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The acoustic behaviour of male *Isophya camptoxypha* bush crickets (Orthoptera: Tettigonioidea) in the Uzh river valley: preliminary findings

Andriy KOVALCHUK[1] and Taras PUSHKAR[2]

[1]*Department of Zoology, Faculty of Biology, Uzhhorod National University, Narodna Square, 3, Uzhhorod City, 88000, Zakarpattya, Ukraine; e-mail: a_koval54@ukr.net (corresponding author)*
[2]*Schmalhausen Institute of Zoology, NAS of Ukraine, Bohdan Khmelnitsky street, Kyiv, 01054, Ukraine*

Abstract: The research article presents a study of acoustic behaviour of the bush cricket *Isophya camptoxypha* from Ukrainian Carpathians. However, it has also been discovered in forest meadows located in the Uzh River valley, which is part of the Danube catchment basin. The article discusses the unique stridulations of this species in vivo and in natural settings, as well as the acoustic interactions between male bush-crickets during duet singing. This study provides valuable insights into the intricate acoustic behaviour of *Isophya camptoxypha*.

Key words: acoustic signals, singing in duet, Zakarpattya

INTRODUCTION

Ten "solid" species (one occur in two subspecies) of the bush-cricket genus *Isophya* Krauss, 1902, have been reported in Ukraine, and four species of this genus have been confirmed in Zakarpattya province based on investigations conducted by Bey-Bienko (1954, 1964), Harz (1969), Heller et al. (2004), Zhantiev et al. (2017), Lykovych & Kovalchuk (2019), and Kovalchuk (2023). Isophyas are insects that typically do not migrate actively, with one notable exception known for *Isophya taurica* (Bey-Bienko, 1954). Long-term population survival and large fluctuations in population size distinguish these insects in their small local habitats. Isophyas appear to benefit greatly from active acoustic communication for long-term survival of their populations in such remote locations. As a result, scientists have paid attention to this characteristic, and over the past 50 years, a flurry of research into their singing has taken place (Zhantiev & Dubrovin 1977, Heller 1988, Nagy et al. 2003, Orci et al. 2010, Iorgu & Iorgu 2011, Iorgu 2012, Guzik & Guzik 2022).

One of the most important aspects of this kind of research is the possibility of taxonomic identification of species with very similar morphologies, like the "camptoxypha" subgroup of the "*Isophya pyrenea* species complex" based on the males' songs. This subgroup derives its name from *Isophya camptoxypha* (Fieber, 1853). It is composed of several species that are morphologically similar to each other (Chobanov et al. 2013), *I. camptoxypha* (Fieber, 1853), *I. ciucasi* Iorgu et Iorgu 2010, *I. dochia* Iorgu 2012, *I. nagyi* Szövényi, Puskás et Orci 2012, *I. posthumoidalis* Bazyluk 1971, *I. sicula* Orci, Szövényi et Nagy 2010, and *I. bucovinensis* Iorgu, Iorgu, Szövényi et Orci, 2017. In a variety of habitats, members of the "camptoxypha" subgroup can be found close to each other (Iorgu 2012: p. 15, fig. 75). Iorgu (2012) discusses as well on the high intra- and interpopulational morphological variability of the "camptoxypha" subgroup, which makes identification of individuals of *I. camptoxypha* (=*I. brevipennis*) from older collections extremely challenging, if not impossible (Puskás 2015). As a result, oscillographic analysis of acoustic signals appears to be the primary method for recognizing potentially new and closely related species within this subgroup (Iorgu 2012).

Until now, only two Zakarpattyan *Isophya* species have had their acoustic signals studied: *Isophya stysi* Čejchan, 1957 (Zhantiev & Dubrovin 1977, Kovalchuk 2023) and *Isophya posthumoidalis* Bazyluk, 1971 (Kovalchuk 2023).

According to Iorgu et al. (2018), the acoustic signals of males in the "camptoxypha" subgroup can be classified into three clusters. *I. camptoxypha* males' songs belong to the first cluster, consisting of a single syllable that may be repeated in a very long series. The primary goals of our study were to investigate whether there are significant differences in individual characteristics of male songs from different parts of the Uzh Valley, and to examine the peculiarities of solo and duet singing by male bush crickets.

MATERIAL AND METHODS

Four live males of *I. camptoxypha* were collected in 2017 from two locations: Mt. Ostra in the Polonynian Beskids and Mt. Stinka in the Verkhovyna Dividing Range. These locations are situated in the Eastern Beskids, a geographical transliteration commonly used in geological and geographical research, as exemplified by Földvary (1988) (see Figs 1 & 2, and Table 1).

