SONG STRUCTURE VARIABILITY IN THREE *PHYLLOSCOPUS* SPECIES: WILLOW WARBLER (*PH. TROCHILUS ACREDULA*), WOOD WARBLER (*PH. SIBILATRIX*), AND GREENISH WARBLER (*PH. TROCHILOIDES VIRIDANUS*)

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Introduction

The song structure of many passerine birds is greatly variable. Various explanations have been offered for this fact (Catchpole, Slater, 1995). It is well known that in addition to variability in types of song (repertoire) there is variability of song structure within each type of song (Kroodsma, 1982; Searcy et al. 1995; Hailman, Ficken, 1996). For example, within one song type of Chaffinch (*Fringilla coelebs*) the number of similar elements in the phrase of one type may vary from 2.7 to 7.9 (Slater, Ince, 1979). Most research studies the difference in song types more carefully, and usually does not pay great attention to variation within each song type. However, it is proposed that these variations may be functional and can transmit useful additional information to males and females of many species of birds (Kroodsma, 1982). This proposal is based on the fact that birds of some species can recognise small variation within song type (Searcy et al., 1995). These facts allow as to suggesting that a small variation within song structure might transmit important information to other birds. Song variability can be related to attraction of females and to interaction with them (Kroodsma, 1976; Catchpole, 1982; Catchpole, Leisler, 1996; Hasselquist et al., 1996), as well as to the interaction between males (Brémond, 1966; Krebs, 1977; Staicer, 1996). It is possible that variability within song type may be related to attraction of females, to breeding success and/or to the interaction between males.

The first step in studying this prediction is describing the variation of fine song structure. Our goal is to describe four levels of song structure variability: 1) repertoire of elements, 2) number of similar elements per phrase, 3) number of phrases per song, 4) combination of phrases. We investigate the variability of song structure between and within song types; individual and specific variations of fine song structure; and whether or not variations correlate with the ability of a male to attract a female, with breeding success, and/or with different stages of the breeding season. The final task of this paper is to identify tools which will allow us to compare the songs of different species of birds, and to find similarities and differences in the song composition of relatively close species. The aim of this paper is to study song structure variation of three relatively close *Phylloscopus* species: Willow Warbler (*Phylloscopus trochilus acredula*), Wood Warbler (*Ph. sibilatrix*), and Greenish Warbler *(Ph. trochiloides viridanus*).

We chose these species because of their relatively simple song organisation. The beginning and the end of songs are well defined. The songs of Willow Warbler have been described by many authors (Shubert, 1976; Martens, 1996), and it is known that they are considerably variable. The songs of Greenish Warbler are little studied (Martens, 1980; Марова, 1989), but according to these studies its songs are less variable. The songs of Wood Warbler were studied by H. Temrin (1986), and these are even less variable. However, all noted authors did not pay special attention to the variation within song type. The variability of Willow Warbler songs was recently described by Gil and Slater (2000), but this detailed analysis was mainly devoted to reper-

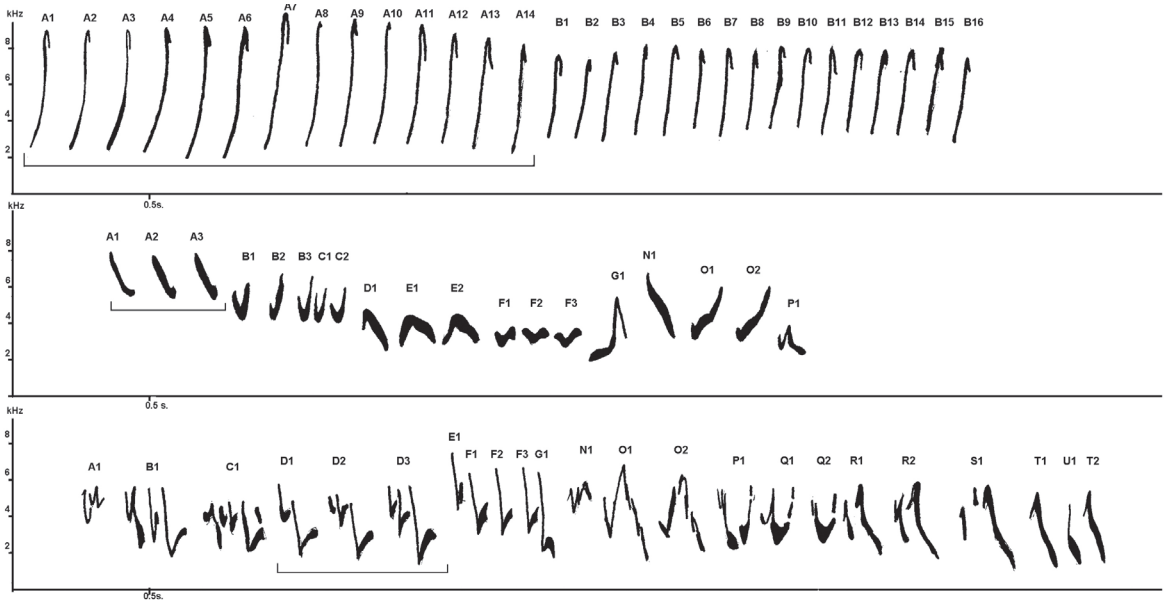

Fig. 1. *Songs of three Phylloscopus species, from up to down: Wood Warbler (Phylloscopus sibilatrix), Willow Warbler (Phylloscopus trochilus acredula), Greenish Warbler (Phylloscopus trochiloides viridanus).*
The similar elements are marked with the one capital letter. The examples of phrases are underlined. The capital letter coincides to the type of phrase.
Рис. 1*. Песни трёх видов пеночек, сверху вниз: пеночка-трещотка, пеночка-весничка, зелёная пеночка.*
Сходные элементы обозначены одной заглавной буквой, примеры фраз подчеркнуты сплошной линией.

toire of elements and combination of phrases, while other characteristics were not taken into account.

Methods

The study was carried out at the Zvenigorod Biological Station (the Moscow Region) and at the Kostroma Biological Station (the Kostroma Region) from 1993–1997. Three test-sites were chosen. All of them were situated in mixed forest. Two (N2 and N3) were located at the Zvenigorod Biological Station and one (N1) at the Kostroma Biological Station. Their areas were 30 ha., 12 ha., and 14 ha. respectively.

More attention was paid to studying Willow and Wood Warblers. At the beginning of breeding seasons birds of these species were captured using song playback to lure them into a mist-net. Eight male and three female Willow Warblers and 3 male and 1 female Wood Warbler were ringed with standard and coloured rings and marked with grease-paint.

In each area the territories were mapped. During the investigations every test-site was visited several (4–8) times per day, so we assume that non-marked birds could be identified by their locations. The females' appearance on the male's territory and courtship behaviour were recorded. We tried to find the nests of all birds observed. In all, the singing and breeding behaviour of 16 Willow Warbler males, 8 Wood Warbler males, and 9 Greenish Warbler males were observed.

