An unusually diverse courtship vocal repertoire in the lesser mouse-eared bat (*Myotis blythii*) results from flexible recombination of a limited set of syllables

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Abstract:
Acoustic signals are the primary medium for communication. Nevertheless, the diversity of bat vocal repertoires remains poorly known. Recently, several studies have demonstrated that males of some species produce highly versatile songs during courtship, suggesting that this still poorly understood phenomenon may also occur in other species. We investigated the courtship vocalisations of 28 individuals of the lesser mouse-eared bat *Myotis blythii* in five underground sites in southern Ukraine (Eastern Europe). We analysed the spectrographic structure and syntax of nearly 9,000 bat vocalisations. We identified nine syllable types forming phrases, and different phrases were combined into vocalisation units (hereafter referred to as vocalisations). The number of syllables within phrases and the number and order of phrases within vocalisations were highly variable. We identified 689 phrase orderings (vocalisation types) and 1,423 variants resulting from variable repetition of syllables within phrases (vocalisation variants), of which only 20 vocalisation types and 19 vocalisation variants accounted for more than 1% of the total analysed repertoire. Transition structure was weak (i.e., the frequency with which one phase was followed by another), as no single phrase transition accounted for more than 9% of all adjacent transitions. Phrase types also exhibited only weak positional biases within vocalisation units, indicating limited sequential structuring. These results suggest a low level of stereotypy and a dynamic expansion of courtship vocal display through phrase reassertion and variable repetition of a limited number of syllables. This strategy makes the courtship vocal repertoire of *M. blythii* one of the most diverse vocal systems described in mammals. Given its structural complexity and its production by males during the mating season at courtship sites, the analysed vocal repertoire qualifies as song.

Keywords: acoustic communication, bat song, combinatorial vocal system, phrase structure, vocal sequence organisation, courtship behaviour.

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30 ***Introduction***

31 Many animals use acoustic signals to communicate with conspecifics in a variety of social contexts
32 (Bradbury and Vehrencamp 1998). The structure and complexity of these signals vary with the
33 behavioural context, and natural, social and sexual selection play important roles in shaping
34 communication systems and signal design (August and Anderson 1987; Morton 1977). Repertoire size
35 therefore depends on the communication system and the type of selection shaping it.

36 Some species possess larger vocal repertoire than others and use a greater diversity of sounds to
37 convey information about mate quality, the location of conspecifics or food, and the presence of
38 predators. High levels of acoustic complexity are particularly evident in courtship vocalisations, with
39 many examples from bird songs emitted mainly for mate attraction and territory defence against rivals.
40 Courtship signalling is a major component of partner choice and has therefore evolved largely through
41 sexual selection. Female preference, in particular, is known to drive the evolution of complex and
42 elaborate song repertoires in birds (Catchpole and Slater 2008; Collins 2004; Marler and Slabberkoorn
43 2004; Bradbury and Vehrencamp 1998).

44 The complexity of courtship vocal repertoires can be expressed by the number, combination, and order
45 of sound types (often referred to as elements or syllables) produced by an individual. Courtship
46 displays may range from simple call repertoires to elaborate songs. In general, calls are relatively short
47 vocalisations that may consist of one or multiple element types and can serve a variety of functions,
48 whereas songs are longer and more complex, consisting of multiple element types combined in a fixed
49 or variable sequential order and are most often associated with sexually selected contexts such as
50 mate attraction or rival deterrence (Engesser and Townsend 2019; Catchpole and Slater 2008).

51 The rules governing the order in which elements can be arranged are referred to as syntax (Marler
52 1977). Two forms of syntax have been proposed: phonological (combinatorial) and lexical
53 (semantical). The former describes how smaller, individually meaningless vocal units are combined
54 into larger structures, whereas the latter refers to the corresponding changes in meaning (Marler 1998).
55 Phonological syntax is widespread in animal communication systems, whereas evidence for lexical
56 syntax is scarcer (Engesser and Townsend 2019; Marler 1998).

57 A wide range of animals, including songbirds, bats, rodents, primates, hyraxes, whales and
58 amphibians, combine sound elements into higher order sequences or songs of varying structural
59 complexity (e.g. Cholewiak et al. 2013; Pasch et al. 2013; Arnold and Zuberbühler 2006; Clarke et al.
60 2006; Holy and Guo 2005; Batzli and Henttonen 1993; Mitani and Marler 1989). Well- studied
61 songbirds expand their song repertoires either by adding distinct song types with different functions or
62 by flexibly modifying the phonological structure of a primary song depending on context (reviewed in
63 Engesser and Townsend 2019; Smotherman et al. 2016; catchpole and Slater 2008).

Methods and terminology developed for the study of bird song are increasingly applied to bat vocalisations, and there is growing evidence of comparable levels of vocal repertoire complexity in bats and birds (e.g., Collier and Parsons 2022; Vernes 2017; Bohn et al. 2016; Smotherman et al. 2016). Despite the diversity of bats (more than 1,500 species), mating behaviours and courtship signalling have been described in only around 50 species (about 3.5% of all bats) (Gillam and Fenton 2016; McCracken and Wilkinson 2000).

At least a dozen bat species use songs during courtship. Most produce complex multi-syllabic acoustic signals used in male advertisement, whereas other studied species produce simpler courtship calls consisting mainly of repeated elements (reviewed in Bohn et al. 2016; Gillam and Fenton 2016; Knörnschild et al. 2016; Smotherman et al. 2016). So far, some of the most complex song repertoires have been described in males of lesser short-tailed bats *Mystacina tuberculata* (Collier and Parsons 2022; Toth and Parsons 2018), greater sac-winged bats *Saccopteryx bilineata* (Knörnschild et al. 2016; Behr and von Helversen 2004; Davidson and Wilkinson 2002), Brazilian free-tailed bats *Tadarida brasiliensis*, broad-eared bats *Nyctinomops laticaudatus* (Bohn et al. 2016; Bohn et al. 2009), and false vampire bats *Megaderma lyra* (Bohn et al. 2016; Schmidt 2013; Leippert 1994). These species are mainly tropical or widely distributed American or African species. Among European bats, detailed studies of courtship song exist only for Nathusius' pipistrelle *Pipistrellus nathusii* (Jahelková et al. 2008), while several other species have been reported to produce songs or simpler advertisement calls (Russ and Racey 2007; Furmankiewicz 2005; Pfalzer and Kusch 2003; Lundberg and Gerell 1986). However, the structural organisation and repertoire diversity of courtship vocalisations remain poorly documented in most European bat species.

Here, we investigate the courtship vocalisation of the lesser mouse-eared bat *Myotis blythii* at the north-eastern edge of its range in eastern Europe. This species belongs to the complex of five cryptic large mouse-eared bat species within the genus *Myotis* (Furman et al. 2020). Male calling activity in roosts during mating season have been previously described only in one species of this group, the greater mouse-eared bat *Myotis myotis* (Staňková et al. 2023; Furmankiewicz 2021*a*; Pfalzer and Kusch 2003; Zahn and Dippel 1997, Printz et al. 2025, 2026). Detailed information on the vocalisations of *M. blythii* is currently lacking, and description of its courtship behaviour remains scarce (Horáček and Gaisler 1986). This species forms large mating aggregations in underground sites, where males produce prolonged courtship vocalisations, making it a suitable model for studying the structure and diversity of mating vocal displays.