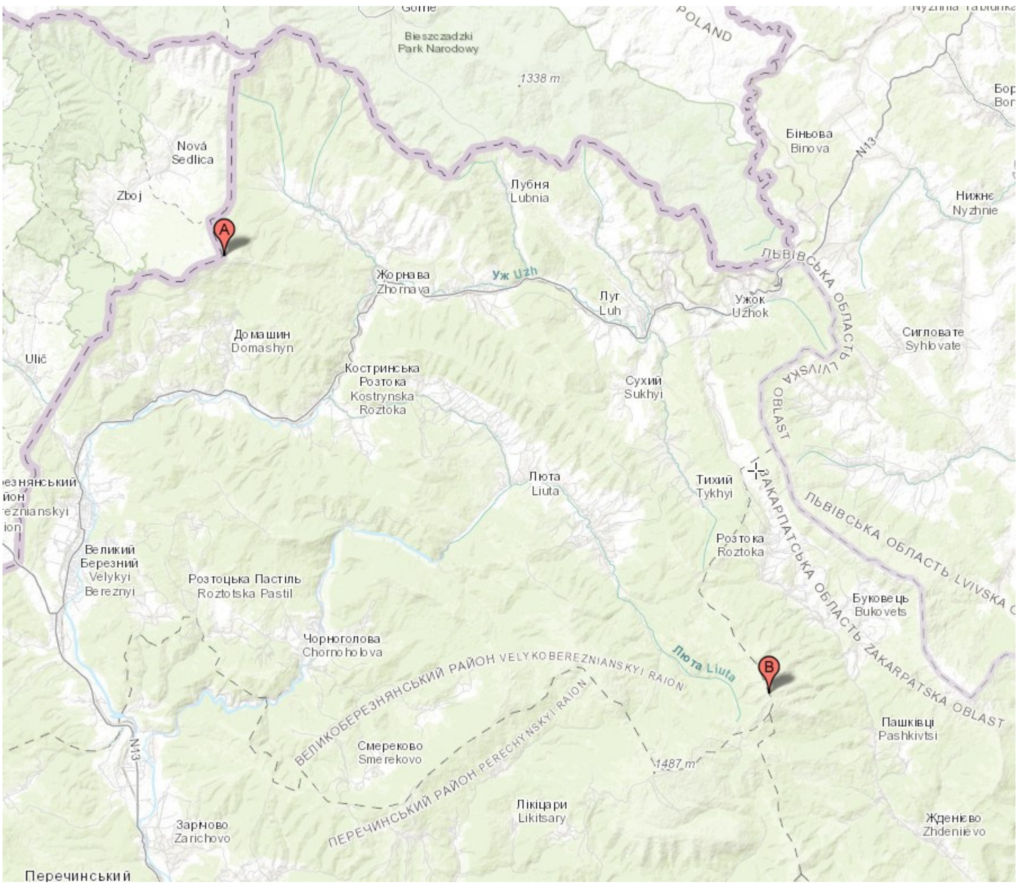


Fig. 1. *Isophya camptoxypha* locations in the Uzh river valley: A – Mt. Stinka, B – Mt. Ostra (in ACME Mapper 2.2.).

Acoustic recordings were made to analyse the singing characteristics of the males, both when they were singing solo and when they were engaged in duet singing. Male *I. camptoxypha* bush-crickets

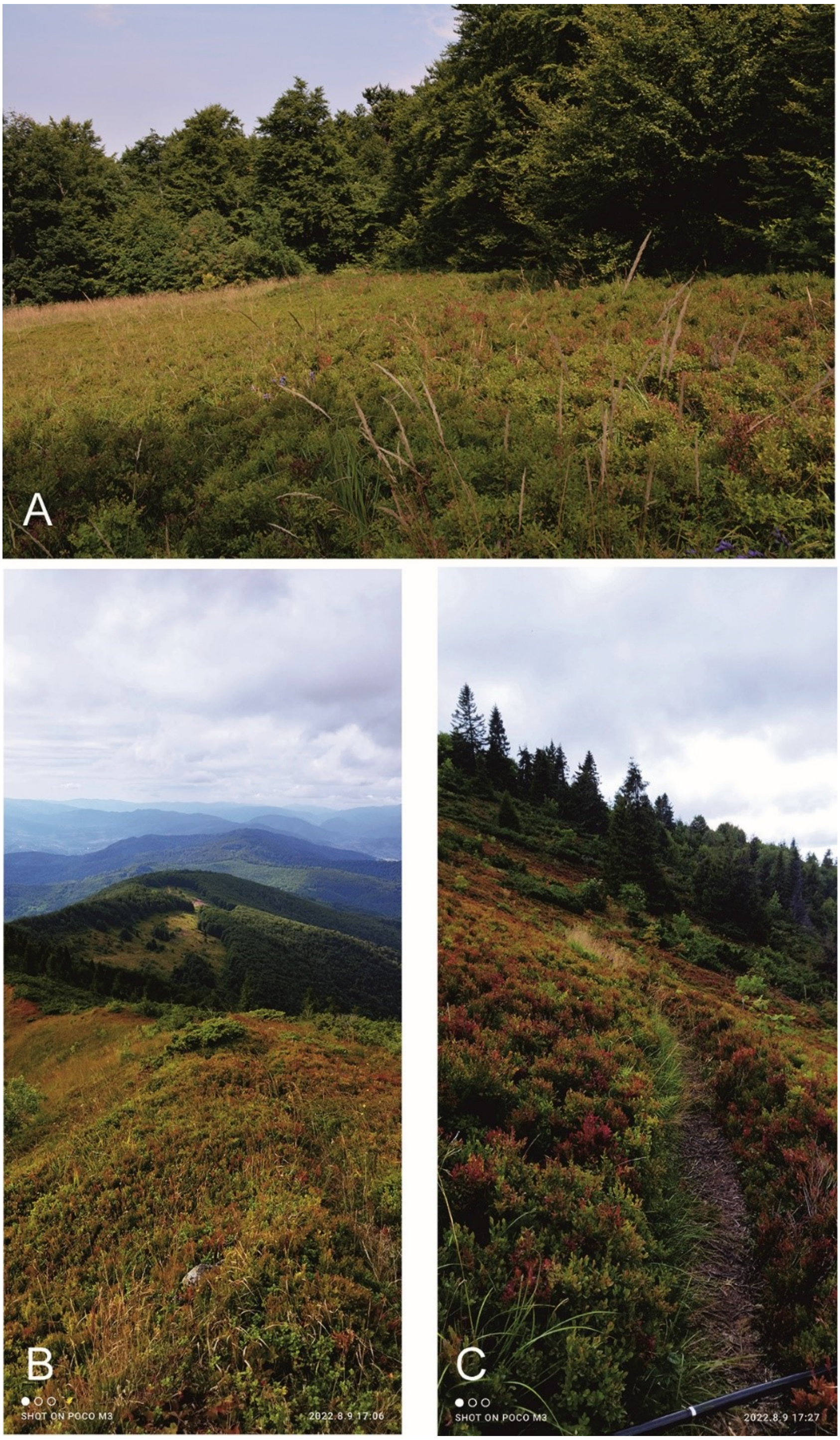


Fig. 2. Typical habitats of *Isophya camptoxypha*: A – Mt. Stinka (Aug 22, 2019), B, C – Mt. Ostra (Aug 9, 2022). Photos by A. Kovalchuk.

typically produce songs composed of several series of syllables. In our study, the characteristics of these syllable series were measured between 12 and 35 times, while the characteristics of individual syllables were measured between 190 and 361 times per male. All measurements, except for those of one male in its natural environment (the measurements were carried out from 4pm until 5pm), were conducted in a laboratory where the bush crickets were housed in plastic food cages of 5–10 litres capacity, with natural forage plants provided to aid their adaptation. The feeding plants were sprayed by water to keep suitable humidity for bush-crickets. Temperature (between 25–27 degrees Celsius) was not actively regulated during this series of experiments but remained relatively stable compared to natural conditions, especially in September.