Song recordings

Sequences of songs (10–15 min.) were recorded by singing posts. Every male was recorded from 3 to 10 times. To study the variability of songs through the day the males were recorded several times per day in morning (4:00–9:00), middle of day (9:00–17:00), and evening (17:00–23:00) hours. To study the variability of songs throughout the breeding season, recordings were taken at different stages of the breeding cycle. We choose three stages of the breeding cycle: the beginning of the breeding season — territory advertisement, female attraction; the middle stage of the breeding season — laying and hatching of eggs; the end of the breeding season — feeding the young in a nest, feeding fledglings.

Recordings were made using a Sony Cassette CFM-31S one-cassette tape-recorder and an Aiwa TP-550 Dictaphone with an external MD-380A dynamic microphone, with drive frequency up to 16 kHz.

Fine song structure

2000 songs of Willow Warbler, 1000 songs of Wood Warbler and 1000 songs of Greenish

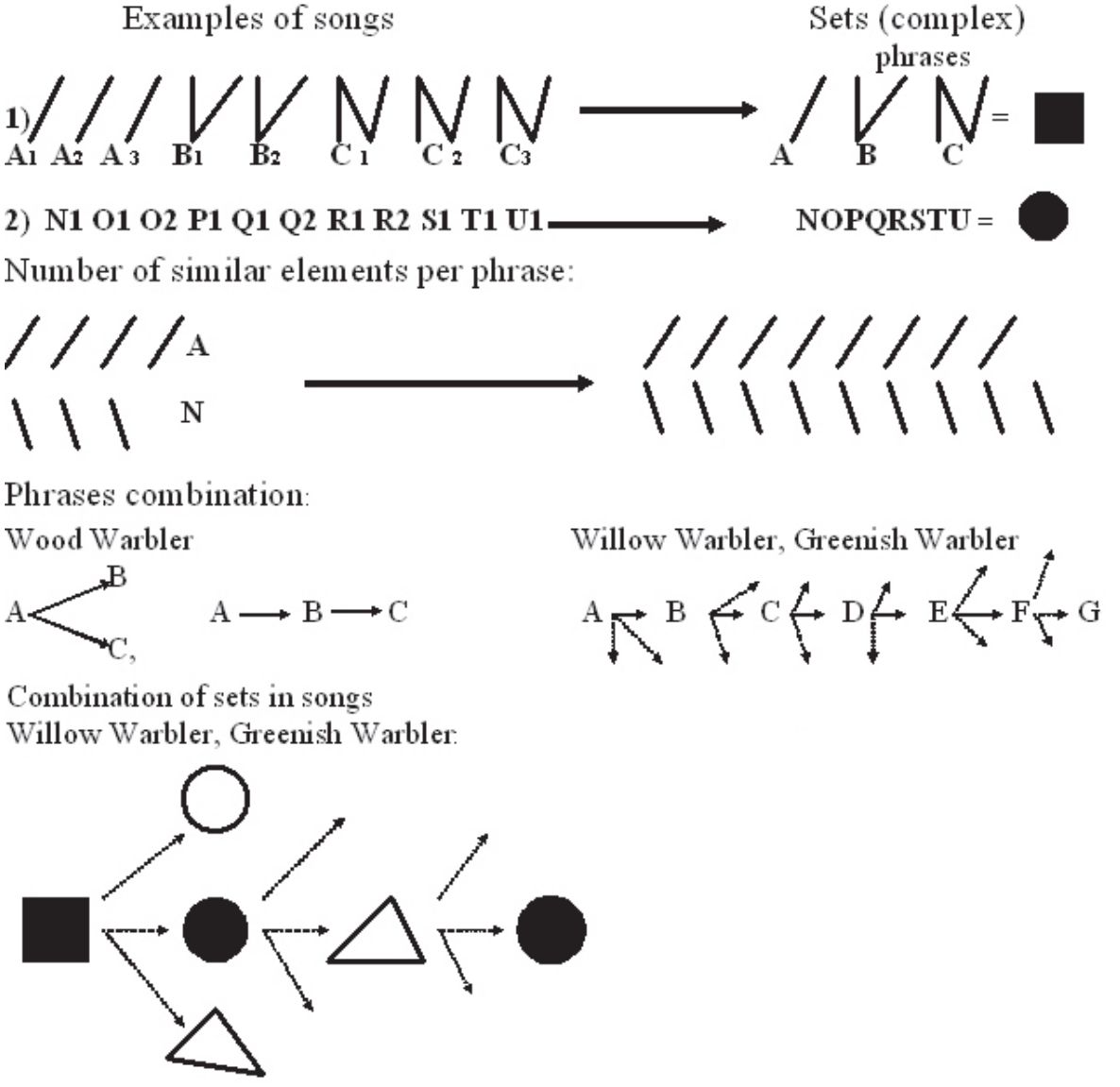

Fig. 2. *Scheme of song structure variability in three Phylloscopus species: Willow Warbler (Phylloscopus trochilus acredula), Wood Warbler (Ph. sibilatrix), and Greenish Warbler (Ph. trochiloides viridanus).*

Рис. 2. *Схема изменчивости структуры песни у трёх видов пеночек рода Phylloscopus: пеночки-веснички (Phylloscopus trochilus acredula), пеночки-трещотки (Ph. sibilatrix) и зелёной пеночки (Ph. trochiloides viridanus).*

Warbler were analysed with Avisoft-light and Avisoft-Pro programs (R. Specht) using broadband filters.

The songs of all species are composed of elements, which normally repeated several times before switching to a new one.

We define song elements and phrases in the following manner:

Element — a non-interrupted fragment of a song or a group of fragments which are isolated by gaps greater than the gaps between them (fig. 1). Elements with similar form of frequency modulation were called similar elements, in other words those elements belonging to one type of element;

Phrase — a sequence of similar elements (fig. 1). The type of element defines phrases.

Four levels of song structure variability were taken into account: repertoire of elements; number of similar elements per phrase; number of phrases per song; combination of phrases.

Statistics

Nonparametric statistical tests were used to analyse the data.

Results

Basic song description

Songs of Wood Warbler begin as a rule with short, poorly modulated elements, which performed in a wide band of frequencies (from 2 up to 10 kHz.) (fig. 1, 2). Elements from the middle and last parts of songs are also show poor frequency modulation. Their frequency band rang-