In this study, we investigate the structure and diversity of the courtship vocal repertoire of *M. blythii*, including the combinatorial organisation of vocal elements and the extent to which vocal sequences exhibit non-random structural patterns. Specifically, we quantify (i) the diversity and organisation of vocal elements (their combination and ordering, i.e. phonological syntax) and (ii) variation among syllable types based on their spectral and temporal characteristics. Together, these analyses provide

the first comprehensive description of this repertoire and thus lay the foundation for future studies investigating the relationship between vocal structure and behavioural function.

Materials and Methods

Study species and sites

The complex of large mouse-eared bats is widespread across Europe where it is represented by two species, the greater mouse-eared bat *Myotis myotis* (Borkhausen, 1797) and the lesser mouse-eared bat *Myotis blythii* (Tomes, 1857) [= *M. b. oxygnathus* (Monticelli, 1885; terr. typ.: Italy)]. They occur sympatrically throughout most of their distribution range and often share the same maternity and winter roosts (Dietz et al. 2009). These species are quite similar morphologically and not always easy to distinguish without detailed examination, for example of tooth row length (Dietz et al. 2009).

We studied *M. blythii* in southern Ukraine, within a zone of allopatric distribution, which eliminated the probability of confusing the two cryptic large mouse-eared bats species.

The study sites comprised five abandoned limestone mines in the SW of the Podolian Upland (numbers 1 and 2 in Fig. 1) and in the Crimea (numbers 3–5 in Fig. 1), in Vinnytsia, Odesa Oblasts and in the Autonomous Republic of Crimea, respectively. The sites were as follows: site 1 – part of the GRK-K mine complex; site 2 – ZGN-K mine; site 3 – part of the R-20 et al. mine complex (Ak-Monayski mines); site 4 – part of the mine complex, from R-21 to R-24 (Petrovski mines); site 5 – R-7 mine (one of the Bulganakski mines) (Fig. 1). All sites are included in the list of internationally important underground bat sites (https://www.eurobats.org/activities/intersessional_working_groups/underground_sites).

All mines are extensive underground systems of corridors and chambers excavated about 50–100 years ago. All of them were occupied by *M. blythii* year-round: sites 1 and 2 by several dozen individuals (Godlevska et al., 2010; 2022); sites 3 and 4 by big maternity and hibernation aggregations, and site 5 by big winter and summer aggregations (without juveniles) (Godlevska et al. 2009; L. Godlevska, unpubl.). In August and September, these sites function as mating grounds. Numerous males (from several individuals to hundreds) perch singly on the ceilings of the mines. At the Crimea sites, they occurred at short distances from one another, forming dense aggregations. In contrast, males at the Podolian Upland sites were much less numerous, perched at considerably greater distances from each other, and did not appear to form large aggregations comparable to those observed in Crimea. Many of these males vocalise at night time from their perching sites. Some are joined by one to three females, occasionally by up to six females, for mating. Example video recordings of bat aggregations at site 5 (Crimea) are provided in Supplementary Materials (Appendix 1).

We recorded bat vocalisations in all five sites in late August (sites 1, 2) and early September 2009 (sites 3–5). We aimed to record individual vocalising males. Whenever possible, the recorded individual was captured after recording to confirm its sex and age. In total, we recorded 28 individuals, of which 19 were identified as males and seven were assumed to be male based on their behaviour, i.e., vocalisation patterns similar to confirmed males and solitary perching behaviour (cf. McCracken and Wilkinson 2000, Walter and Schnitzler 2019, Zahn and Dippel 1997, Horáček and Gaisler 1986). All confirmed and probable males perched singly on the ceilings. The remaining recordings included one individual recorded in a pair of bats and one confirmed male recorded while in a pair. Each individual or pair was recorded only once, for a maximum duration of about one hour.

The number of recorded individuals and vocalisations per site was as follows: site 1 – 3 confirmed males and 4 probable males, and 3,198 vocalisation units (between 72 and 1,131 per male); site 2 – 6 confirmed males and 3,592 vocalisation units (between 78 and 1,294 per male); site 3 – 7 confirmed males, 1 probable male and 1 individual in a group of 2 bats, and 1,413 vocalisation units (between 16 and 556 per male); site 4 – 1 confirmed male, 2 probable males and 1 male in a group of 3 bats, and 352 vocalisation units (between 2 and 317 per male); and site 5 – 1 confirmed male, 1 probable male, and 421 vocalisation units (76 and 345 per male). In total, we recorded 8,976 vocalisation units.

Recording of courtship vocalisations

We recorded bats using a condenser CM16 ultrasound microphone (frequency response +/-3 dB between 10 and 150 kHz) connected to an Avisoft UltraSoundGate416 base unit and a laptop running Avisoft-RECORDER software (Avisoft Bioacoustics, Berlin, Germany). We recorded at 16-bit resolution and a sampling rate of 250 kHz.

We positioned the microphone in front of the vocalising bat, as close as possible, i.e., about 1–3 m from its head. We recorded each individual for about 30–60 minutes, depending on its vocal activity. These recording sessions were designed to obtain high-quality, representative samples of courtship vocalisations from a large number of males rather than to conduct detailed behavioural observations. As each session represented only brief snapshots of the males' activity while exhibiting the typical courtship behaviour described above, they generally captured a single, relatively uniform behavioural context rather than a broad range of behavioural or social situations potentially influencing vocal production. Consequently, the present study focuses on describing the structural organisation of courtship vocalisations rather than on testing relationships between vocalisation patterns and behavioural context.

We analysed the recordings with the computer program Avisoft-SASLab Pro ver. 4.40 (Avisoft Bioacoustics, Berlin, Germany) with a Blackman window and an FFT size 512. We selected only

high-quality recordings with minimal background noise for further analysis. We described courtship vocalisations using syntactic and spectro-temporal parameters.

Syntax analysis

At the syntax level, we identified the number and type of *syllables* and *phrases* and their ordering within discrete larger units (Marler 1977), which we termed *vocalisation units* (hereafter referred to simply as *vocalisations*) (Fig. 2), following terminology used in previous studies of bat courtship repertoires (Bohn et al. 200, Knörnschild et al. 2014, Smotherman et al. 2016, Toth and Parsons 2022). A continuous sequence of different vocalisation units was considered a courtship *song*.

The basic unit of each vocalisation unit was a *syllable*, defined as the smallest continuous trace on the spectrogram, separated by a silent gap shorter than 20 ms. We distinguished syllable types based on their spectrographic pattern, specifically the form of frequency modulation or constancy over time (Kanwal et al. 1994). We named the syllable types based on their modulation pattern; however, for syntax analyses, we applied one-letter code based on syllable shape or previous description by Zahn and Dippel (1997).

We grouped syllables occurring consecutively separated by gaps shorter than 20 ms into *phrase*. We distinguished only monosyllabic phrases (i.e. composed of a single syllable type). Therefore, there was a one-to-one correspondence between phrase types and syllable types, and both were assigned the same names. We treated closely spaced phrases as forming a single *vocalisation unit*.

