ISSN 1062-3590, Biology Bulletin, 2016, Vol. 43, No. 9, pp. 1249–1255. © Pleiades Publishing, Inc., 2016.
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Spatial Structure of the Population and Reproductive Success of the Bluethroat (*Luscinia svecica,* Turdidae, Aves) in the South of the Saratov Trans-Volga Region

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Received February 29, 2016

Abstract—The present study was performed in the dry steppe subzone of the Saratov Trans-Volga region during six breeding seasons (years 2010–2015). Habitat features that affected the structure of bluethroat (*Luscinia svecica*) population were analyzed. The biotopes present in the area investigated differed greatly with regard to the dynamics of environmental conditions during the breeding season. Population density and spatial distribution of nesting territories in each habitat were used to characterize habitat selection, and the breeding productivity was used to assess the result of this selection. Bluethroat population density was always higher in uniformly suitable habitats that provided favorable conditions for nest building and feeding. Part of the population occupied habitats of a lower quality; however, these habitats might be used as "reserve habitats" during breeding seasons characterized by extreme conditions of the environment. Moreover, the contribution of a number of reproductive parameters to the overall breeding productivity was assessed. The present study showed that the starting date and length of fertile period, as well as nest mortality, are the major parameters that determine the variation in breeding productivity between different habitats and seasons. The results are discussed in view of the contributions of population groups to reproduction.

Keywords: spatial structure of the population, reproductive success, habitat choice, *Luscinia svecica*

DOI: 10.1134/S106235901611011X

INTRODUCTION

Maximal possible adaptation to environmental conditions is the major prerequisite for habitat selection by a bird. Therefore, the choice made by an individual at a specific moment is a result of natural selection.

The process of habitat selection depends on abiotic factors, resource availability, competition, and predator activity. These effects shape the structure of all ecosystems. The choice of a habitat, in its turn, has a considerable effect on population dynamics, community structure, and ecosystem functioning. Therefore, research on the process of habitat selection can make an important contribution to understanding the structure of ecosystems. Moreover, the understanding of habitat selection strategies in individual species may result in identification of essential characteristics of a habitat that are important for the prediction of species distribution and population viability.

Habitat selection is a hierarchical sequence of behavioral responses that can lead to non-uniform habitat use and the related effects on survival and adaptation of the individuals (Hutto, 1985; Block and Brennan, 1993).

Two aspects of habitat selection that play a key role in the understanding of the adaptive significance of non-uniform habitat use are the demonstration of selection and the assessment of the adaptive capacity of the individual with regard to the choice made. Firstly, habitat selection involves the making of successive decisions, and thus it is necessary to outline the effects of the environmental conditions on the choices made by an individual. One should remember that a certain decision is influenced both by the benefits of a specific choice and by the costs of implementation of this choice. Secondly, the preference for a certain habitat may be a manifestation of adaptation, even though enhanced adaptation of individuals to this habitat is not observed. A positive correlation between population density in a certain habitat and the quality of this habitat does not necessarily exist. The characteristics that influence habitat selection cannot be defined if the information on the behavior and the life events of individual animals is unavailable.

Finally, many factors not directly related to habitat structure (nest mortality rate, competition, and social interactions in the population, to name a few) affect the selection of habitat by birds as well. It is important to identify the extent of the influence of these factors on the choice made by an individual and the benefits related to this choice.

The bluethroat (*Luscinia svecica* L. 1758) used as the model species in the present study has a broad living range and occurs in diverse biotopes. The bluethroat prefers semi-secluded habitats near water bodies in most of the nature zones; the birds prefer small shrubs and avoid completely open areas (Ryabitsev, 2008). Numerous studies showed that the presence of a discontinuous tree and shrub canopy and a water body in the vicinity are the most important factors that define the location of nests. The bluethroat feeds on the ground, and therefore vegetation should not hinder the search for food (for instance, tall vegetation hinders the movement of birds and is therefore avoided); on the other hand, convenient nest-building sites (thick shrubs that prevent the access of predators) are important as well. Thus, the topoarchitecture of communities preferred by the bluethroat can be classified as a "moderate ground canopy surrounded by open space" (Ravkin, 1978; Yudkin, 2002). The presence of a water body ceases to be a decisive factor if the appropriate structure of vegetation can be formed in the absence of a water body (Berndt and Holzel, 2012).