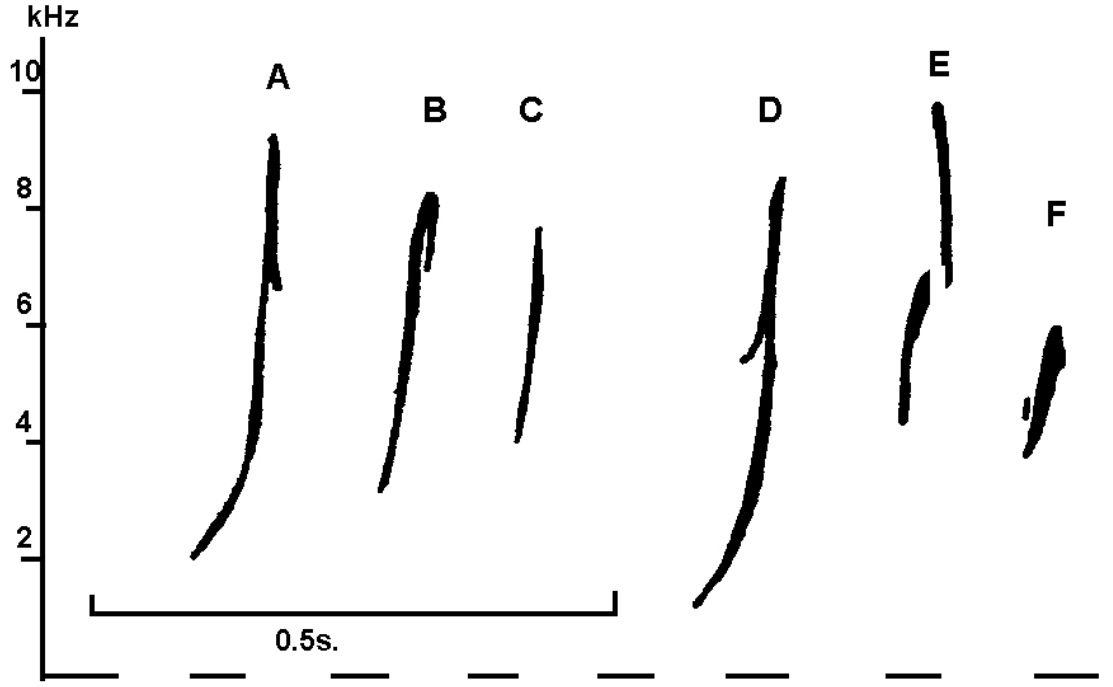

Fig. 3. *Different elements of song in the Wood Warbler (Phyllocopus sibilatrix).*
Рис. 3. *Разные элементы песни пеночки-трещотки.*

es from 3 up to 9 kHz. From time to time songs may begin or finish with a series of calls, which may be considered as phrases of song.

All elements in Greenish Warbler songs show great frequency modulation. The first element is performed, as a rule, in a rather narrow band of frequencies, from 5 up to 8 kHz. Other elements are more often performed in a wide band of frequencies from 2 up to 8 kHz (fig. 1, 2).

Songs of Willow Warbler begin with high-frequency elements (band of frequency from 4 up to 8 kHz.), the middle phrases consist of elements performed in a frequency band from 2.5 up to 6 kHz, and last phrases more often consist of low-frequency elements (from 2 up to 3.5 kHz.) (fig. 1, 2). Initial elements of songs display poor frequency modulation. The form of frequency modulations of elements from the middle and the last phrases of songs is very variable.

Fine song structure, individual and specific variability

Repertoire of elements

Wood Warbler. Each male sings from 2 to 5 different elements. In all, 6 elements were found in songs of 8 males (fig. 3). Three of them were found only in the song of one male, others (1–3) were shared among different males.

Elements sung by the male from the Kostroma Region have the same shape of frequency modulation as do elements of males from the Moscow Region.

We did not find any difference in repertoire of elements through the day.

Seven males sang all elements through the breeding cycle. However one male sang 5 elements in the beginning of the breeding cycle (before a female appears) (162 songs), and only 4 elements at the end of the breeding cycle (youth feeding) (33 songs). This fact may be linked to the small number of recorded songs.

Greenish Warbler. Each male sings from 33 to 35 elements. Most of them are common to all males (fig. 4). The number of elements is correlated positively with the number of recorded songs ($R = 0.56$, $p < 0.05$ Spearman Rang Correlation) (fig.4). The absence of 3–5 elements in songs of 3 male seems to be linked with the insufficient number of recorded songs.

Males from the Moscow Region sang the same repertoire of elements, as did males from the Kostroma Region. The repertoire of elements varies from one recording to another, but this variability does not depend on the time of day. The number of different elements increases a little to the end of the breeding cycle, but the difference is not significant ($p > 0.4$, Kolmogorov-Smirnov, $p > 0.1$ Spearman Rang Correlation).

Willow Warbler. Each male sings from 40 to 200 elements (fig. 5). Most of the elements are

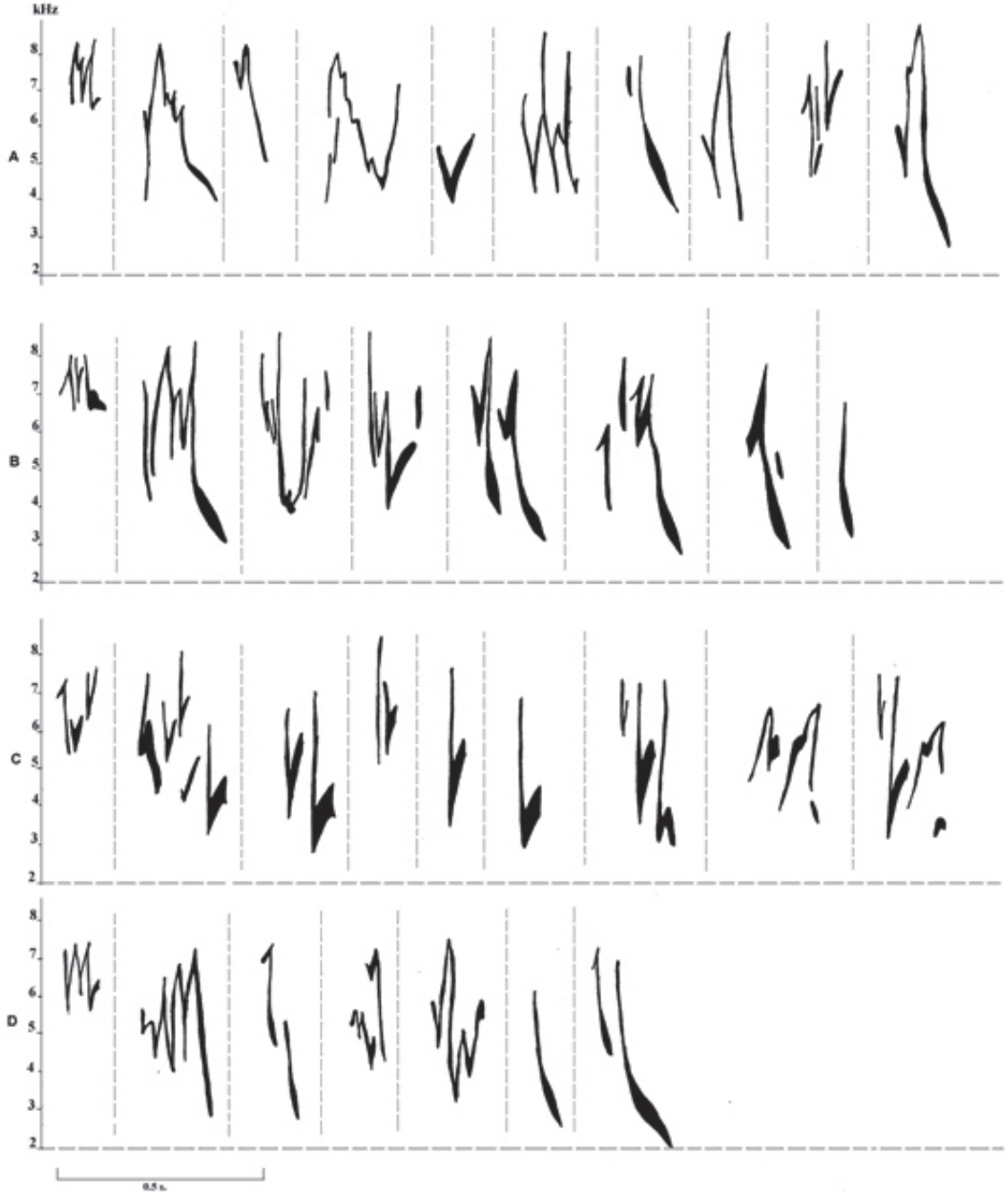

Fig. 4. *Different elements of song in the Greenish Warbler (Phylloscopus trochiloides viridanus). Fine interrupted lines separate one element from another. A, B, C, D — different sets of phrases.*
Рис. 4. *Разные элементы песни зелёной пеночки, тонкая прерывистая линия отделяет один элемент от другого. A, B, C, D — разные комплексы фраз.*

individual, only a few (2–9 for each male) are shared among several males. The number of elements is correlated positively with the number of recorded songs ($R = 0.53$, $p < 0.0002$ Spearman Rang Correlation).