We classified discrete vocalisation units and the number and types of syllables within them visually ("by eye", Kershenbaum et al. 2016, Catchpole and Slater 2008), based on the criterion that intervals separating units were longer than those between neighbouring syllables and phrases within a unit (Fig. 2). All classifications were performed by the same observer (JF) to ensure consistency of visual classification.

We defined a vocalisation unit as a unique combination of phrases or syllables. We used the term vocalisation unit consistently for all analysed groups of syllables or phrases, including short units composed of only one or two syllables. We classified vocalisation units into types and variants, following the terminology by Bohn et al. (2009), Bohn et al. (2016), and Collier and Parsons (2022). A *vocalisation (unit) type* was a unique sequence of phrases that did not include syllable repetition within a phrase, whereas a *vocalisation (unit) variant* was defined as a unique sequence of all syllables including their repetitions within a vocalisation (Fig. 2).

Spectro-temporal measurement

In the temporal domain, we measured syllable duration (ms). In the spectral domain, we measured four parameters (kHz) of syllables: i) peak frequency (frequency with maximum energy density in the mean spectrum); ii) maximum frequency; iii) minimum frequency; and iv) bandwidth. Sample sizes for measured syllables are provided in Table 1.

Statistical analysis

All analyses were performed in R v. 3.5.1 (R Core Team 2022) with statistical significance set at $p < 0.05$.

We used the chi-square test to examine differences in the proportions of syllable types, vocalisation types, and vocalisation variants. These analyses were based on 8,976 vocalisations recorded from 28 individuals of *M. blythii*.

For all spectral and temporal parameters, we calculated mean and standard deviation (SD) for each identified syllable types. To investigate differences among syllable types, we performed a multivariate analysis of variance (MANOVA) using five acoustic parameters, with hypothesis testing based on Wilks' Lambda. Following a significant MANOVA result, we performed univariate ANOVAs to test differences among syllable types for each acoustic parameter.

To estimate the expected number of vocalisation types and variants relative to sample size, we applied rarefaction analysis to assess repertoire diversity and sampling completeness. We calculated frequency matrices for vocalisation types and variants, both for the entire dataset and per individual, and plotted rarefaction curves using the vegan 2.6-4 package (Oksanen et al. 2022). The number of recorded vocalisations per individual ranged from 2 to 1,294. Specifically, eight individuals contributed between 72 and 157 vocalisations, six individuals between 441 and 694 vocalisations, and three individuals between 962 and 1,294 vocalisations. Therefore, we rarefied the data set to three standardised sample sizes: 100, 500 and 1000 vocalisations.

To investigate phrase transition patterns and the positional distribution of phrases within vocalisations, we analysed the phrase adjacency matrix in the R package 'Matrix'. We visualised the transition structure as a network graph using the closeness centrality and betweenness centrality metrics implemented in the R package "igraph". This approach allowed us to identify phrase transition patterns and assess the structural organisation of vocal sequences.

In addition, we analysed the positional distribution of phrase types in the first three positions of vocalisations, as well as in single-phrase (isolated) vocalisations, using the chi-square goodness-of-fit tests. We focused on first, second, third, and isolated phrase types because the single-phrase (isolated) and three-phrases vocalisations together constituted 96% of the analysed repertoire.

Results

Syllable types and acoustic parameters

We identified nine syllable types, labelled V, W, A, M, K, I, L, C, and S to facilitate syntax analysis (Fig. 3). The principal frequency modulation patterns and general spectro-temporal characteristics of each syllable type, along with example audio files, are provided in the Supplementary Materials (Appendices 2 and 3, respectively).

We identified several modifications in frequency modulation patterns within each syllable type (Fig. 3), suggesting that the syllable repertoire may be even more diverse. However, we did not further analyse these modifications or investigate their underlying causes.

Syllable types differed significantly in both temporal and spectral parameters (MANOVA: Pillai = 0.939, df = 7, 5019; F = 165.8, $p < 0.0001$). The highest variation was observed in syllable duration, which ranged from very short pulses (**I:** 3.5 ms ± 1.6, mean ± SD) to very long pulses (**C:** 142.4 ms ± 54.5, mean ± SD). The remaining acoustic parameters showed comparatively lower variation among syllable types (Table 1).

Syntax of vocalisations

Proportions of syllable types **–** Syllable types occurred in significantly different proportions across all analysed vocalisations (Chi-square test, $\chi^2 = 115.54$, df = 8, $p = 0.0001$). Syllable types V and type I were the most frequent, accounting for 33.53% and 32.24% of all syllables, respectively. The remaining syllable types occurred less frequently: W (9.27%), M (7.35%), K (6.60%), L (5.84%), C (4.15%), A (0.67%) and S (0.35%).

Vocalisation length **–** Vocalisations varied in length, ranging from 1 to 15 phrases in vocalization types (defined from phrase sequences, in which consecutive identical syllables were treated as a single monosyllabic phrase) and from 1 to 17 syllables in vocalisation variants (defined from the complete sequence of all identified syllables before grouping consecutive identical syllables into phrases).

Vocalisations were usually composed of two phrases (41.5% of the repertoire), or one and three phrases (26.5% and 21.2%, respectively). In total, 7.2% of vocalisations contained four phrases, whereas between 1.0% and 2.2% consisted of five or six phrases. The remaining vocalisations (< 1%) contained between 7 and 15 phrases (Table 2).

In terms of syllable number, most vocalisations comprised three (32.4%) or four (22.1%) syllables. Single- and double-syllable vocalisations each constituted 14–15 % of the repertoire. Vocalisations containing five, six, seven, and eight syllables accounted for 8.4%, 4.0%, 2.4% and 1.0% , respectively. Vocalisations containing more than nine syllables (up to 17) were rare and accounted for about 0.9% of the analysed repertoire (Table 2).

Vocalisation variation – Overall, we identified 689 vocalisation types differing in phrase order, and 1,423 vocalisation variants differing in syllable repetitions within phrases. Rarefaction analysis indicated that the expected numbers of vocalisation types and variants exceeded the observed values for sample sizes of 100, 500 and 1,000 vocalisations (Fig. 4). The rarefaction curves continued to rise steadily, suggesting high versatility of the courtship repertoire and indicating that additional sampling would likely reveal further variation.

Despite this high diversity, only 20 vocalisation types (2.9%) and 19 vocalisation variants (1.33%), each exceeded 1% of the total analysed sample. The remaining vocalisation types and variants were recorded only once or between 2 and 88 times.

The most common vocalisation types were VI, C, and I (12.14%, 8.53% and 6.32%, respectively) (Fig. 5). Among the 20 most frequent vocalisation types, five consisted of a single phrase (never A, K, L and S), ten consisted of two phrases types, and five contained three phrase types (Fig. 5).

Among the 19 most frequent vocalisation variants, three consisted of a single syllable (C, W, or M), five contained two syllables, eight contained three syllables, and three contained four syllables (Fig. 5). The most common vocalisation variants were C, VII, and III (8.36%, 4.52% and 3.34%, respectively) (Fig. 5).

