance of their populations even in not optimal conditions. This is relevant to relationships within and between species: (1) variety of territorial patterns of conspecifics lets them inhabit quite different sites in the vast ranges, and (2) behavioral variations among different species give them a possibility to settle at the same place.

Compared to conspecifics from the central parts of the ranges, birds in Karelia have a short prebreeding period, less aggressive ways to establish territorial borders, the simplified process of stereotype pair formation. Such reduction of territoriality is mainly caused by the limitation of time suitable for breeding and relatively low population densities in the northern regions. Concerning interspecific variations, Willow Warblers and Chiffchaffs (common species that have been inhabiting the region for evolutionary long time) form highly stable territorial structures, whereas Wood Warblers and Greenish Warblers (species that settled in the region recently) form more labile territorial structures and thus are able to move during a breeding season in search of potential reproductive partners. Besides, the behaviour of Leaf Warblers also varied depending on the level of social tension in populations, habitat structure and volume of sites suitable for

nesting and foraging. Undoubtedly, behavioural diversity is essential for sustaining population stability, changing the borders of species ranges and settlement in new habitats.

ACKNOWLEDGEMENT

We gratefully thank all the researchers and assistants participated in trapping and ringing birds for their helping in our work and anonymous experts for reviewing our paper. We also thank the leadership of the Institute of Biology, Karelian Research Centre, Russian Academy of Sciences, for financial support for the investigations and material resources. Furthermore, the reported study was partially supported by RFBR, project NN. 06-05-64368, 12-04-31872 and 15-05-03493_a.

REFERENCES

- Bianchi V.L. 1914. Птицы, наблюдавшиеся в Олонецкой губернии в июне 1911 года (Birds observed in Government Olonets in June 1911). *Ornithologicheskyy vestnik*, 3: 167 – 173. (In Russian).
- Büchner E.A. 1887. Die Vögel des St.-Petersburger Gouvernements. Beitr. Russ. Reiches. Folge 3. Bd. 2: 1 – 150.
- Enemar A., Klaesson P., Sjöstrand B. 1979. Accuracy and efficiency of mapping territorial Willow Warblers *Phylloscopus trochilus*: a case study. *Oikos*, 33: 176 – 181.
- Geissbühler W. 1954. Beitrag zur biologie des Zilpzalps, *Phylloscopus collybita*. *Orn. Beob.*, 51: 71 – 99.
- Glutz von Blotzheim U.N., Bauer K.M. 1993. Handbuch der Vögel Mitteleuropas. Aula-Verlag, Wiesbaden, 12/II, Passeriformes (3. Teil). Sylviidae: 1 – 1459.

- Howard H.E. 1920. Territory in bird life. London: 1 – 308.
- Jakobsson S. 1988. Territory fidelity of Willow Warbler (*Phylloscopus trochilus*) males and success in competition over territories. *Behav. Ecol. Sociobiol.*, 22: 79 – 84.
- Lapshin N.V. 1978. Поведение пеночки-веснички в предгнездовой период (Behaviour of Willow Warblers in a prebreeding period). In: Fauna and ecology of birds and mammals of taiga North-West USSR. Petrozavodsk: 32 – 39. (In Russian).
- Lapshin N.V. 2000. Biology of the Chiffchaff *Phylloscopus collybita* in the taiga zone of north-western Russia. *Avian Ecol. Behav.*, 4: 1 – 30.
- Lapshin N.V. 2001. Изучение годовых циклов дальних трансконтинентальных мигрантов Палеарктики (на примере пеночек рода *Phylloscopus* Карелии) (The study of annual cycles of far transcontinental migratory birds of Palearctic (in example of *Phylloscopus* warblers of Karelia)). Achievements and problems of ornithology of Northern Eurasia on a boundary of centuries. The Works of the International Conference «Urgent problems of birds' study and protection in East Europe and Northern Asia». Kazan': 394 – 412. (In Russian; resume in English).
- Lapshin N.V. 2004. Биология зеленой пеночки *Phylloscopus trochiloides* (Passeriformes, Sylviidae) в Карелии (Biology of the Greenish Warbler, *Phylloscopus trochiloides* (Passeriformes, Sylviidae), from Karelia). *Zool. Journal*, 83 (6): 715 – 724. (In Russian; abstract in English).
- Lapshin N.V. 2005. Biology of the Wood Warbler *Phylloscopus sibilatrix* (Berchst.) in the taiga zone of north-western Russia. *Avian Ecol. Behav.*, 13: 25 – 46.
- Lapshin N.V. 2009. Specific features of annual cycles in long-distance migrant birds living at the range boundary: the example of the Wood Warbler, *Phylloscopus sibilatrix*, in the taiga zone of Northwestern Russia. *Russian journal of ecology*, 3: 1 – 7.
- Lapshin N.V., Topchieva L.V., Matantseva M.V., Simonov S.A., Malysheva I.E., Kanceroва N.P. 2013. Ecological features of migrating Passerines (analysis with molecular biology techniques involved). *Biology Bulletin*, 40 (10): 815 – 822.
- May D.J. 1949. Studies on a community of Willow Warblers. *Ibis*, 1 (1): 24 – 54.
- Odum E., Kuenzler R. 1955. Measurement of territory and home range size in birds. *Ari*, 72 (2): 128 – 137.
- Ovchinnikova N.P. 1973. Способы установления токовых и гнездовых участков и взаимоотношения между самцами пеночек-трещоток (The ways of establishment of demonstrated and foraging territories and relationships between males in Wood Warblers). *Vestnik LGU*, 3: 19 – 24. (In Russian).
- Ovchinnikova N.P., Firsova L.V. 1971. Весеннее территориальное поведение самцов пеночек-трещоток (The spring territorial behaviour of Wood Warbler males). *Uchenye zapiski LGU*, 50: 179 – 185. (In Russian).
- Piotrowska M., Wesołowsky T. 1989. The breeding ecology and behaviour of the Chiffchaff *Phylloscopus collybita* in primeval and managed stands of Białowieża Forest (Poland). *Acta Ornithol.*, 25: 25 – 76.
- Radesäter T., Jakobsson S. 1989. Song rate correlations of replacement territorial Willow Warblers *Phylloscopus trochilus*. *Ornis Scand.*, 20: 71 – 73.

Ryabitsev V.K. 1993. Территориальные отношения и динамика сообществ птиц в Субарктике (The territorial relationships and dynamics of bird communities in Subarctic). *Nauka*, Ekaterinburg: 1 – 296.

Received: 28.04.2015.

Accepted: 06.07.2015.

Simms E. 1985. British Warblers. Collins, London: 1 – 432.

Zarudny N.A. 1910. Птицы Псковской губернии (The birds of Government Pskov). *Proc. Acad. Sci., division Phys. Math.*, series 8, vol. 25 (2). Pp. 1 – 181. (In Russian).

Zimin V.B. 1988. Экология воробьиных птиц Северо-Запада СССР (Ecology of Passeriformes Birds in the Northwestern Soviet Union). Leningrad: *Nauka*. (In Russian).

Zimin V.B. 2001. Особенности распространения птиц таежного Северо-запада России, реальная и ложная экспансия (по данным кольцевания и контроля за составом меченого населения) (Characteristics of bird spread in taiga North-West Russia, real and false expansion (according to the data of ringing and control of birds)). *Trudy Karel'skogo nauchnogo centra RAN*, 2: 97 – 95. (In Russian).