The repertoire of elements varies from one recording to another, but this variability does not depend on the time of day. Some elements disappear from one recording to the next recording but may appear again in another one. For example, in the middle of the breeding season the number of new elements may vary by 25 elements from one recording (about 50 songs) to another. The number of different elements between two recordings made in one day may consist of 23 elements.

In the beginning of the breeding season males sing a small number of elements (the average is

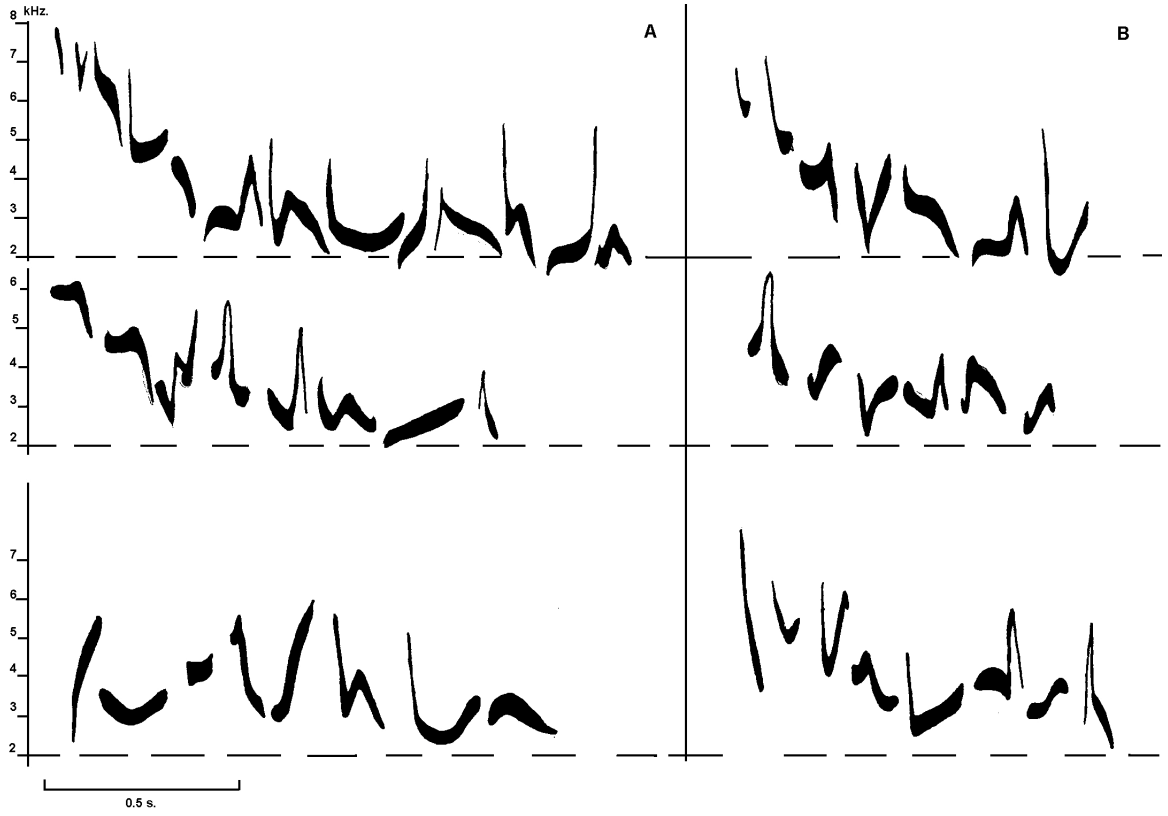

Fig. 5. *The example of different elements of song in the Willow Warbler (Phylloscopus trochilus acredula). The elements which belong to one set of phrases are situated in one line. A — one male, B — another male.*
Рис. 5. *Примеры разных элементов песни пеночки-веснички. Элементы, принадлежащие к одному комплексу, расположены в линию. А — один самец, В — другой самец.*

27.5 ± 7.04). This number increases dramatically at the middle stage of the breeding season (the average is 57.5 ± 8.34), and stays high up to the end (the average is 70.5 ± 7.8). There is the positive correlation between the number of elements and stages of the breeding cycle ($R = 0.67$, $p < 0.0001$, Spearman Rang Correlation).

Number of phrases per song

Wood Warbler. Usually songs consist of two phrases. Rarely this number increases to four (2% of 240 songs) (Table 1).

Greenish Warbler. The number of phrases per song varies significantly (from 1–2 to 30). However, in general about 40–70% of songs consist of 9–12 phrases.

Willow Warbler. The number of phrases per song varies significantly (from 1–2 to 30). However, in general about 40–70 % of songs consist of 8–10 phrases.

Number of elements per phrase

Wood Warbler. The number of similar elements per phrase is 1–40 for the first phrase and 1–45 for the second phrase. In general this number is equal to an intermediate mean of 10–20 elements (67% of all songs) in the first phrase, and 15–25 elements (50% of all songs) in the second. Songs with very short or very long phrases are rare.

The number of similar elements per phrase varies from one song to another. The number of similar elements per phrase also varies from one recording to another. The difference may be significant between recordings of an individual male made on one day and between recordings made on two different days ($p < 0.01$, Kolmogorov-Smirnov, Kruskal-Wallis). At the same time the difference between recordings of an individual male made in the period of territory advertisement and during feeding of fledglings is significant ($p < 0.0001$, Kruskal-Wallis) for the first two recordings and not significant for the other two recordings (fig. 6). In other words recordings of individual males differ one from one another, but this does not seem to be linked to time of day or to stages of the breeding cycle. The same tendency is found also for the second phrase.