Examples of the most frequent vocalisation types and vocalisation variants are shown in Fig. 6 and in the Supplementary Material (Appendix 4 with audio files corresponding to Fig. 6). A complete list of all identified vocalisation types and variants is provided in the Supplementary Material (Appendix 5).

Transitions of vocalisation elements – The most frequent adjacent phrase transitions were from phrase V to phrase I (9.0% of all transitions) and bidirectionally between phrases W and V (approximately 7.0% of all transitions). The next most frequent transitions (about 3.5–7.0%) were from phrases M, K, and L to phrase V, from phrase I to K and V, and bidirectionally between V and L (Fig. 7). Transitions of intermediate frequency (1–3.5%) accounted for about one-quarter of all transitions, whereas nearly two-thirds occurred at low frequencies (<1%).

Overall, 68 of the 72 possible directional transitions between phrase types (94.4%) were observed, indicating that nearly all possible phrase transitions occurred at least once during courtship vocalisations. Thus, although most phrase transitions were infrequent, a small number of recurring transitions formed a highly connected core centred on phrases V, I, L, and W. Notably, transitions between some phrase pairs were asymmetric, as exemplified by the much more frequent transition from V to I and M to V than their reverse transitions, indicating directional preferences in phrase ordering. Nevertheless, no single transition dominated the transition network. Even the most frequent transition accounted for only 9.0% of all transitions, whereas a large number of transitions occurred at frequencies below 1%. Together, these patterns were reflected in an overall transition network that

was only weakly structured and contained numerous low-frequency links between a wide variety of phrase combinations (Fig. 7).

Positions of vocalisation elements – Analysis of phrase distribution within vocalisations showed that phrase position (first, second, third, or isolated – i.e. single-phrase vocalisations) was non-random. Phrases V and M were most frequently used as first elements (chi-square goodness-of-fit test, $\chi^2 = 7443.97$, df = 8, $p < 0.0001$), whereas phrases I and V predominated in the second and third positions (chi-square goodness-of-fit test, $\chi^2 = 11220.25$, df = 8, $p < 0.0001$, $\chi^2 = 3049.15$, df = 8, $p < 0.0001$, respectively). Phrases C and I were the most frequently produced in isolation as single-phrase vocalisations ($\chi^2 = 2193.15$, df = 8, $p < 0.0001$). Although phrase-type distribution across positions was statistically non-random, positional biases were moderate. The most frequent phrases at given positions accounted for only 23.2–41.4% of vocalisations composed of at least two elements, while the remaining phrases were distributed more evenly across positions (Table 3). This pattern suggests limited sequential structuring.

Discussion

Our study presents the first detailed description of courtship vocalisations in male *Myotis blythii*. The primary aim was to characterize the structural organisation and diversity of this repertoire rather than to investigate the behavioural functions of individual vocalisation types. Consequently, the present analyses do not allow reliable assignment of specific functions to particular vocalisation types or variants. Instead, we focused on describing the courtship vocal repertoire as a whole, encompassing the diversity of vocalisations produced during mating displays. The courtship vocal repertoire is likely to comprise vocalisations serving several different functions, including territorial defence of display sites, attraction of females, deterrence of rival males, and vocalisations emitted before, during and after copulation. Similar vocalisations have been described in these behavioural contexts in the closely related species *M. myotis* (Printz et al. 2026), where they are all considered components of the courtship vocal repertoire, and some of them have been produced by males for setting territorial boundaries and attracting females. Given the close structural similarity between many vocalisations described here and those reported for *M. myotis*, we assume that the repertoire documented in the present study encompasses many, and probably most, of the vocalisation types associated with different functions during courtship. However, assigning specific behavioural functions to individual vocalisation types in *M. blythii* will require dedicated behavioural observations of individually identified males over longer periods and, ideally, experimental approaches such as playback experiments.

Nine syllable types were combined into 689 vocalisation types and 1,423 variants, revealing an exceptionally large vocal repertoire. Rarefaction curves did not reach an asymptote, indicating that the observed diversity likely underestimates the full repertoire size.

The structure of vocalisations further illustrates how this diversity arises. Most of the nine syllable types were emitted in grouped units (phrases), which were combined in varying orders to form vocalisation types. Most vocalisations consisted of one to three phrases, although sequences of up to 15 phrases also occurred. Additional variation arose from differences in syllable number within phrases, producing variants of up to 17 syllables. We also observed subtle modifications in frequency modulation within each syllable type. Because these variations were not classified separately, the true syllable repertoire may be even more diverse than reported here.

Only a small proportion of all analysed vocalisation types and variants occurred frequently, with 20 of the 689 vocalisation types (2.9%) and 19 of the 1,423 vocalisation variants (1.33%) occurring more than 1% of the time. Most sequences were rare and often recorded only once or twice. Importantly, rare vocalisations did not appear to result from interruptions, as they occur between other vocalisations without extended pauses.

Despite this extensive variation, sequential organisation of vocalisations was weak. Phrase transitions lacked strong structural regularity, dominant transition pairs were rare, and positional biases, although statistically non-random, were moderate. Some phrases nevertheless occurred more frequently in particular positions within vocalisations (Table 3), indicating limited positional preferences. In addition, the frequent occurrence of certain phrases (C and I) as isolated vocalisations may function as independent signalling units, although their precise communicative roles remain unclear. At the same time, the observed positional biases of some phrase types suggest that vocal sequences are not entirely unconstrained, with certain elements occurring in specific structural positions more frequently than expected from their overall frequency within the analysed repertoire. Taken together, these observations suggest that vocalisations are assembled flexibly rather than according to a fixed syntactic template.

Similar partial structuring of vocal sequences, combining flexible recombination with non-random positional tendencies, has been reported in other animal vocal systems (e.g., Kershenbaum et al. 2014) and in the courtship songs of *M. tuberculata*, where sequences show hierarchical organisation despite considerable individual variation (Collier and Parsons 2022). Most vocalisations appeared to be constructed dynamically through phrase reassertion and variation in syllable number rather than through fixed hierarchical rules.

This dynamic rearrangement of phrases and variable repetition of a limited set of syllables generated many structurally distinct sequences with low similarity, suggesting that males of *M. blythii* expand their repertoire primarily through flexible recombination of a limited set of syllables rather than by

increasing the number of distinct syllable types. Such flexible song organisation has so far been rarely documented in bats. Most described mating repertoires are performed in a relatively stereotyped manner (Jahelková et al. 2008; Bohn et al. 2009, 2013, 2016; Nardone et al. 2017). For example, songs of male *M. tuberculata* exhibit non-random hierarchical organisation, while still allowing individual variation (Collier and Parsons 2022), whereas male *Saccopteryx bilineata* increase repertoire size by adding distinct song types (Behr and von Helversen 2004). In this context, the vocal behaviour of *M. blythii* appears broadly comparable to that of other bat species in which complex courtship songs have evolved.