Territorial behavior was reported in the bluethroat, at least during the time when the birds claim the nesting territories. This type of behavior is likely to serve for the attraction of a breeding partner, rather than for the protection of food resources or the prevention of mating between the female and a stranger male, as was assumed earlier (Smiseth and Amundsen, 1995). However, considerable intraspecies (inter-populational) variation of the degree of territorial behavior and territory overlap (the inverse parameter) has been demonstrated. The structure can be (1) rigidly territorial, (2) rigidly territorial during a certain period, (3) flexibly territorial, or (4) non-territorial (Turcokova et al., 2011). Thus, population density itself can depend on the features of the social structure and have an ambiguous influence on habitat quality.

The aims of the present work included the assessment of bluethroat distribution in different habitats in the dry steppe subzone of the Trans-Volga region. Biotopes characterized by dramatically different dynamics of conditions during the nesting season alternate in this area. The population density parameter and the characteristics of the spatial distribution of the nesting territories were used to characterize the habitat selection. The result of the choice was assessed using the data on breeding productivity of the bluethroat in different habitats and the contribution of individual components to the overall reproductive success.

MATERIALS AND METHODS

The study was performed in the dry steppe subzone, in the D'yakovskii forest and in its vicinity (Saratov oblast, Krasnokutskii raion, D'yakovka village, 50°31′ N, 46°47′ E). D'yakovskii forest is the largest forest outlier in the south of the European part of Russia; it is located in the extreme south of the Saratov Trans-Volga region, in the middle reaches of the River Eruslan, at the border of Volgograd oblast. The forest consists of patches of birch, aspen, and oak tree stands that alternate with sandy-steppe open areas, damp meadows, glades, and thickets of small steppe shrubs (Neronov, 2005; Shilova and Neronov, 2010).

The material was collected in April–July during six nesting seasons (the years 2010–2015). Four major types of habitats occupied by the bluethroat were identified in the area investigated, and study plots were marked in each habitat.

(1) Habitat of the steppe type is composed of fallows of different age. Wormwood (*Artemisia* sp.), needle grass (*Stipa* sp.), and sheep fescue (*Festuca valesiaca* Gaud.) predominate in the herb tier. Thickets formed by the shrub form of oldman wormwood (*Artemisia abrotanum* L.) and isolated groups of other shrubs (mostly blackthorn (*Prunus spinosa* L.) of not more than 1.5 m in height are found in the area as well. Local depressions (balkas) flooded by melt water occur. The area of the study plot was 31 ha.

(2) Habitat of the riverine type extends as a narrow strip (not more than 50 m in width) along the Eruslan River. Vegetation is composed by cane thickets, tall herbs, and shrubs (willow *Salix* sp., oleaster (*Elaeagnus angustifolia* L.), and blackthorn) of not more than 2–4 m in height. Trees (maple ash *Acer negundo* L., white poplar *Populus alba* L., and others) form isolated groups and usually reach 6–7 m in height. The area of the study plot was 23 ha.

(3) Habitat of the forest type is located within the D'yakovskii forest and composed of forest fragments of 0.1 to 10 ha with highly diverse tree stands. Deep hollows overgrown by willows and sedge grass (and less often, cane) are common in the area; these hollows are flooded by melt waters in the spring and often remain flooded during the entire season. Patches of steppe with shrubbery are formed near the edges of the groves and at sites where the trees were partially cut down. Meadowsweet (*Spiraea hypericifolia* L.), blackthorn, and hawthorn (*Grataegus curvicepala* Lindm.) predominate among the shrubs. Groves alternate with fragments of psammophyte-cereal steppe. The area of the study plot was 57.5 ha.

(4) The coastal lake is a hollow flooded by water during the melting of snow in the spring. Part of the site remained flooded during the humid years, but drying-out of the water was observed during most years. The vegetation was formed by cane (*Phrágmites austrális* (Cav.) Trin. ex Steud.) thickets of up to 2.5 m in height; dry canes of the previous year were found in the area until the end of May, and new shoots overtook the area quickly afterwards. The area of the study plot was 2.4 ha.