In the beginning of the breeding season the difference in the number of similar elements per initial phrase is significant between male N4 and

Table
Таблица

Variability limits of songs in three species of Leaf Warblers
Пределы изменчивости песен у трёх видов пеночек

	Phylloscopus sibilatrix 1000 songs of 8 males 1000 песен 8 самцов	*Ph. trochiloides viridanus* 1000 songs of 9 males 1000 песен 9 самцов	*Ph. trochilus acredula* 2000 songs of 16 males 2000 песен 16 самцов
Number of different elements (repertoire) Репертуар элементов	2–6	33–35	45–200
Number of similar elements per phrase / Число сходных элементов во фразе	1–45	1–6	1–16
Number of phrases per song Число фраз в песне	1–4	1–30	1–30

other males and between male N3 and male N1 ($p < 0.001$, Kruskol-Wallis) (fig. 6). The difference in the number of similar elements per initial phrase is not significant between males N1, N2 and N5. The difference in the number of similar elements per initial phrase is significant between all males ($p < 0.0001$, Kruskol-Wallis) if we compare the summary data on all stages of the breeding season (fig. 6). The same tendency is also found for the second phrase.

Males N1, N2 and N3 bred successfully. Males N4 and N5 were noticed at the test-site during a short time period (4–6 days), after which they disappeared. It is possible that these two males were unmated or advertising the secondary territory. As shown in fig. 6, male N4 had the maximal number of similar elements per phrase, whereas males who bred successfully sung small or intermediate numbers of similar elements per phrase. Hence the ability of a male to attract a female does not seem to be linked to the number of similar elements per phrase.

Greenish Warbler. The number of similar elements per phrase varies little. Phrases consist of 1 or 2–3 similar elements. As a rule the number of elements in a particular type of phrase remains constant both for songs of one male and for songs of different males. Rarely does the number of elements increase to 5–6 (2 %).

Willow Warbler. The number of similar elements varies greatly in the first three phrases (from 1 to 9, rarely 16). The median mean of the element number in first phrases of all males is equal to 2–4. The number of similar elements remains considerably high, up to 5–9 (median — 2) until the eighth or ninth phrase. At the end of the song the number of similar elements per phrase is less variable. Songs with very short or very long phrases are rare.

We have analysed the variability in the number of similar elements per first two phrases. The number of similar elements per first and second phrase for an individual male varies from one song to another. The number of similar elements per phrase for an individual male varies from one recording to another (fig. 7). The difference may be significant between recordings made in one day and between recordings made on two different days ($p < 0.001$). At the same time the difference between recordings of individual males made during different stages of the breeding cycle is significant for some days and not for others. For example, recordings of male N4 made on 23.05.95 in the morning and on 04.06.95 and 08.06.95 in the middle of day do not differ significantly in the number of similar elements per initial phrase (fig. 7). Also there is no difference between recordings made on 26.05.1995 in the morning and on 6.06.1995 in the morning and in the middle of the day. At the same time there is a significant difference between these two groups of recordings ($p<0.001$, Kruskol-Wallis). Besides, the recordings made on 19.06.1995 in the morning and in the evening hours do not differ significantly in the number of similar elements per initial phrase, but these two recordings differ significantly from the recording made on 19.06.1995 in the middle of day. In other words, recordings of an individual male differ from one another, but this does not seem to be linked to time of day or to stages of the breeding cycle.

In the beginning of the breeding season the difference in the number of similar elements per

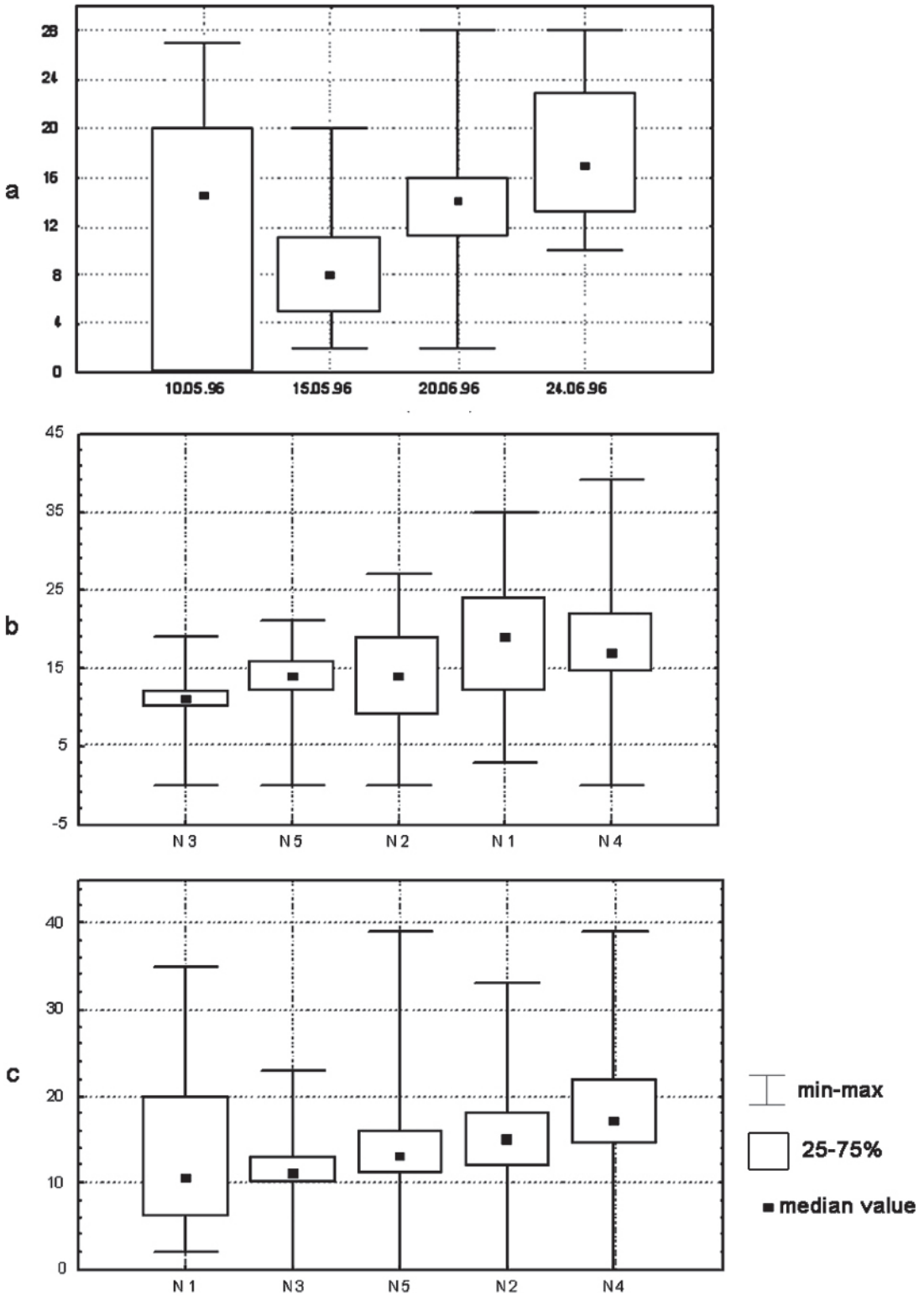

Fig. 6. *The number of similar elements per first phrase in songs of the Wood Warbler.*
*a — different recordings of male N4; 15.05.1996 laid the first egg, 19.06.1996 the fledglings left the nest; * show two recordings, which do not differ one from another; b — the beginning of the breeding season (N4 — 45 songs, other birds — 50 songs); c — the summary data (N1 — 100 songs, N2 — 184 songs, N3 — 105 songs, N4 — 45 songs, N5 — 167 songs).*