The high variability and weak sequential structuring observed here are consistent with a structurally improvisational mode of song production, in which males recombine a limited set of syllable types rather than reproduce fixed, stereotyped sequences. Similar flexible combinatorial systems, characterised by low stereotypy and high sequence diversity, have been described in other mammalian and avian courtship displays (e.g., Bohn et al. 2009; Kershenbaum et al. 2014), where repertoire expansion results from dynamic recombination of elements rather than strict hierarchical organisation. Comparative studies in birdsong have demonstrated that flexibility in phrase ordering and element repetition can arise from dynamic assembly rules instead of fixed syntactic templates (Kroodsma et al. 2009).

Importantly, the structural complexity of the vocalisations, together with their production by males at mating sites during the breeding season, supports their classification as song. Although hierarchical organisation was weak, the presence of multi-element sequences, combinatorial organisation, and prolonged emission during courtship fulfil widely accepted criteria for song in animal communication (Smotherman et al. 2016; Kershenbaum et al. 2014; Catchpole and Slater 2008).

These findings position *M. blythii* among the growing number of bat species exhibiting song-like courtship displays and suggest that elaborate vocal signalling may be more widespread among bats than previously assumed. To date, structurally complex courtship vocalisations have been documented in several phylogenetically and ecologically diverse taxa, including molossid bats such as *Tadarida brasiliensis* and *Nyctinomops laticaudatus*, emballonurids such as *Saccopteryx bilineata*, and the mystacinid *Mystacina tuberculata*. These systems differ markedly in the organisation of vocal elements, ranging from hierarchically structured sequences to more flexible combinatorial patterns (Collier and Parsons 2022; Toth and Parsons 2018; Bohn et al. 2016; Bohn et al. 2009; Behr and von Helversen 2004; Davidson and Wilkinson 2002, 2004). In European bats, detailed descriptions of complex advertisement vocalisations remain relatively scarce. Most species, such as *Plecotus auritus*, *Pipistrellus pygmaeus*, *Pipistrellus pipistrellus*, and *Myotis nattereri*, have been reported to produce structurally simpler courtship calls (Schmidbauer and Denzinger 2019; Furmankiewicz et al. 2013; Furmankiewicz 2005; Lundberg and Gerell 1986). In contrast, the advertisement vocalisation of *Pipistrellus nathusii* has been described as song, consisting of three main motifs (analogous to

phrases), often supplemented by accessory motifs that form a principal syntagmatic sequence with additional structural variants (Jahelková et al. 2008). Within this comparative context, the vocal behaviour of *M. blythii* appears notable for the degree of variability generated through the recombination and rearrangement of a limited set of syllable types, rather than for the absolute size of the repertoire. Given that structurally similar courtship vocalisations have also been described in the closely related *Myotis myotis*, which also exhibits a lek mating system (Staňková et al. 2023; Rainho and Furmankiewicz 2021*a*; Zahn and Dippel 1994, Printz et al. 2025, 2026), song production may represent a shared behavioural trait within the large mouse-eared bat complex and potentially occur in other congeners.

Large vocal repertoires are more commonly documented in birdsongs. Some songbirds produce more than 1,500 song types and rarely repeat identical sequences due to highly variable syllable ordering. In contrast, other species maintain distinct song types composed of largely non-overlapping syllable sets (Catchpole and Slater 2008). Exceptional repertoire sizes occur in species such as the northern mockingbird *Mimus polyglottos*, superb lyrebird *Menura novaehollandiae*, nightingale *Luscinia megarhynchos* and brown thrasher *Toxostoma rufum*, the latter exceeding 2,000 song types. Most songbirds, however, fall between these extremes, with repertoires ranging from a few to several hundred song types (reviewed in Catchpole and Slater 2008). Although the vocal repertoire of *M. blythii* is built from only nine syllable types, their extensive combinatorial use has generated more than 600 vocalisation types identified thus far. Importantly, this remarkable repertoire size results from combinatorial diversity rather than from a large inventory of syllable types. In this respect, *M. blythii* ranks among the most variable mammalian vocal systems known and approaches the repertoire sizes reported for the most extreme songbird species.

Several hypotheses have been proposed to explain large repertoire sizes. In birds, repertoire diversity and versatility may reduce listener habituation and prevent vocal fatigue (Catchpole and Slater 2008). Repertoire size can also depend on population size and density and may be shaped by social interactions (Laiolo and Tella 2008; Bitterbaum and Baptista 1979). Group size and demographic complexity within animal populations have been shown to influence various aspects of communication complexity (Pollard and Blumstein 2011), as was observed in primates (McComb and Semple 2005), sciurid rodents (Pollard and Blumstein 2012), and birds (Freeberg 2006, Bitterbaum and Baptista 1979).

Males *M. blythii* often form large aggregations comprising hundreds of individuals, as was the case at three of our study sites. Similar assemblages were described by Horáček and Gaisler (1986) in caves in Kirghizia, where males divided cave walls into small territories (~1 m^2), a pattern consistent with our observations in Crimea. In contrast, behavioural observations of courtship vocalisations in the sibling species *M. myotis*, conducted in considerably smaller mating roosts occupied by only 6–20 males (Printz et al. 2025), identified only 14 distinct vocalisation types, whereas multisyllabic

vocalisations combining different elements were exceptionally rare (Printz et al. 2026). This repertoire appears considerably less diverse than that described here for *M. blythii*. This difference may, at least in part, reflect differences in the social environment, as larger aggregations are likely associated with more frequent male–male interactions, repeated encounters with different females, and a greater diversity of social situations, potentially favouring the production of a broader and more variable vocal repertoire. Under such conditions, competition among numerous males for females, together with eavesdropping on neighbours' songs, may help explain the large size of the mating vocal repertoire. Eavesdropping and learning songs from males sharing the same roost have also been suggested as factors explaining the complex courtship songs of *M. tuberculata*. Males of this species are lek breeders and display in close proximity to one another (Carter and Riskin 2006), producing mating vocal repertoires with one of the highest levels of variability reported in bats (Collier and Parsons 2022; Toth and Parsons 2018).

In songbirds, polygyny is positively correlated with song complexity and repertoire size (Read and Weary 1990), suggesting that strong sexual selection may promote elaborate vocal displays (Smotherman et al. 2016). Song complexity may play a role in both territorial defense and female choice (Krebs and Davies 1993). In bats, however, direct evidence linking courtship song complexity to female choice remains limited (Lundberg and Gerell 1986; Davidson and Wilkinson 2004; Behr et al. 2009; Eckenweber and Knörnschild 2013).

The complexity of male songs in some bats has also been linked to male-male interactions. For example, in *Saccopteryx bilineata* and *Carollia perspicillata*, interactions between males and territorial defence, together with female choice, have been suggested to influence courtship song complexity. Male *C. perspicillata* produce simpler songs than those of *S. bilineata*, possibly because the former species engages in frequent physical territorial conflicts, whereas males of *S. bilineata* often resolve territorial disputes through display rather than aggression and rely more strongly on female choice (Knörnschild et al. 2016).