Table 1. Locations where the bush-crickets where caught.

Locations	Date	Geographical location	Altitude, m	Males
Stinka	Aug 06, 2017	N 49.00664 E 22.54609	1003	2
Stinka	Sep 18, 2017	"		1
Ostra	Sep 11, 2017	N 48.83194 E 22.87805	1250	1
Total				4

For our bioacoustic investigation, we used a TASCAM DR-40 linear recorder, sometimes in conjunction with a 3 m-long RC-10 cable for distant recording. This allowed us to measure frequency responses up to 48 kHz, which was sufficient to evaluate most of the male bush-cricket song characters and their spectra (Iorgu & Iorgu 2011: p. 443, fig. 7-3; Zhantiev et al. 2017).

All data were obtained using Audacity 2.1.3, and noise cleaning was carried out usually in Adobe Audition 1.5. The resulting data were analysed using STATISTICA ver. 10, and the figures in the article were produced using Avisoft SASLab Lite, ver. 5.2.15, Audacity, ver. 3.3.3, FastStone Capture for Windows, ver. 7.7, and CorelDRAW X6.

When comparing statistical indicators, we used three levels of confidence in the observed differences between the features (Siegel & Wagner 2022): a statistically significant test result (if $p < 0.05$), a highly statistically significant result (if $p < 0.01$), and a very highly statistically significant result (if $p < 0.001$).

RESULTS

Bioacoustic characters

Isophya camptoxypha male song pattern from Ukrainian Carpathians, tested by us under controlled conditions, resembles that described by Heller et al. (2004), Orci et al. (2010), and Iorgu et al. (2017, 2018). A discrete song unit consists of one or more series of syllables (Ss) (Fig. 3A). Each Ss can be uniform or sometimes subdivided by gaps (e.g., 'AIAI...AAAAA..AA.AAA..AAA') and may include initiating syllables (AI) before a somewhat longer gap without after-clicks, as well as smaller "closing" syllables (CS) at the end (Fig. 3B).

To conduct statistical comparisons and draw conclusions, we identified the following indicators in a male calling song (Fig. 3A):

a) Syllable (Syl): one complete cycle of tegmina movement, consisting of a row of discrete sound impacts known as impulses, each corresponding to a tooth on the oscillogram (Figs. 3C, 4A). It is usually followed by one or rarely two separate impulses, the after-clicks, whose period duration is calculated from the end of a syllable's main body, in milliseconds (A-c).

b) Syllable duration (SD), in ms (Fig. 4A).

c) Syllable peak frequency (SPF), in kHz (Fig. 4B).

d) Number of impulses (NI) in a syllable (Fig. 4A).

e) Syllable repetition period (SRP), in ms: the time elapsed from the beginning of a syllable to the beginning of the next syllable.

f) Series of syllables (Ss): a natural sequence or series of syllables, sometimes interrupted by short gaps (1–2 seconds), especially in the presence of so-called initial syllables. The number of syllables in a series (NSs) was also calculated. This variable is distributed log-normally and requires logarithmic transformation (Fig. 5 and Table 2).

g) Duration of a male response (DMR), in ms: measured during duet singing of males, this is the distance between the initial and initiated male syllables in the elementary duet cycle and is dependent on dominance.

The large number of valid observations for these variables allowed us to draw preliminary conclusions about possible directions for further research.

Solo call songs of males

Table 2 presents the main statistical indicators for individual singing males. The table reveals that there are significant differences in the first five indicators, while the number of syllables in a series (NSs) is a more variable indicator that may have limited value, particularly since it can be influenced by factors such as the time of day when the measurement was taken.

Table 2. Characteristics of solo call songs of *I. camptoxypha* males. Note: Male #M1' is Male #M1 *in natura*. Durations in ms. All abbreviations used in the tables are explained in the text. Differences between Type 1 and 2 are explained in the subsection "Individual differences".

No	Characters	n	$\overline{X}$	±S	Min	Max
1.	Male 1, caught 06.08.2017, Mt. Stinka loc. A, *in vivo*. Type 1					
	SD	300	75	7	64	88
	SPF	300	22.1	0.6	21	24
	NI	300	25.9	3.1	20	32
	1st A-c	162	162	25	104	242
	SRP	292	512	63	387	866
	NSs (lnX)	40	18(2.89)	3(1.04)	1	121
2.	Male 2, caught 06.08.2017, Mt. Stinka, loc. A, *in vivo*. Type 1					
	SD	325	60	4	50	68
	SPF	325	21.8	0.9	20	24
	NI	325	23.3	1.3	21	28
	1st A-c	321	126	10	70	218
	SRP	320	445	41	354	609
	NSs (lnX)	58	37(3.62)	4(1.32)	2	1072
3.	Male 1', caught 06.08.2017, Mt. Stinka loc. A, *in natura*. Type 1					
	SD	190	73	6	47	87
	SPF	190	22.6	1.5	19	29
	NI	190	29.2	2.0	25	34
	1st A-c	107	149	12	117	197
	SRP	181	513	66	380	696
	NSs (lnX)	13	9(2.10)	4(1.34)	1	47
4.	Male 3, caught 18.09.2017, Mt. Stinka, loc. A, *in vivo*. Type 2					
	SD	361	61	4	51	74
	SPF	361	22.5	1.3	21	25
	NI	361	21.2	1.5	15	24
	1st A-c	179	139	10	117	182
	2nd A-c	24	210	55	162	450
	SRP	353	386	32	322	643
	NSs (lnX)	14	32(3.47)	2(0.56)	10	57
5.	Male 4, caught 13.09.2017, Mt. Ostra, loc. B, *in vivo*. Type 1					
	SD	305	63	6	39	79
	SPF	305	24.2	0.7	21	26
	NI	305	20.7	2.6	11	28
	1st A-c	217	140	12	103	198
	SRP	296	380	53	305	867
	NSs (lnX)	34	21(3.04)	2(0.71)	4	79