Рис. 6. *Число сходных элементов в первой фразе песен пеночки-трещотки.*
*а — разные записи самца N4; 15.05.96 откладка 1-ого яйца, 19.06.96 слётки покинули гнездо; * обозначает записи, которые достоверно не отличаются друг от друга; b — начало сезона размножения (N4 — 45 песен, для других самцов по 50 песен); с — обобщенные данные по всему сезону размножения (N1 — 100 песен, N2 — 184 песен, N3 — 105 песен, N4 — 45 песен, N5 — 167 песен).*

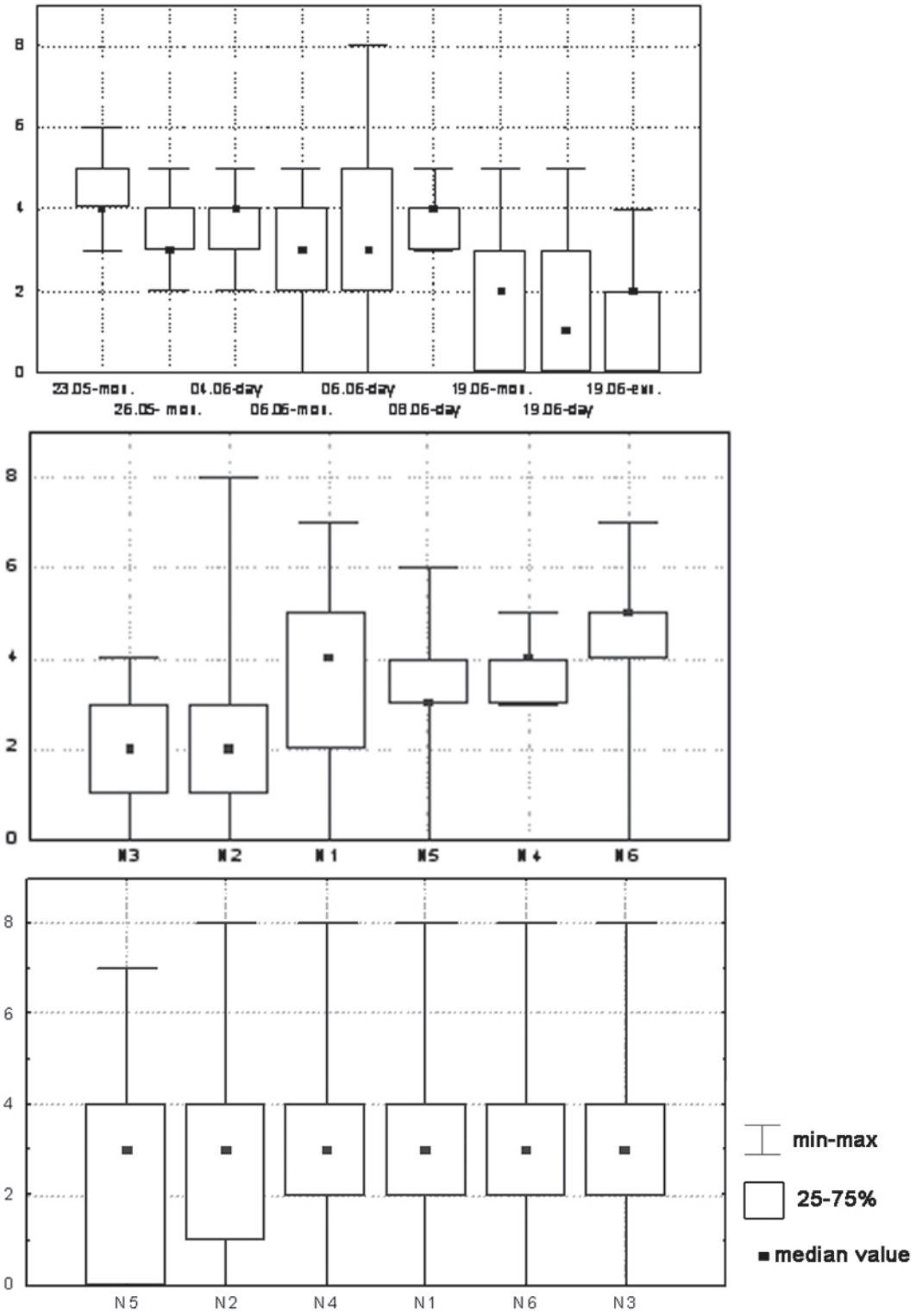

Fig. 7. *The number of similar elements per first phrase in songs of the Willow Warbler.*
a — different recordings of male N4; 25–29.05.1995 laying the eggs by first female, 10.06.1995 young hatching; 23.06.1995 the fledglings left the nest; about 29.05.1995 second female started to lay the eggs; mon. — morning, day — the middle of the day, evn. — evening hours; b — the beginning of the breeding season (50 songs for each bird); c — the summary data (the number of songs for each bird is N1 — 239 songs, N2 — 170 songs, N3 — 436 songs, N4 — 385 songs, N5 — 147 songs, N6 — 165 songs.).

Рис. 7. *Число сходных элементов в первой фразе песни пеночки-веснички.*
а — разные записи самца N4; 25–29.05.95 откладка яиц первой самкой, 10.06.95 вылупление; 23.06.95 — вылет слётков; около 29.05.95 начало кладки у второй самки; mon. — утро, day — дневное время, evn. — вечерние часы; b — начало сезона размножения (50 песен на каждого самца); c — обобщенные данные по всему сезону размножения (число проанализированных песен: N1 — 239, N2 —170, N3 — 436, N4 —385, N5 — 147, N6 — 165).

initial phrases is significant between the males N6 and other males ($p < 0.0001$, Kruskol-Wallis) (fig. 7). There is no difference in the number of similar elements per initial phrase between males N1, N4 and N6 and on the other hand between males N2 and N3. However, there is significant difference in the number of similar elements per initial phrase between these two groups ($p < 0.001$, Kruskol-Wallis). When we compare the summary data on all stages of the breeding season as show in fig 7, there is no difference in the number of similar elements per initial phrase between males N1, N3, N4, and N6, and on the other hand between males N2 and N4. However, there is significant difference in the number of similar elements per initial phrase between these two groups ($p < 0.001$, Kruskol-Wallis).

Males N1, N2, N5 and N6 bred successfully and fed 3, 4, 5 and 5 fledglings respectively. The female of male N3 laid 5 eggs, but she was eaten by a predator during the hatching stage. Male N3 advertised its territory up to the end of the breeding season but remained alone. Male N4 has two females at his territory. The first female successfully fed 5 fledglings. The male participated in feeding the young from the first nest. There was a Cuckoo (*Cuculus conoris*) in the second nest. Male N4 did not feed the cuckoo. Since six males were able to attract females, the ability of a male to attract a female does not seem to be linked to the number of similar elements per phrase. As shown in fig. 7, breeding success does not seem to be linked to the number of similar elements per phrase either. The polygamous male has a big, but not the biggest number of similar elements per initial phrase. Hence, the ability to attract a secondary female may be partially linked with the number of similar elements per phrase, but this link is not strong.