The mating system of *M. blythii* resembles lekking behaviour and may be classified as a seasonal multi-male/multi-female polygynous system (McCracken and Wilkinson 2000). Males establish small territories within mating sites and attract females acoustically. Increased repertoire size may therefore enhance mating success without the need for frequent physical aggression. Indeed, we rarely observed aggressive interactions between males of *M. blythii* at the studied underground mating sites. Horáček and Gaisler (1986) reported that males particularly active in performing loud acoustic courtship display were not necessarily more successful in attracting females, suggesting that additional cues, such as chemical signals from facial glands, may also influence female choice. Silent individuals were also observed in our study. Moreover, recent studies suggest that olfactory cues, including male facial gland secretions, may also contribute to female mate choice in *M. myotis* (Printz et al. 2025). Thus, acoustic complexity may represent only one component of a multimodal signalling system.

Nonetheless, elaborated singing may allow males to advertise their quality and compete through display rather than physical confrontation.

Our study reveals extraordinary diversity in the courtship vocal repertoire of *M. blythii*. This diversity arises from flexible recombination and variable ordering of a limited set of syllables and phrases, generating numerous vocalisation types and variants. The production of these vocal sequences appears to rely on dynamic assembly of vocal units with weak hierarchical structuring, possibly facilitated by large male aggregations and a polygynous mating system with low levels of aggression. Given their structural complexity and their production by males at mating sites during the breeding season, these vocalisations fulfil widely accepted criteria for song. Together, these findings add to growing evidence that combinatorial vocal systems occur across a range of animal taxa and highlight bats as a promising model for comparative studies of vocal communication.

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Tables

Table 1. Acoustic parameters of nine syllable types in the courtship vocalisations of *M. blythii*, with ANOVA statistics for variation among syllable types.

Syllable	N	Duration (ms)	Frequency of maximum energy (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Bandwidth (kHz)
		mean ± 95% CI	**mean ± 95% CI**	**mean ± 95% CI**	**mean ± 95% CI**	**mean ± 95% CI**
cFM (V)	1139	8.14 ± 5.69	49.0 ± 14.63	35.0 ± 10.8	87.2 ± 14.9	52.2 ± 20.14
dSFMs (W)	706	28.7 ± 16.4	46.8 ± 15.31	37.1 ± 12.7	85.4 ± 15.6	48.2 ± 21.50
ArFM (A)	58	8.52 ± 3.40	51.0 ± 14.08	38.6 ± 14.8	87.8 ± 13.9	49.1 ± 23.43
uSFMs (M)	366	34.6 ± 14.69	49.6 ± 15.19	40.6 ± 14.2	85.5 ± 16.0	44.9 ± 23.25
UFM (K)	396	5.40 ± 1.88	52.1 ± 13.81	44.1 ± 14.2	82.0 ± 17.3	37.8 ± 24.95
DFM (I)	1205	3.49 ± 1.26	46.6 ± 11.45	36.3 ± 9.3	93.5 ± 14.5	57.2 ± 18.42
bDFM (L)	552	4.49 ± 1.41	43.9 ± 12.75	32.8 ± 9.3	88.2 ± 13.9	55.4 ± 16.72
SFMl (C)	605	142.4 ± 54.5	43.1 ± 16.44	31.8 ± 11.8	85.1 ± 15.6	53.2 ± 18.73
S (squawk)	24	526.7 ± 162.8	21.6 ± 3.34	3.41 ± 1.21	92.3 ± 12.3	88.9 ± 13.0
ANOVA	(df=8, 5042)	F= 3622 P<0.0001	F=30.8 P<0.0001	F=75.8 P<0.0001	F=35.2 P<0.001	F=56.7 P<0.0001
R2		0.852	0.045	0.106	0.051	0.081

Table 2. Distribution of the number of phrases and syllables per vocalisation unit in the vocal display of *M. blythii*.

	Number of elements in vocalisation units			
	Number of phrases (excluding syllable repetition) = vocalisation type		Number of syllables (including syllables repetition) = vocalisation variant	
Number of phrases or syllables per vocalisation units	N	Proportion (%)	N	Proportion (%)
1	2382	26.54	1323	14.74
2	3725	41.50	1255	13.98
3	1900	21.17	2912	32.44
4	643	7.16	1980	22.06
5	197	2.19	752	8.38
6	95	1.06	361	4.02
7	24	0.27	215	2.40
8	5	0.06	96	1.07
9	2	0.02	42	0.47
10	2	0.02	17	0.19
11	-	-	10	0.11
12	-	-	2	0.02
13	-	-	5	0.06
14	-	-	-	-
15	1	0.01	3	0.03
16	-	-	2	0.02
17	-	-	1	0.01

Table 3. Proportion (%) of phrases occurring as first, second, third and isolated phrase in vocalisation types of the vocal display of *M. blythii*. Because only monosyllabic phrases were distinguished, phrase types correspond one-to-one with syllable types and are denoted by the same letters. The two highest values in each column are shown in bold.

Phrase	First	Second	Third	Isolated
A	1.5	0.4	0.7	0.3
C	0.8	2.0	4.8	**32.2**
I	1.5	**41.4**	**34.6**	**23.8**
K	19.5	3.0	3.7	3.4
L	1.8	10.5	19.2	0.3
M	**27.3**	0.9	1.4	10.2
S	1.0	0.3	0.1	1.9
V	**31.8**	**33.1**	**23.2**	17.3
W	14.8	8.5	12.3	10.7

731 **Figure captions**

732 Fig. 1. Study sites of *M. blythii*: 1 – GRK-K mine complex, 2 – ZGN-K mine, 3 – R-20 et al. mine
733 complex (Ak-Monayski mines), 4 – R-21 to R-24 mine complex (Petrovski mines), 5 – R-7 mine (one
734 of the Bulganakski mines).

735 Fig. 2. Examples of the division of the vocalisation units into syllables and phrases, and their
736 classification into vocalisation types and variants.

737 Fig 3. Syllable types and their variations identified in courtship vocalisations of *M. blythii*.

738 Fig. 4. Relationship between the number of vocalisations analysed and number of identified
739 vocalisation types (A) and vocalisation variants (B) based on rarefraction analysis. Horizontal lines
740 indicate three rarefaction sample sizes (100, 500, and 1000 vocalisations). Vertical lines show the
741 expected numbers of vocalisation types and variants at these sample sizes.

742 Fig. 5. Proportion of the most frequent vocalisation types (A) and vocalisation variants (B) (>1% of
743 the analysed vocal repertoire).

744 Fig. 6. Examples of the most frequently produced vocalisation types (phrase ordering). Corresponding
745 vocalisation variants (syllable ordering) are given in parentheses.

746 Fig. 7. Network of phrase transition showing the ordering of phrases within vocalisations. Nodes
747 represent phrase types and arrows indicate transitions between them. Arrow thickness is proportional
748 to transition frequency, and proportions of individual transitions are given indicated along the
749 connecting lines.

751 **Supplementary Online Materials**

752 Appendix 1. Example video recordings of mating aggregations of *M. blythii*:

753 Mov 1_Site 3_copulating pairs and group of three individuals

754 Mov 2_Site 5_aggregation of individuals (some silent and some vocalising); vocalisations of summer
755 aggregation of approximately 100 individuals can be heard in the background

756 Mov 3_Site 5a_aggregation of individuals and copulating pair

757 Mov 4_Site 5a_aggregation of individuals and copulating pair

758 Mov 5_Site 5a_copulating pairs

759 Appendix 2. Description of identified syllable types in courtship vocalisations of *M. blythii*.

760 Appendix 3. Sound files with examples of syllable types found in courtship vocalisations of *M. blythii*
761 showed in Fig. 3.