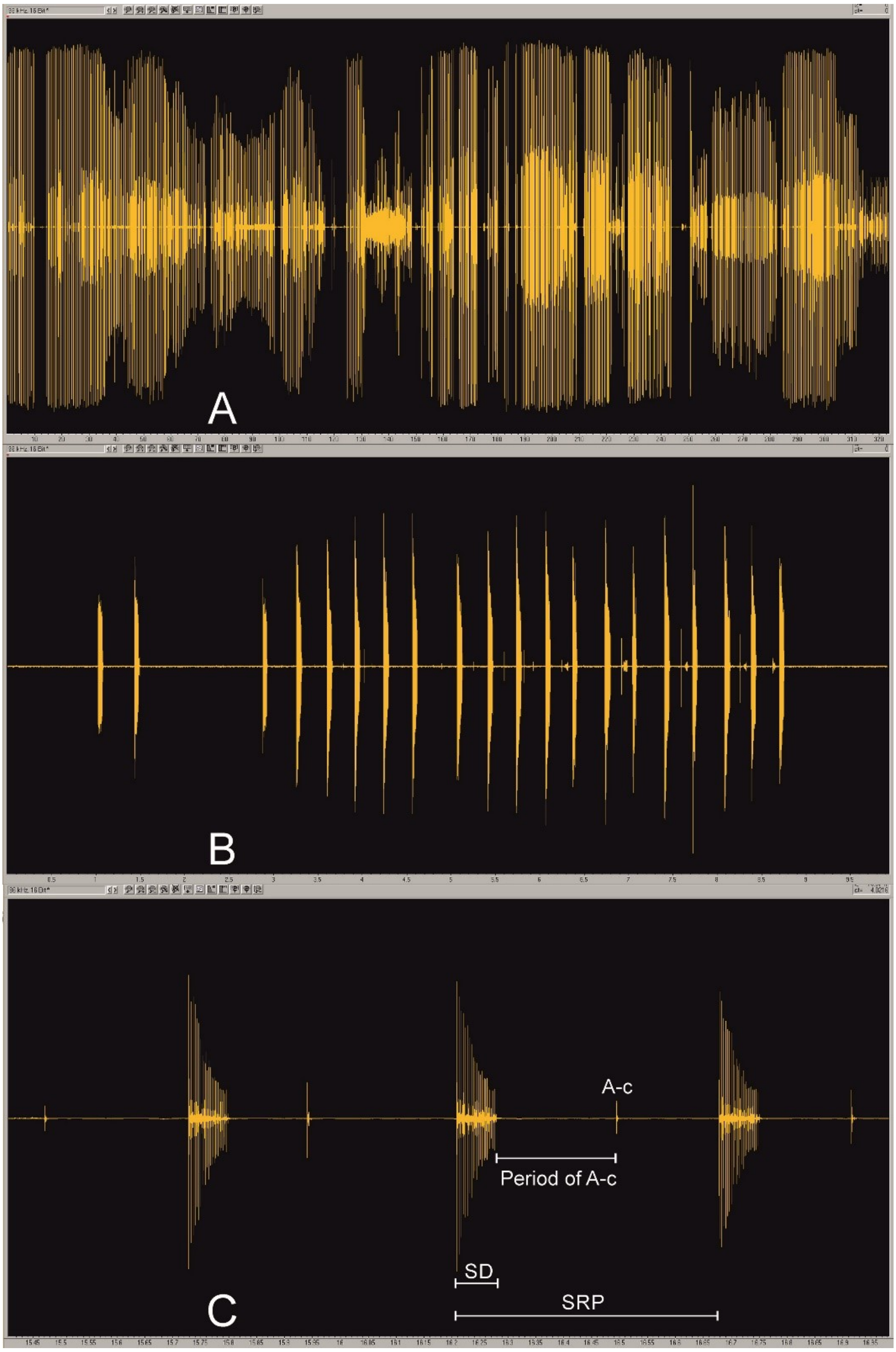


Fig. 3. Song of *I. camptoxypha* males: A – oscillogram of a song of #M1 from Mt. Stinka (file 170807_0128S34D12, recorded *in vivo*, 7 Aug 2017); B – an Ss of a male's song, Mt. Ostra (file 170914_0526_rep, recorded *in vivo*, 14 Sep 09.2017); C – the first three syllables from an Ss of #M1', Mt. Stinka (file 170806_0083S34D12, recorded *in natura*, 6 Aug 2017).