Some of the habitats bordered on each other, but the character of seasonal resource dynamics in the habitats was essentially different, and thus comparative assessment of the breeding settlements in these areas was possible.

The assessment of population density at the stationary study plots in the habitats selected was based on the results of yearly censuses and mapping of the nesting territories (Morozov, 1992). The birds were captured by mist nets of 7 and 10 m in length during the morning hours; the nets were installed near the nests identified and in other parts of the territory investigated throughout the breeding season. The birds captured were treated according to the standard procedure (Vinogradova et al., 1976; Svensson, 1992). The sex and the age was recorded. All birds were divided into two cohorts: one-year old individuals and birds aged two years or more. The birds were ringed with numbered aluminum rings and three colored rings, so that the subsequent identification of individuals did not require capturing. The total number of adult individuals ringed during the 6 years of research was 524. Nestlings and fledglings were ringed with single numbered rings.

The "distance to nearest neighbor" approach was used to describe the characteristic features of the distribution of nesting territories at the study sites. The coefficient R calculated according to this approach characterizes the deviation of the distribution under investigation from a random distribution. The distribution is considered random at $R = 1$ (or in the case of absence of a statistically significant difference between R and 1), uniform at $R > 1$, and groupwise at $R < 1$ (Clark and Evans, 1954). The distance between the nest and the nearest nest occupied at the time of assessment was calculated. The calculation was performed for the day of the beginning of hatching in each nest. The results of GPS mapping were processed with the OziExplorer 3.95.4s software in order to calculate the distances.

The nests were searched for and monitored (every 2 to 3 days) in order to assess the reproductive parameters. The stage of the nesting cycle (building/egg laying/hatching/feeding nestlings), clutch size or number of young, breeding result, and the individual marks of the parents were registered. The total number of nests monitored was 318.

Breeding productivity of the bluethroat was assessed according to a procedure reported previously (Ricklefs and Bloom, 1977). The advantage of this method consists in the possibility of assessing the breeding productivity of the entire population and the contribution of each parameter to nesting success (Paevskii, 2008) without the need to monitor each nest from the moment of building until fledging. The procedure enables the comparison of nesting settlements in different habitats and the assessment of year-to-year variability. Breeding productivity can be presented as a function of "direct" (obtained by direct monitoring) breeding parameters. These parameters include clutch size C (average for each habitat), length of the nest cycle from clutch initiation to fledging T (our observations showed that $T = 29$ days), breeding success S (proportion of individuals that fledge, %), and nest mortality rate (proportion of nests failing per day) m, %. The calculations also involve a number of "indirect" parameters, such as F (expected rate at which young are fledged in a large population (yong fledged/pair · day)):

$$F = C \times S \times I,$$

I—rate of nest initiation (clutches per pair per day);

p_s, p_f—probability that a nest successfully fledges (at least one young) or that a nest fails before fledging.

r_s, r_f—delay before a new clutch is laid after successfull fledging/nest failure. The average value for the population was $r_s \pm SE = 10.4 \pm 0.8$ days if the first nesting cycle was successful, and $r_f \pm SE = 6.6 \pm 1.2$ days in case of the first nest was fail.

B—length of fertile period (in other words, the period of the initiation of egg laying in the population) calculated according to the formula:

$$B = 15\exp(-\sum Pi \ln Pi),$$

where Pi the proportion of clutches laid by the population during a 15-day interval i. The intervals used in the original procedure (Ricklefs and Bloom, 1977) were 30 days long, but we found the 15-day intervals more appropriate for intraspecies comparisons within a single geographical area, since the necessary increase of assessment sensitivity could be attained in this case.

Breeding productivity P was expressed as the number of fledglings per pair per season.

$$P = F \times B.$$

Part of the males in the population investigated showed polygyny with overlapping breeding cycles (Batova and Nemchenko, 2014), and therefore the number of fledglings per female per season was assessed.

The raw data were processed using the STATISTICA 8.0 (StatSoft Inc., 2008).