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763 Appendix 5. A complete list of all identified vocalisation types (phrase ordering) and vocalisation
764 variants (variable syllable repetitions within phrases) in courtship vocal display of *M. blythii*.
765 Vocalisation types are highlighted in bold and grey. Each vocalisation type represents a unique
766 sequence of phrases, whereas vocalisation variants correspond to different numbers of syllable
767 repetitions within the same phrase sequence.

Tables

Table 1. Acoustic parameters of nine syllable types in the courtship vocalisations of *M. blythii*, with ANOVA statistics for variation among syllable types.

Syllable	*N*	Duration (ms)	Frequency of maximum energy (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Bandwidth (kHz)
		mean ± 95% CI	mean ± 95% CI	mean ± 95% CI	mean ± 95% CI	mean ± 95% CI
cFM (V)	1139	8.14 ± 5.69	49.0 ± 14.63	35.0 ± 10.8	87.2 ± 14.9	52.2 ± 20.14
dSFMs (W)	706	28.7 ± 16.4	46.8 ± 15.31	37.1 ± 12.7	85.4 ± 15.6	48.2 ± 21.50
ArFM (A)	58	8.52 ± 3.40	51.0 ± 14.08	38.6 ± 14.8	87.8 ± 13.9	49.1 ± 23.43
uSFMs (M)	366	34.6 ± 14.69	49.6 ± 15.19	40.6 ± 14.2	85.5 ± 16.0	44.9 ± 23.25
UFM (K)	396	5.40 ± 1.88	52.1 ± 13.81	44.1 ± 14.2	82.0 ± 17.3	37.8 ± 24.95
DFM (I)	1205	3.49 ± 1.26	46.6 ± 11.45	36.3 ± 9.3	93.5 ± 14.5	57.2 ± 18.42
bDFM (L)	552	4.49 ± 1.41	43.9 ± 12.75	32.8 ± 9.3	88.2 ± 13.9	55.4 ± 16.72
SFMI (C)	605	142.4 ± 54.5	43.1 ± 16.44	31.8 ± 11.8	85.1 ± 15.6	53.2 ± 18.73
S (squawk)	24	526.7 ± 162.8	21.6 ± 3.34	3.41 ± 1.21	92.3 ± 12.3	88.9 ± 13.0
ANOVA	(df=8, 5042)	F= 3622 P<0.0001	F=30.8 P<0.0001	F=75.8 P<0.0001	F=35.2 P<0.001	F=56.7 P<0.0001
R2		0.852	0.045	0.106	0.051	0.081

Table 2. Distribution of the number of phrases and syllables per vocalisation unit in the vocal display of *M. blythii*.

	Number of elements in vocalisation units			
	Number of phrases (excluding syllable repetition) = vocalisation type		Number of syllables (including syllables repetition) = vocalisation variant	
Number of phrases or syllables per vocalisation units	N	Proportion (%)	N	Proportion (%)
1	2382	26.54	1323	14.74
2	3725	41.50	1255	13.98
3	1900	21.17	2912	32.44
4	643	7.16	1980	22.06
5	197	2.19	752	8.38
6	95	1.06	361	4.02
7	24	0.27	215	2.40
8	5	0.06	96	1.07
9	2	0.02	42	0.47
10	2	0.02	17	0.19
11	-	-	10	0.11
12	-	-	2	0.02
13	-	-	5	0.06
14	-	-	-	-
15	1	0.01	3	0.03
16	-	-	2	0.02
17	-	-	1	0.01

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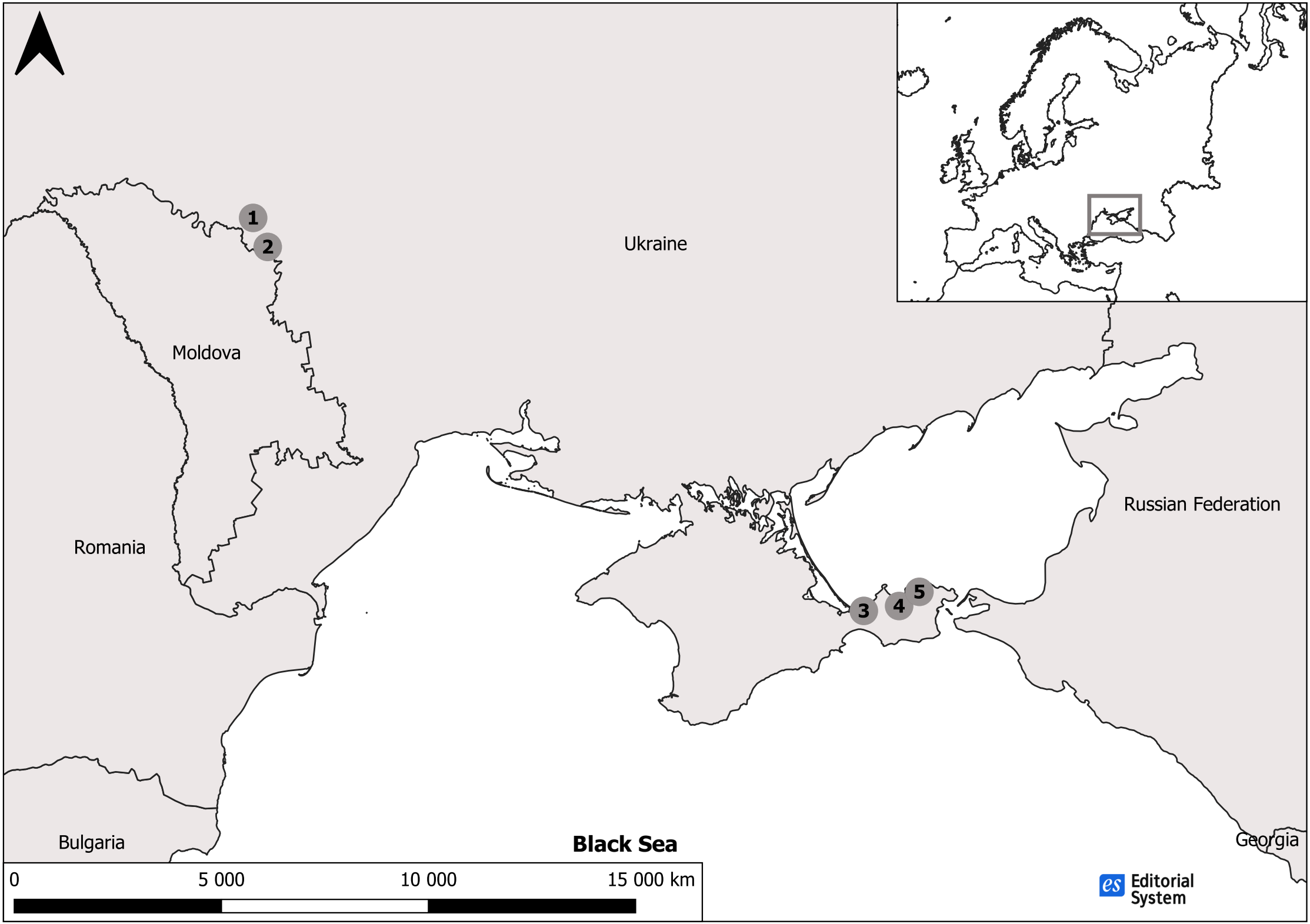
Table 3. Proportion (%) of phrases occurring as first, second, third and isolated phrase in vocalisation types of the vocal display of *M. blythii*. Because only monosyllabic phrases were distinguished, phrase types correspond one-to-one with syllable types and are denoted by the same letters. The two highest values in each column are shown in bold.