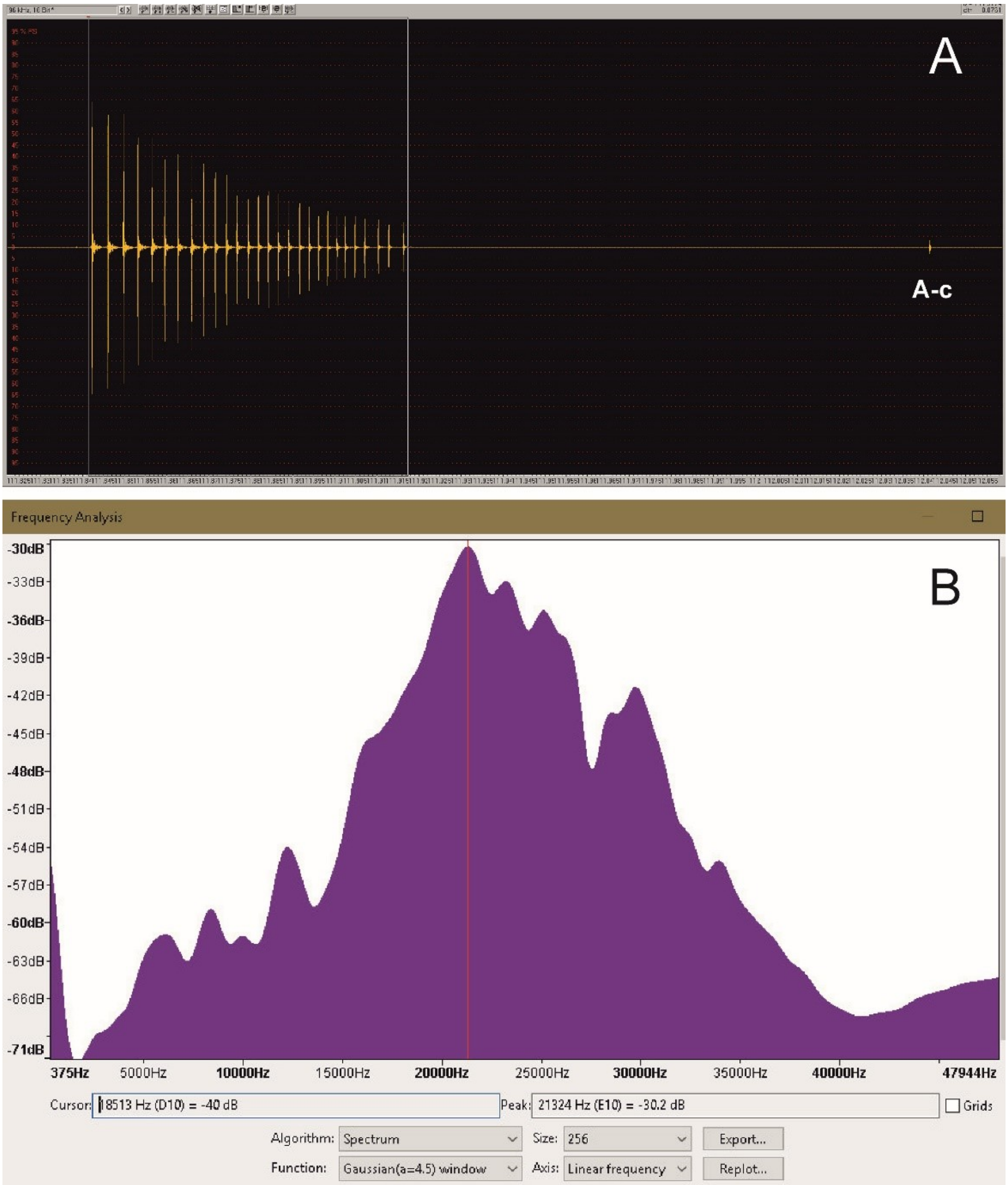


Fig. 4. Characteristics of *I. camptoxypha* male song: A – typical syllable of the song with 28 impulses (NI) and an after-click (A-c) on the right, with the main body duration (SD) indicated by two vertical lines. The oscillogram has been cleaned of noise. This example is from #M1' recorded on Aug 6 in natura at Mt. Stinka. B – spectrum of an Ss from #M4 (file 170919_0613), with a peak frequency of 21.3 kHz indicated by the red line in Audacity 3.2.5.

Individual differences

Exploring the uniqueness of each male's song is essential, necessitating the identification of key parameters that best distinguish individuals. Within this context, the reliability of these distinctions becomes a paramount criterion for assessing each male's 'individuality.' For instance, we considered Male 1 from Mt. Stinka as a separate individual and conducted both *in natura* and *in vivo* acoustic signal measurements to determine if his stridulation uniqueness persisted under experimental conditions. Additionally, factors such as season, weather, altitude, and environmental temperature can exert influence. Consequently, distinct local singing patterns may develop among geographically isolated groups of bush-crickets.

It should be noted that all males can be divided into two groups based on the number of after-clicks in a syllable: Type 1, with one after-click after the main syllable body (SD), and Type 2, with two after-clicks.

The most critical individual indicator is SD, which was found to be highly significant and unique to each male ($p < 0.001$). The number of impulses (NI) in SD is equally important, and differences between individual males in NI were also highly significant ($p < 0.001$).

The first A-c of the bush cricket under study is characterized by a distinct, separate sound impulse that follows the main syllable of the male song. This feature is observed after almost every syllable, with an average range of distance values between 126 and 162 ms (Table 1). Additionally, males with longer SRP exhibit a later occurrence of the after-click.

Less commonly, the second after-click is present in fewer than 10% of all syllables, and not all males exhibit it in their songs (Table 2). The second after-click occurs at a distance that is one and a half times further from the main syllable than the first and does not show any significant correlation with the first after-click.

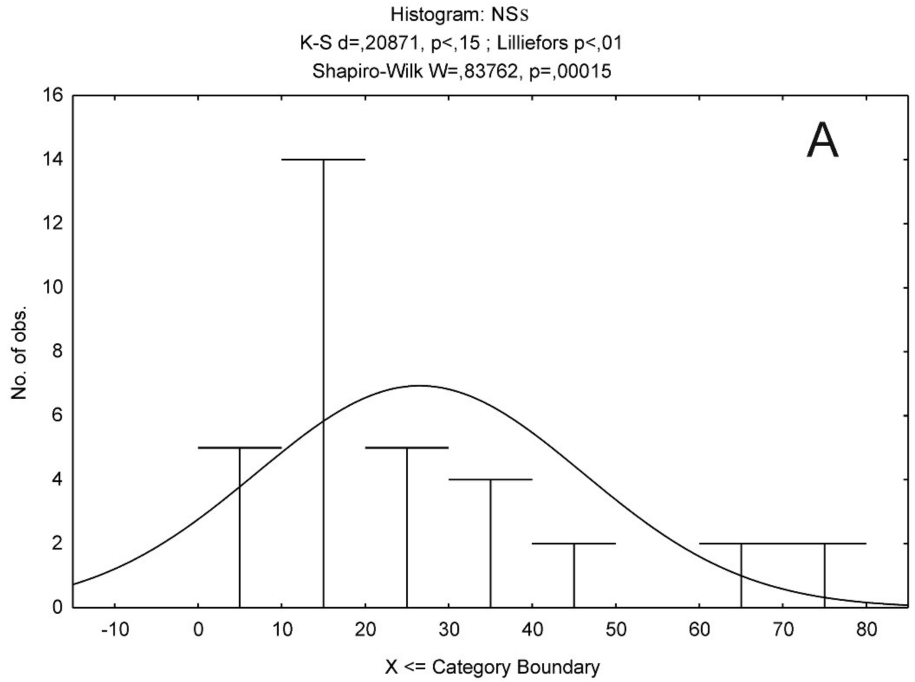
In males captured during the autumn season (#M3 and #M4), there was no statistically significant difference in the A-c periods. However, in all other cases, differences among males in A-c were highly significant ($p < 0.001$). Notably, #M3 (type 2) and #M4 (type 1) males exhibited differences in syllable type (as shown in Table 2). Therefore, it can be concluded that both A-c (after-click) duration and syllable type play a crucial role in identifying individual male bush crickets.