RESULTS

Structure of the Bluethroat Population

The density (pattern) and spatial structure of the bluethroat population in the major habitats were inferred from the results of site censuses. Population density was the highest in the riverine habitat complex (24.1 pairs/10 ha) and in the coastal lake area (22.7) and much lower in the steppe (8.9) and especially in the forest (1.8). This difference is due to non-uniform distribution of favorable microhabitats within the habitats investigated. Habitats of the riverine type form a narrow strip along the river and therefore the population density is elevated, as is common for all ribbon-like habitats. This habitat provides all conditions required by bluethroats: namely, nest building sites well protected from predators by the shrubs and tall herbs and sites with a low herb tier well adapted for feeding. The coastal lake area is a homogeneous habitat that borders on open steppe areas not suitable for nesting. However, the coastal lake area does not provide good opportunities for feeding, and therefore the birds that nesting in this area feed in the open steppe areas. Tall and thick vegetation that provides good protection for the nest building sites is one of the advantages of the coastal lake area. Some of the habitats of the steppe type are overgrown by shrubs, while others are not, and only the microhabitats overgrown with shrubs are used for nest building by the bluethroat. The habitat of the forest type is mosaic and consists of fragments with dramatically different environmental conditions. Bluethroats build nests at the edges of groves that border on the steppe overgrown with shrubs or in humid depressions with shrub vegetation.

The "distance to nearest neighbor" approach revealed differences in the distribution of individual nesting territories in the three habitats. Uniform distribution was observed in both the riverine habitat and the coastal lake area during all years ($R = 1.29 \pm 0.026$, $p < 0.001$; $R = 1.88 \pm 0.35$, $p < 0.05$, respectively), and the population density was high: therefore, continuous settlements were formed. The distribution of the nesting territories in the steppe habitat was aggregated ($R = 0.65 \pm 0.028$, $p < 0.001$), with high local density within the aggregations and some unoccupied sites. Distribution of the nesting territories in the forest did not show a significant deviation from a random distribution ($R = 0.91 \pm 0.095$, $p > 0.1$); as a rule, the territories occupied by neighboring pairs did not border on each other. Thus, the breeding populations of the bluethroat in the major habitats are distributed according to characteristic spatial patterns, regardless of the absence of distinct boundaries between the biotopes identified.

Breeding Productivity

Analysis of the overall breeding productivity revealed a lower value of this parameter in the forest habitat during all seasons: the number of fledglings per female per season never exceeded three in this habitat (table). On the other hand, the breeding productivity in the steppe habitat never dropped below five fledglings per female per season. The values for the riverine habitat and the coastal lake area varied considerably between years. One may assume greater stability of the conditions in the forest and steppe habitats or the compensation of the varying conditions by the selection of a specific nesting territory, since continuous bluethroat settlements of a uniform density were not formed in either habitat.

Analysis of components of the overall breeding productivity revealed different levels of spatial and temporal variability for different parameters. For instance, the average clutch size did not vary between years and habitats. However, the trend to clutch size decrease during a season was apparent. This trend, previously reported by Ryzhenkova (2012), is apparent from the smaller size of repeated (following first nest destruction or abandonment) or second (after successful hatching of the first clutch) clutches as compared to the first clutches. The average clutch size for a specific year and habitat depends on the probability of nest destruction to a certain extent. Each subsequent clutch becomes smaller as a female makes repeated efforts to resume breeding. Importantly, the presumed dependence of clutch size on the female's age was not proven.

Length of fertile period, breeding success, and nest mortality rate were much more prone to changes related to the variation in environmental conditions. The fertile period was always short in the forest habitat, this being an important reason for low breeding productivity. The length of fertile period in the steppe and riverine habitats seldom changed by more than 7 days in either direction. The abrupt end of nesting due to the early drying-out of steppe vegetation in 2014 formed the only exception. One should remember that the time of the beginning and end of nesting is as important as the duration of the beginning of the egg laying period. The breeding season usually begins earlier in the steppe habitat due to the earlier disappearance of the snow cover and development of herbaceous vegetation. However, differences in this parameter are usually more pronounced when breeding seasons are compared, whereas the two most productive bluethroat habitats compared during the same season show little difference.