Phrase combination

Wood Warbler. Most males sing two song variants. Each male's initial phrase is usually the same for both variants. Two males sang two variants of second phrase (for example the song A–B and A–C). Very rarely the sequences A–B–C were noticed (fig. 2). The first (0.7 % of all songs) or the second phrase (7.2% of all songs) may be skipped. From time to time the song may begin or finish with a series of calls.

Greenish Warbler. In Greenish Warbler songs the number of different elements (different types of elements) is not large in the first phrases, its number increases dramatically in the middle phrases, and decreases a little in the final phrases (fig. 8). Usually the appearance of one type of element in the first phrase (for example A) leads to the regular, successive performance of other types of elements, which are attached to the first one in the following phrases. The tendency to sing sets (complexes) of 4–11 phrases was found (fig. 2). The probability of singing the whole complex varies from 0.7 to 1. It is more probable (0.85–1) that a bird will sing the first (1–5) phrases of the set than that he will sing the last phrases. Sometimes the probability of singing the set of phrases decreases to 0.3–0.5. Every male sings 3–4 sets of phrases, which are common to all birds recorded. Every set of phrases can be sung as one song. However, male Greenish Warblers may sing one song with up to 4–5 different sets of phrases (table 1). The alternation of sets in the song is relatively free (fig. 2).

We did not find any correlation between phrase combination and time of day. In one recording a bird may repeat one set of phrases without any variation up to 25 times, and after that sing 1–3 copies of another set of phrases or some variations of the first set. In the next recording made on the same day a bird may sing long songs which combine different sets of phrases and very rarely repeat the same set of phrases several times (2–5).

The sets of phrases are relatively strong in the beginning of the breeding season (until the young hatch), and the number of different elements per phrase is small (fig. 8). In the middle of the breeding season the number of different elements in each phrase increases (fig. 8). In other words, songs became more variable. At the end of the breeding season the number of different elements in each phrase decreases and songs again became more stable. However, these differences in song structure are not significant ($p > 0.05$, Spearman Rank Correlation, Kolmogorov-Smirnov).

Willow Warbler. In Willow Warbler songs the number of different elements (different types of elements) is not large in the first phrases, its number increases dramatically in the middle phrases, and decreases a little in the final phrases (fig. 2). Usually the appearance of one type of element in the first phrase (for example A) leads to the regular, successive performance of other types of elements which, are attached to the first

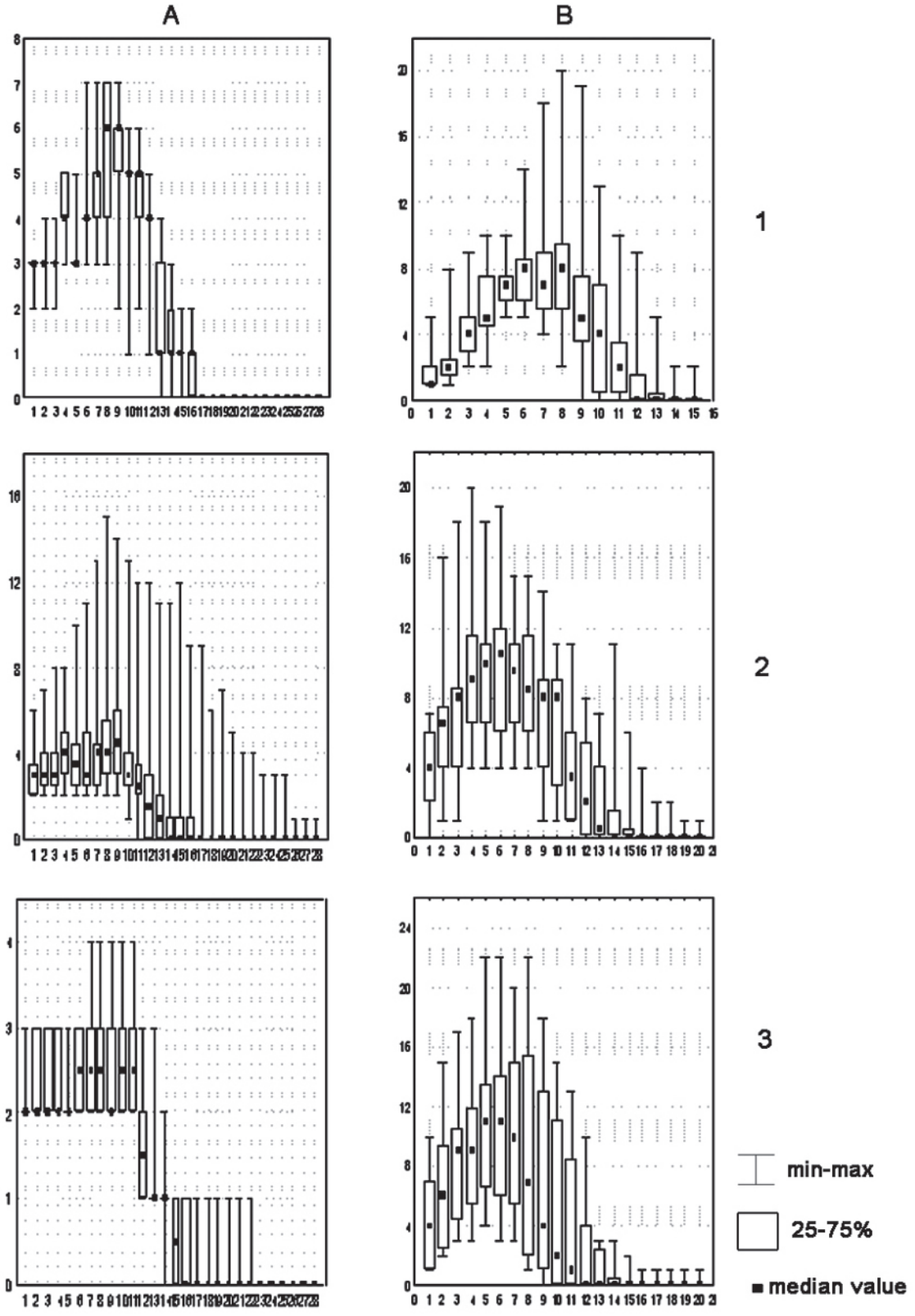

Fig. 8. *The number of different elements (types of elements) in phrases of songs of: A — Greenish Warbler (Phylloscopus trochiloides viridanus), B — Willow Warbler (Ph. trochilus acredula); 1 — the beginning of the breading season; 2 — the middle of the breeding season; 3 — the end of the breeding season. The axe Y shows the number of different elements in phrases; the axe X shows the phrase numbers.*

Рис. 8. *Число разных элементов (типов элементов) во фразах песен: А — зелёной пеночки (Phylloscopus trochiloides viridanus), В — пеночки-веснички (Ph. trochilus acredula); 1 — начало сезона размножения; 2 — середина сезона размножения; 3 — конец сезона размножения. По оси Y показано количество разных элементов во фразах; по оси X порядковый номер фразы.*

one in the following phrases. The tendency to sing sets (complexes) of 4–8 phrases was found. The probability of singing the whole complex varies from 0.4 to 6. It is more probable (0.7–1) that a bird will sing the first (1–5) phrases of the set than that he will sing the last phrases. Sometimes the probability of singing the set of phrases decreases to 0.1. Different males sing from 2 to 7 sets of phrases, which are usually individual to the single bird. Every set of phrases can be sung as one song. Sometimes, male Willow Warblers also may sing one song with up to 2–3 different sets of phrases. The alternation of sets in the song is relatively free (fig. 2).