The maximum frequency spectrum of a song is an important indicator, but the question is how to measure it. Should we find the maxima of each syllable's main body in a song or consider the song as a whole (Ss)? Experimental findings showed that SPF (syllables' peak frequency) values are significantly underestimated when considering Ss (Fig. 4B, Table 2).

As it turned out, only in one case there were no differences in SPF, namely between males from Mt. Stinka: #M1' and #M3. However, in all other cases, the differences were highly significant. Thus, SPF is as well powerful indicator suitable for describing individual males of *I. camptoxypha*.

The syllable repetition period (SRP) also proved to be good indicator of male individuality. In only one case, for male #M1 *in vivo* and *in natura* (#M1'), there were no differences. In all other pairwise comparisons, differences were observed with varying degrees of significance. Therefore, this indicator can also be used as an additional one in characterizing the singing of individual males.

The comparison of male from Stinka Mountain's singing *in natura* (#M1') and *in vivo* (#M1) produced intriguing results (Table 2). Firstly, the syllable duration for this male was statistically significantly longer in laboratory trials than in field data ($p < 0.001$). At the same time, the differences from other males in this indicator are evidently (Table 2) much more significant! Secondly, there was a highly significant reduction in laboratory SPF when syllable duration decreased (correlation r is significant at the 0.001 level), which did not occur in nature. Thirdly, compared to all other *in vivo* measurements, this male's syllable impulse count was significantly higher in nature. This raises the question: how is the length of the syllable controlled in males' singing? Is it primarily caused by the quantity of impulses or the alteration in the gap between impulses? The relationship between the number of impulses and syllable duration is also less apparent in natural settings than in the laboratory (correlation r is significant at 0.001 level). Thus, the logical conclusion is that numerous processes regulate the length of the syllable in male songs under normal circumstances.



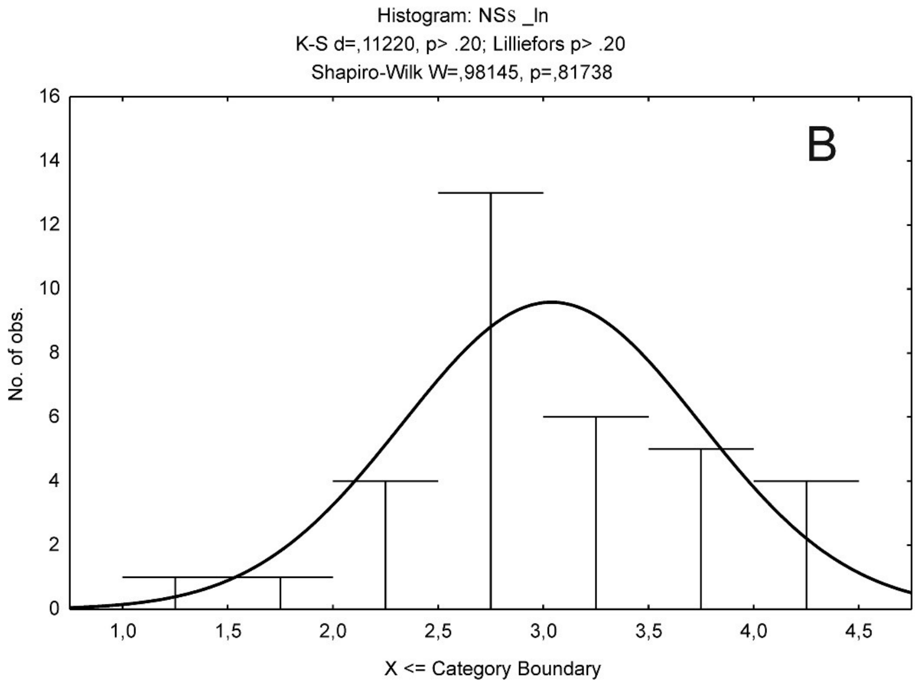


Fig. 5. The NSs' distribution (n = 34) of the male from Mt. Ostra data before (A) and after (B) normalization by logarithms.

As a result of the close relationship between syllable duration (SD) and syllable repetition period (SRP), an increase in SD immediately results in an increase in SRP. Therefore, this is likely one of the main strategies that *I. camptoxypha* males use to control their singing.

While drawing far-reaching conclusions from a single individual is inappropriate, our aim was not to perfectly replicate all environmental factors in a laboratory setting, which is practically impossible. Male singing in the wild presents a complex challenge, as various factors, some more influential than temperature, come into play. Consider, for instance, the intermittent winds of highlands, a variable that's demanding to model. It's evident that the general characteristics of a male's song can exhibit a wide range of variation. The authors' primary objective has been to identify which song syllable characteristics warrant more in-depth investigation in the future and which are too variable to be reliably informative. In the case of male #M1, the conditions during the measurement (#M1') in the sunny meadow with a gentle breeze were favourable.