The contributions of reproductive success and the rate of nest destruction to breeding productivity are opposite, but it would be erroneous to state that these two parameters compensate for each other. The factors of reproductive success include the relative abundance of unfertilized eggs, embryonic death, and partial destruction characteristic of nests built on the ground in the steppe zone. Analysis of the spatiotemporal dynamics of these parameters shows that different habitats can provide for maximal reproductive success during different seasons. For instance, the values of this parameter were uniformly low in the steppe and forest habitats, slightly higher in the riverine habitat, and maximal in the coastal lake area in 2015, whereas the values of 2014 were similarly high for the steppe and riverine habitats and extremely low in the forest habitat. The nest mortality rate showed a similar trend, but the high levels of reproductive success are

Values of the major reproductive parameters in the habitats investigated

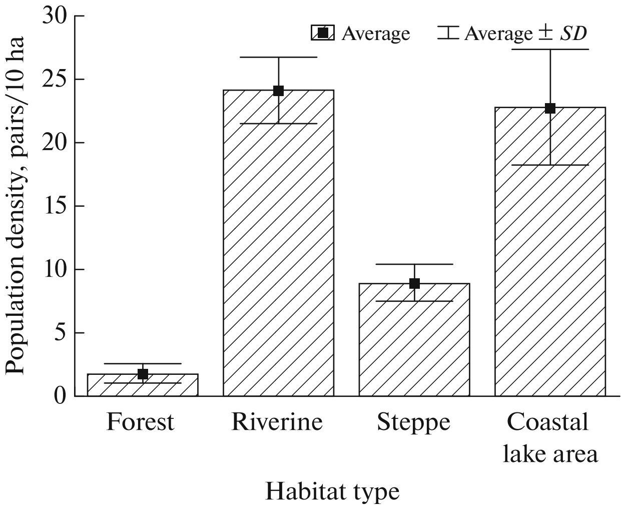
Habitat type	Year	*C* ± *SE*	*S* ± *SE*	*F*	*I*	*m*	*Ps*	*Pf*	*B*	*P* ± *SE*
Steppe	2010	5.07 ± 0.20	0.84 ± 0.11	0.12	0.03	0.01	0.76	0.24	45.81	5.63 ± 0.039
	2011	5.15 ± 0.22	0.86 ± 0.07	0.12	0.03	0.01	0.89	0.11	48.11	5.72 ± 0.027
	2012	4.82 ± 0.15	0.64 ± 0.10	0.12	0.04	0.03	0.38	0.62	65.32	7.55 ± 0.050
	2013	5.25 ± 0.19	0.59 ± 0.11	0.11	0.04	0.03	0.42	0.58	60.87	6.87 ± 0.059
	2014	5.00 ± 0.18	0.82 ± 0.07	0.12	0.03	0.01	0.69	0.31	48.02	5.89 ± 0.013
	2015	4.78 ± 0.17	0.51 ± 0.10	0.11	0.04	0.05	0.22	0.78	49.2	5.33 ± 0.017
Forest	2010	4.63 ± 0.27	0.73 ± 0.15	0.12	0.04	0.03	0.45	0.55	21.86	2.60 ± 0.041
	2011	4.67 ± 0.32	0.67 ± 0.11	0.09	0.03	0.01	0.69	0.31	28.35	2.66 ± 0.040
	2012	4.50 ± 0.63	0.00 ± 0.24	0.00	0.10	0.27	0.00	1.00	28.35	0.00 ± 0.900
	2013	4.50 ± 0.30	0.55 ± 0.17	0.08	0.03	0.02	0.50	0.50	30.64	2.58 ± 0.069
	2014	4.00 ± 0.38	0.15 ± 0.16	0.03	0.05	0.08	0.11	0.89	29.4	0.94 ± 0.061
	2015	4.67 ± 0.46	0.50 ± 0.27	0.1	0.04	0.05	0.22	0.78	28.35	2.97 ± 0.114
Riverine	2010	4.90 ± 0.14	0.50 ± 0.08	0.09	0.04	0.03	0.39	0.61	43.24	3.92 ± 0.023
	2011	4.67 ± 0.28	0.80 ± 0.10	0.11	0.03	0.01	0.68	0.32	54.20	6.07 ± 0.057
	2012	4.90 ± 0.16	0.58 ± 0.10	0.10	0.04	0.03	0.44	0.56	70.95	7.19 ± 0.056
	2013	5.00 ± 0.16	0.52 ± 0.09	0.11	0.04	0.05	0.26	0.74	59.33	6.58 ± 0.053
	2014	5.10 ± 0.19	0.78 ± 0.08	0.13	0.03	0.02	0.58	0.42	66.62	8.46 ± 0.064
	2015	5.05 ± 0.18	0.60 ± 0.10	0.13	0.04	0.05	0.27	0.73	47.23	6.01 ± 0.028
Coastal lake area	2014	4.83 ± 0.35	0.47 ± 0.15	0.09	0.04	0.04	0.36	0.64	15	1.29 ± 0.027
	2015	4.00 ± 0.32	0.67 ± 0.17	0.12	0.05	0.06	0.2	0.8	44.27	5.43 ± 0.054