We did not find any correlation between phrase combination and time of day. The song structure may vary greatly in one recording and remain relatively constant in another recording made on the same day.

The sets of phrases are relatively strong in the beginning of the breeding season (until the young hatch), and the number of different elements per phrase is small (fig. 8). In the middle of the breeding season the number of different elements in each phrase increases, the songs become more variable, and sets of only 2–3 phrases may remain (fig. 8). At the end of the breeding season the number of different elements in each phrase dramatically increases, the songs become quite variable, and sets of phrases nearly disappear (fig. 8). The difference in song structure is significant between the beginning, the middle, and the end of the breeding season ($p < 0.05$, Kolmogorov-Smirnov, Spearman Rank Correlation). Interestingly, the one unmated male sang sets of phrases throughout the breeding season.

Discussion

Our results show that study of the variability of four levels of song structure (1. Repertoire of elements; 2. Number of similar elements per phrase; 3. Number of phrases per song; 4. Combination of phrases) allows the comparison of different species of birds. Variability across four levels of song structure was found in all three *Phylloscopus* species.

All three species strongly differ from each other in the form of frequency modulations and repertoires of elements (table 1). The variability in the number of similar elements per phrase is most pronounced in Wood Warbler, less in Willow Warbler, and is practically absent in Greenish Warbler (table 1). Nevertheless, in some situations the variability in the number of elements per phrase of Willow Warbler songs becomes equivalent to the variability of their number in Wood Warbler (table 1). Sometimes we noticed the increase/decrease in the number of similar elements per phrase in Greenish Warbler. Variability in the quantity of phrases and in phrase combination is most pronounced in the songs of Greenish and Willow Warbler. While the combination of phrases is greatly pronounced in the songs of Willow Warbler, the combination of sets of phrases is manifested best in songs of Greenish Warblers. It is interesting to notice that in some cases the combination of phrases is observed in the songs of Wood Warbler. Nevertheless, despite the specific song variability, sometimes changes in song structure of one species are realised in a way characteristic for another species.

The great variation at all levels of song structure found in all three species allows us to suppose that the concept of song type poorly describes the song versatility of these species. This was shown earlier for Willow Warbler (Gil, Slater, 2000). It seems to be more productive to describe the versatility of different levels of song organisation, which lets us compare different species of birds. This approach may be useful due to the fact that the variation in the number of elements per phrase, as well as the versatility of phrase combination, have been described for many passerine species (Dobson, Lemon, 1976; Панов, Костина, 1978; Slater, Ince, 1979; Slater et al., 1980; Kroodsma, 1989; Hultsch, Todt, 1989).

It is well known that the ability to sing, as well as the activity of singing and repertoire size of some species, are positively correlated with a high level of testosterone and other hormones in blood (Nottebohm et al., 1987; Canady et al., 1988; Beletsky et al., 1990; DeVoogd et al., 1991; Cynx, Nottebohm, 1992; Lampe, Espmark, 1994; Wingfield, 1994; Wingfield, Hahn, 1994). In songs of Willow Warbler the repertoire of elements and the phrase combination change significantly through the breeding season. This fact allows us to suggest that these song characteristics may reflect the level of sexual hormones in blood. Thus, it is interesting to note that the repertoire of elements in

songs of single male Willow Warblers did not increase dramatically towards the middle and end of the breeding cycle, and the structure of sets of phrases remained stronger than the structure of sets of mated males (Goretskaia, 2005; Goretskaia, 2007). These facts may reflect the difference in the hormonal level between mated and single males. Moreover, the structure of sets of phrases in songs of the single polygamous male also remains more constant than the song structure of other mated males, which may also be related to a higher level of sexual hormones (Goretskaia, 2005; Goretskaia, 2007).

Our results show that the repertoire of elements is not linked to time of day, female attraction, breeding success, or stage of the breeding season for the Wood and Greenish Warbler. The number of different elements per phrase is not linked to time of day, female attraction, or the stages of the breeding season for the Wood, Greenish, and Willow Warblers. Likewise, phrase combination is not linked with time of day, female attraction, or stages of the breeding season for the Wood and Greenish Warblers, and poorly linked for the Willow Warbler. However, all these characteristics vary greatly in songs of the three studied species. This may be related to the other functions of bird song. It is well known that one of the functions of bird song is support of neighbour relationships and the structure of the nesting community (Catchpole, Slater, 1995; Searcy, Yasukawa, 1996). That leads us to suppose that the great variation in the number of elements per phrase and in phrase combination, which appears to be poorly linked to individual features, to time of day, and to the stages of the breeding cycle, reflects male-male interaction and provides some information for neighbouring males. Recently it has been shown that the initials phrases of Willow Warbler songs became longer in the high density population as well the songs as a whole became longer and more variable (Goretskaia, 2004). The significant role of within-song type variations in signalling aggression level was also shown in the Ortolan Bunting *(Emberiza hortulana)* (Osiejuk, 2001). Moreover, it was shown that the Wood Warbler reaction to playback depends on structure (the number of similar elements and the tempo) of the second phrase (Goretskaia, Vallet, 2000). According to these the next question has to be the studying of the versatility of different song levels in relation to interaction between males.

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Изменчивость структуры песни у трёх видов пеночек рода *Phylloscopus*: пеночки-веснички (*Phylloscopus trochilus acredula*), пеночки-трещотки (*Ph. sibilatrix*) и зелёной пеночки (*Ph. trochiloides viridanus*)

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Для воробьиных птиц характерно исполнение изменчивой по структуре песни, причём, хорошо известно, что в дополнение к исполнению разных типов песен, птицы могут вносить вариации и в сами типы (Kroodsma, 1982; Searcy et al., 1995; Hailman, Ficken, 1996). Изменения тонкой структуры песен были изучены у трёх представителей рода пеночек: *Phylloscopus trochilus acredula* (2000 песен), *Ph. sibilatrix* (1000) и *Ph. trochiloides viridanus* (1000). Изучение структуры песни проводили на четырёх уровнях её организации: 1) репертуар элементов; 2) число сходных элементов во фразе, 3) число фраз в песне; 4) комбинирование фраз. В ряду пеночка-трещотка, зелёная пеночка и пеночка-весничка изменчивость на каждом уровне составляет соответственно: 1) до 6, 35 и 200 различных элементов, 2) до 40, 6 и 10 сходных элементов во фразе, 3) до 4, 25 и 25 фраз в строфе, 4) комбинирование фраз слабее выражено у пеночки-трещотки. У зелёной пеночки и пеночки-веснички описана тенденция к исполнению комплексов из 3–5 фраз. Изменчивость в числе сходных элементов во фразе, в числе фраз в песне и в комбинаторики фраз, видимо, не связана напрямую со временем суток, способностью привлекать самку и фазой репродуктивного цикла. Обсуждаются возможные функции изменчивости тонкой структуры песен у птиц.