We used two log-normally distributed traits (NSs and the gap or interval duration between Ss) to examine the general characteristics of *Isophya* males' songs. The logarithm of the values was employed to obtain comparable results. On average, the length of Ss ranges from 5 to 20 seconds, with an interval of 2–5 seconds between them. The number of syllables in an individual song is highly variable, fluctuating from 9 to 37 on average from one individual to another. Additionally, the lowest values were obtained in natural settings, possibly due to measurements conducted during late afternoon hours. It's worth noting that the maximum number of syllables in a song can exceed 1000 (Table 2) when recorded during the night-time, as observed in the case of #M2 between 3 am and 4 pm.

The NSs may be more of a species characteristic, although this assertion needs to be verified with additional data from diverse habitats. Concerning the interval duration between Ss, this indicator is even more variable than the previous one and highly dependent on the time of day. The most intense singing of tested bush crickets is observed in the evening and at night.

Intraspecific duet singing of *I. camptoxypha* males

Intraspecific duet singing of I. camptoxypha was investigated by placing males together in a plastic cage. Upon placement, the males immediately synchronized their singing. The first male (#M1) acted as the dominant initiator, while the second male (#M2) acted as the "initiated" or subdominant. We suspect that there may be other, less pronounced cases of dominance, depending on the singing characteristics of the males in the duet. It is likely that dominance was determined by the length of individual syllables, as differences in other characteristics were not significant (Table 3).

Both males in the duet adjusted their singing to emphasize their individual characteristics, presumably due to competitive motives. This led to a reliable increase in the duration of syllables, the frequency of the sound spectrum's maxima, and the number of impulses in each syllable. Synchronization of singing resulted in a slight reduction in the duration of #M1's syllable repetition period (SRP) and an extension of #M2's SRP. The same trend was observed in the after-click (A-c) duration, as #M1 reduced the spawning time, while #M2 increased it. Additionally, #M2 generated A-c much less frequently.

Significant changes in the duet's singing structure were observed, with a change in dominance position from #M1 to #M2. This phenomenon was rare and only occurred in 5–6% of measures, and it was possible only within the so-called transient distance, where a regular syllable of #M2 was delayed (Fig. 6B, C). Interestingly, in this situation, #M1 decreased the values of the main syllable characteristics, while #M2 increased them (Table 3). The duration of males' response (DMR) also drastically changed for both dominant and subdominant males, with a 2.5 times lengthening that immediately returned to the previous level once #M1 resumed the dominant position.

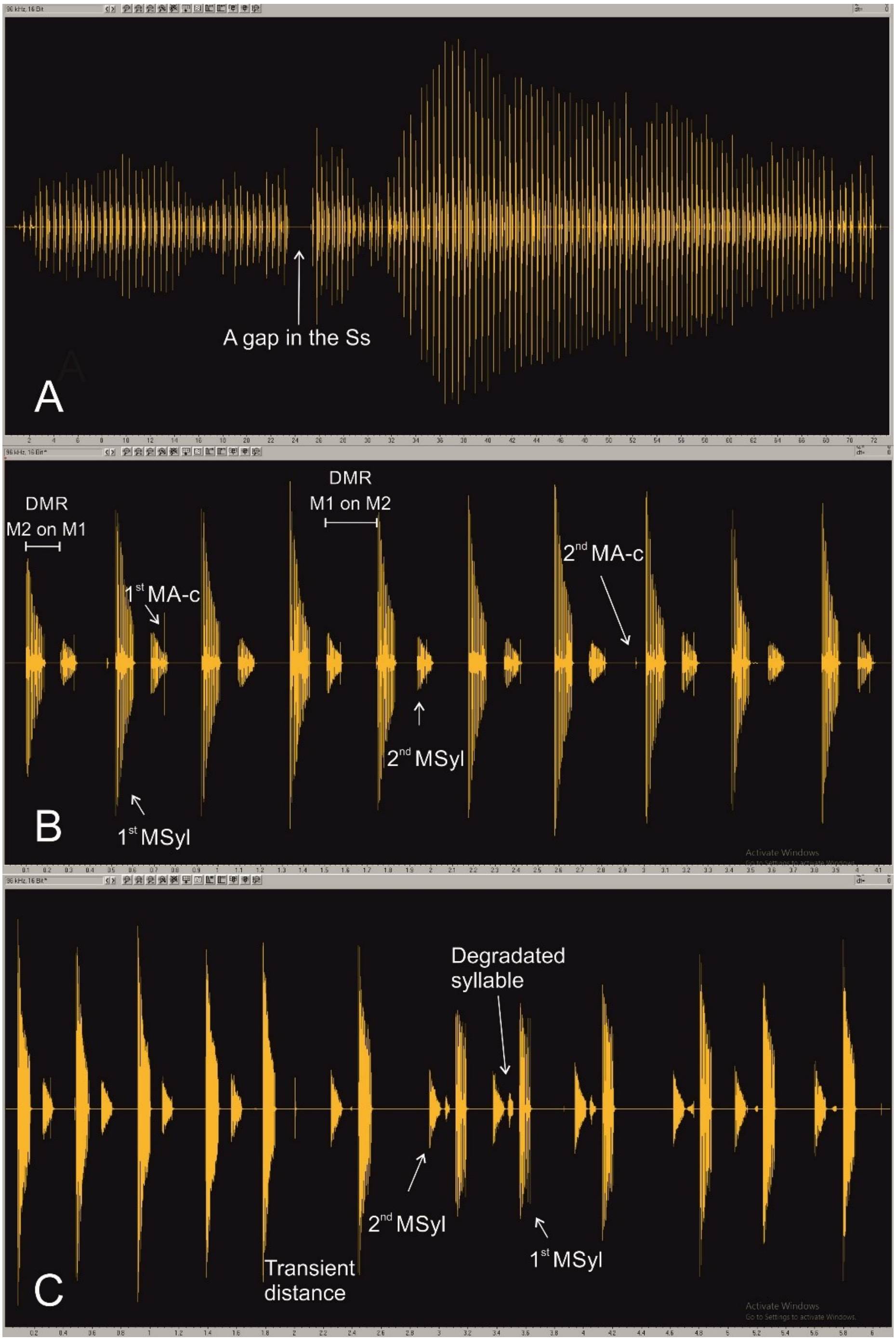


Fig. 6. Duet singing of two males from Mt. Stinka: A – a duet song fragment in an Ss; B – a fragment of the duetting males' song with the 1st male's (#M1) more powerful syllable acting as the dominant; C – a change in dominance to the 2nd male (#M2). MS represents the male's song syllable, used by either #M1 or #M2. Additional notes can be found in the text.