C—clutch size, *S*—breeding success, *F*—expected rate at which young are fledged in a large population, *I*—rate of nest initiation, *m*—nest mortality rate, *Ps*—probability that a nest successfully fledges, *Pf*—probability that a nest fails before fledging, *B*—length of fertile period, *P*—breeding productivity, number of fledglings per female per season.

not necessarily an unambiguous indication of a low nest mortality rate. The nest mortality rate (*m*) varied considerably between years, but was always similar in neighboring habitats (table). However, the value for the riverine habitat was higher than that for the steppe habitat in half of all cases. The probability of nest mortality is determined by two factors, namely, the presence and number of predators and the quality of nest protection conditions. However, predator pressure cannot be used to characterize the habitats, since the three distinct habitats (riverine, coastal lake, and steppe) border on each other. The forest habitat is detached from the others; moreover, certain predators may be specific for the forest and not attack birds in other areas. Thus, the protective conditions that depend on the dynamics of vegetation development will have a definitive influence on the rate of nest mortality. Therefore, it appears impossible to predict these characteristics for a certain habitat if all data available concern other habitats, and these data cannot be regarded as an unambiguous characteristic of the season in all sites.

DISCUSSION

Analysis of the spatial population structure and the distribution of bluethroat among the habitats revealed three types of nest distribution. The riverine habitat and the coastal lake area somewhat similar to the former habitat turned out to be preferred, as evident from the high and stable population density. High population density and uniform distribution of birds in these areas shows that these habitats are uniformly favorable. The structure of the vegetative tiers in the aforementioned habitats is generally considered typical for the species. However, the habitats with an optimal vegetation structure occupy a relatively small area in the region investigated, and the entire population of the birds cannot fit into these habitats. On the other hand, the fallow-type areas are abundant; in contrast to the zonal steppes, these areas contain patches of shrubbery. Thus, the considerable area of the steppe sites relatively to the total area of the study site accounts for the important role of steppe habitats in the maintenance of bluethroat population structure in the Trans-Volga region, although population density in these habitats is lower than in the riverine and



Average population density of the bluethroat in the habitats investigated for all years of the study.

coastal lake areas. Habitats of the forest type within an insular forest have certain characteristics of a pessimal habitat, such as low population density and random distribution of individual nesting territories.

The results of habitat selection were characterized by the values of breeding productivity and the temporal stability of the former. The part of the population that occupied the steppe habitats was characterized by a stable and high productivity level: productivity seldom reached extremely high values, but never dropped below a certain level. This was primarily due to the early beginning of nest building related to the rapid disappearance of the snow cover and development of the herb vegetation on the open steppe areas well warmed by the sun. Older and more experienced birds are well known to arrive to nesting areas ahead of other conspecifics. This was also true for the bluethroat population in the Trans-Volga region, and the birds that bred in the steppe habitat accounted for the largest part of the older bird group (two years and older) (Batova and Nemchenko, 2014). The early beginning of nesting allows for the preservation of a relatively high average level of breeding productivity, even though the vegetation may dry out, bringing about a decrease in reproductive success in the second nesting cycle.