It's worth noting that the male interaction during duet singing was well harmonized, and overlapping of syllables during synchronous singing wasn't observed. However, in some cases, #M1's after-click occurred at the end of #M2's male's syllable (Fig. 6B, C).

Table 3. Characteristics of the duet male calling songs of *I. camptoxypha* recorded in vivo 7 Aug .2017.

N	Characters	n	$\overline{X}$	±S	Min	Max
			#M1 dominant,			
1	#M1-dom.-SD	351	86	05	55	98
	SPF	351	22.6	0.8	20.7	25.9
	NI	351	27.5	1.9	20	32
	SRP	340	454	54	347	645
	1st AC	268	150	15	150	199
	DMR 2 on 1	340	74	11	52	135
2	#M2-subdom.-SD	345	69	6	38	85
	SPF	345	22.1	0.6	17.6	23.1
	NI	345	23.7	2.3	17	32
	SRP	331	454	54	330	602
	1st AC	52	137	08	091	256
	DMR 1 on 2	334	225	52	126	361
	NSs (lnX)	12	28(3.32)	3(1.10)	3	132
			#M2 dominant			
1	#M2-dom.-SD	23	62	18	30	81
	SPF1	23	21.5	2.2	15.8	23.7
	NI	23	27.3	9.2	12	55
	SRP	9	428	145	195	680
	DMR 1 on 2	6	182	5	177	188
2	#M1-subdom.-SD	13	82	6	74	93
	SPF	13	23.0	1.1	21.2	25.7
	NI	13	23.7	3.8	17	28
	SRP	4	560	80	490	675
	DMR 2 on 1	5	344	104	203	492

DISCUSSION

The bush-cricket species *I. camptoxypha* has a wide distribution in both the Carpathians and Alps. The first studies of *I. camptoxypha* singing were possibly presented in Heller's monograph (1988: fig. 29), where a brief mention of *I. pyrenea* (Serville, 1839) was included. However, the latter is a complex species, and the syllable depicted in this figure most likely does not belong to *I. camptoxypha*. A more detailed understanding of the male song characteristics of this species can be obtained from the work of Heller et al. (2004: fig. 81), where the typical after-click following the main syllable is visible. But so far, no one has reported syllables in the songs of males with two after-clicks (type 2).

It is widely known that male bush-crickets use sound signals to attract females and the partners can sing in duet (Nagy et al. 2003, Theuerkauf et al. 2005). An interesting fact is that males can sing in duets as well, which is a sign of intraspecific interaction. During duet singing, both the dominant and subdominant (or guiding and guided) individuals typically eliminate or significantly reduce the after-click component of the male's song syllables. However, it is possible that some of the initial male's after-clicks, which likely serve to establish the rhythm, may be obscured in the oscillograms by the stronger body of the song syllable.

It is worth noting that prior to our study, Bazyluk (1971) and Theuerkauf et al. (2005) identified *I. camptoxypha* (or *I. brevipennis*) as a fairly common species in the Western Bieszczady, and Liana (1994: p. 145) reported it from "edges in oak forests" in the plain Roztocze of Poland. However, at that time, they were not considered synonyms, and the available equipment did not permit bioacoustic analysis of male singing. Therefore, it is uncertain which species these authors observed. Our acoustic studies of the *Isophya* species belonging to the "*camptoxypha*" subgroup in the immediate vicinity of the border with Poland and Slovakia confidently suggest that it is *I. camptoxypha*. This is the first recorded instance of this species in the Ukrainian part of the Beskids mountain range.

CONCLUSIONS

a) This study represents the first bioacoustic investigation of the bush-cricket *I. camptoxypha* in the meadows in the Eastern Beskids (the Verkhovna Dividing Range and Polonynian Beskids) of the Ukrainian Carpathians.

b) Our initial observations confirm the presence of substantial and significant differences between the *I. camptoxypha* males' acoustic signals.

c) Syllable duration (SD), number of impulses within a syllable (NI), syllable peak frequency (SPF), and after-click duration (A-c) were identified as the most important features for individual identification.

d) Syllable repetition period (SRP) was also found to be an auxiliary indicator of male individuality.

e) Notable differences were observed between *in vivo* and recorded *in natura* song.

f) Our findings reveal significant communication skills of male *I. camptoxypha* during duet singing.

g) Thorough investigation of the bioacoustics of the "*camptoxypha*" species subgroup of *Isophya* bush-crickets is needed, to determine whether closely related species exist in the Ukrainian Carpathians.

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STRESZCZENIE

[**Akustyczny behawior samców zrówieńki karpackiej (*Isophya camptoxypha*) (Orthoptera: Tettigonioidea) w dolinie rzeki Uż: wstępne stwierdzenia**]

Ten artykuł prezentuje wstępne badania nad akustycznym behawiorem zrówieńki karpackiej (*Isophya camptoxypha*), gatunku typowego w środowisku subalpejskim Ukraińskich Karpat na wysokości powyżej 1200 m n. p. m. W roku 2017, cztery żywe samce *I. camptoxypha* zostały zabrane z dwóch różnych lokalizacji Beskidu Wschodniego: z bardziej typowego środowiska na Ostrej Górze w Beskidzie Połonińskim i z łąk powyżej granicy lasu na Górze Stinka w Paśmie Wierchowna, w pobliżu granicy ze Słowacją. Badania pozwoliły na określenie czasu trwania sylab, liczbę impulsów w obrębie sylab, szczyt częstości, a także kluczowe cechy dla identyfikacji osobniczej i komunikacji między samcami *I. camptoxypha*. Te badania ilustrują istotne umiejętności interakcji samców *I. camptoxypha,* gdy angażują się w akustyczny duet.

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