The productivity levels for the riverine habitats with herb and shrub thickets preferred by the species varied considerably from year to year. Breeding productivity was maximal in these habitats during the favorable seasons due to the presence of a microhabitat combination that provided a suitable environment for all types of activities of the birds. A large number of studies pointed at higher reproductive success (number of fledglings per unit territory) of the bluethroat in areas with a greater variability of the vegetative cover (Geslin et al., 2002). However, the preference for this habitat evident from high population density and uniform spatial distribution of nesting territories was not necessarily successful, since the breeding productivity was much lower than in the steppe habitat during certain seasons. This may be due to a shorter fertile period, a delayed beginning of this period, or the large number of predators attracted to the only water body during the arid years. In other words, a choice based on species-specific stereotypes is not necessarily the best. This probably applies to the coastal lake area as well, but the amount of data available is still insufficient for drawing conclusions.

The data on low population density and random distribution of nesting sites in the forest area investigated combined with the data on productivity point at the unfavorable character of this habitat for the bluethroat. The predominance of one-year old birds in the forest habitat confirms this assumption (Ryzhenkova, 2012). The forest can be regarded as a pessimal habitat, but the birds continue to nest in the forest from year to year, albeit at a low population density. Several explanations for this fact are possible. Firstly, the size of the favorable habitats may be insufficient for all birds that arrive to the area. This hypothesis can be confirmed by the detection of partnerless individuals (mostly males, but some females as well) in the population. Thus, younger and less experienced individuals are forced to settle in a less suitable habitat. Part of the population is faced by a choice of not breeding during a specific season or trying to breed in a less favorable habitat. Secondly, the forest may play a role of a certain "reserve habitat." For instance, the forest habitat may turn out more favorable than others during a very arid year. Finally, population viability is defined by the strategy of the distribution of reproductive attempts given the essentially unpredictable character of the breeding season.

Thus, the pattern of habitat use by the bluethroat in the area investigated was the following. Maximal population density and uniform distribution were observed in complex herb and shrub communities formed at the riverine sites and in the humid lowlands (coastal lake areas). However, the productivity of this habitat choice varied between years, and therefore the breeding productivity of this part of the population varied considerably. Bluethroats differentiated between fallows of different types upon nesting. The area occupied by fallows was much greater than that of the riverine sites, whereas the productivity was maintained at a stable and high level, but did not reach the maximal values. The sites within an insular forest were occupied in a sparse and non-uniform manner; these sites provided the reserve part of the population with a breeding opportunity, but the breeding productivity was low. Still, part of the birds settled in this area every year. One can assume that the nest distribution pattern described above provides for stable reproduction in the population under unstable environmental conditions. Habitat selection in birds is determined by evolutionary factors. Stable differences between the population density in different habitats prove that birds choose the same nesting sites every year and assess the advantages of the habitats. The result of habitat choice is ambiguous and depends on the conditions of the season, that is, a certain habitat may be more or less favorable depending on the characteristics of a specific season. As a result, habitat type combined with breeding productivity allow for the assessment of the role of each biotope in the maintenance of the population structure and the preservation of the species in the area over many years. Habitats of the forest type can be regarded as pessimal under the conditions described; these habitats serve as breeding grounds for the young individuals incapable of competing for habitats of a higher quality. However, forest habitats may play the role of reserve habitats upon a drastic change of the environmental conditions. The contribution of steppe and riverine sites to the overall reproductive success of the population is not entirely defined by the density of the nesting territories and the area occupied by the biotopes in question, since the conditions of a specific breeding season exert an effect as well. Thus, a stable state and the reproduction of a population are maintained due to predominant success of breeding in a specific part of the population.

ACKNOWLEDGMENTS

We are grateful to S.A. Shilova, O.V. Burskii, A.V. Chabovskii, E.N. Ryzhenkova, M.A. Sukhova, Yu.I. Akimova, and I.L. Gershenzon for assistance during all stages of the work.

Financial support for the present work was provided by the Russian Foundation for Basic Research (15-04-08491-a).

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Translated by S. Semenova