Phrase	First	Second	Third	Isolated
A	1.5	0.4	0.7	0.3
C	0.8	2.0	4.8	**32.2**
I	1.5	**41.4**	**34.6**	**23.8**
K	19.5	3.0	3.7	3.4
L	1.8	10.5	19.2	0.3
M	**27.3**	0.9	1.4	10.2
S	1.0	0.3	0.1	1.9
V	**31.8**	**33.1**	**23.2**	17.3
W	14.8	8.5	12.3	10.7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Ukraine
Moldova
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Russian Federation
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Figure 2

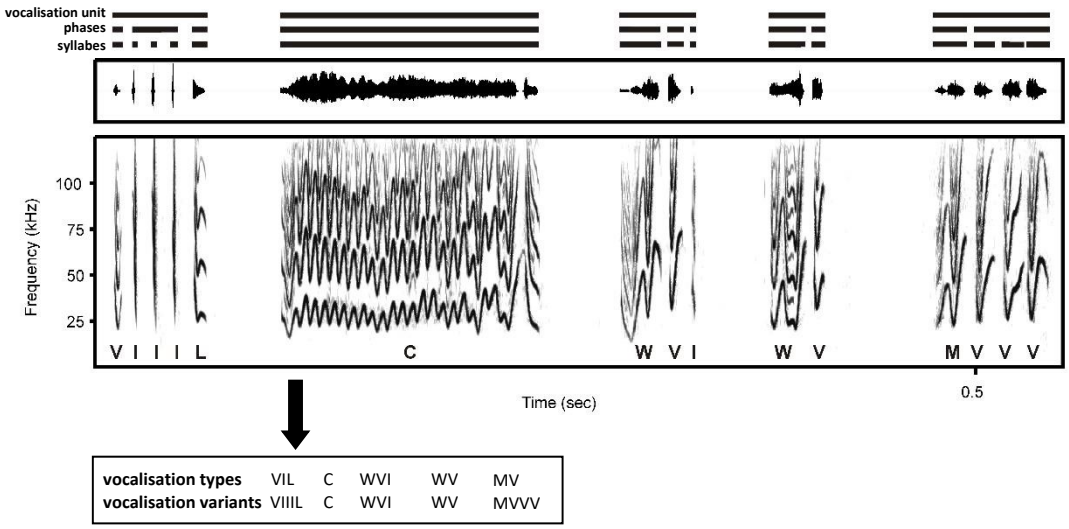

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Figure 3

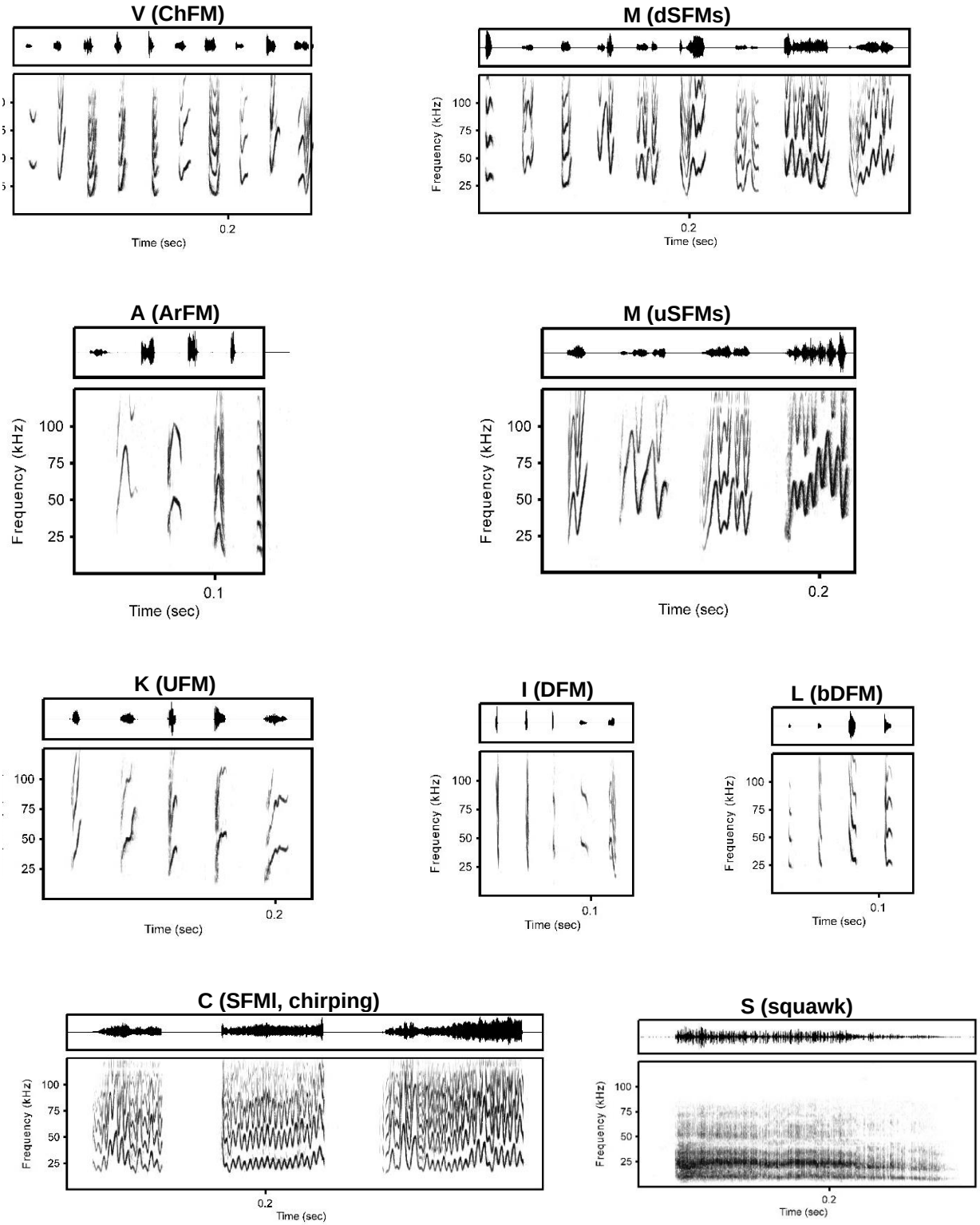

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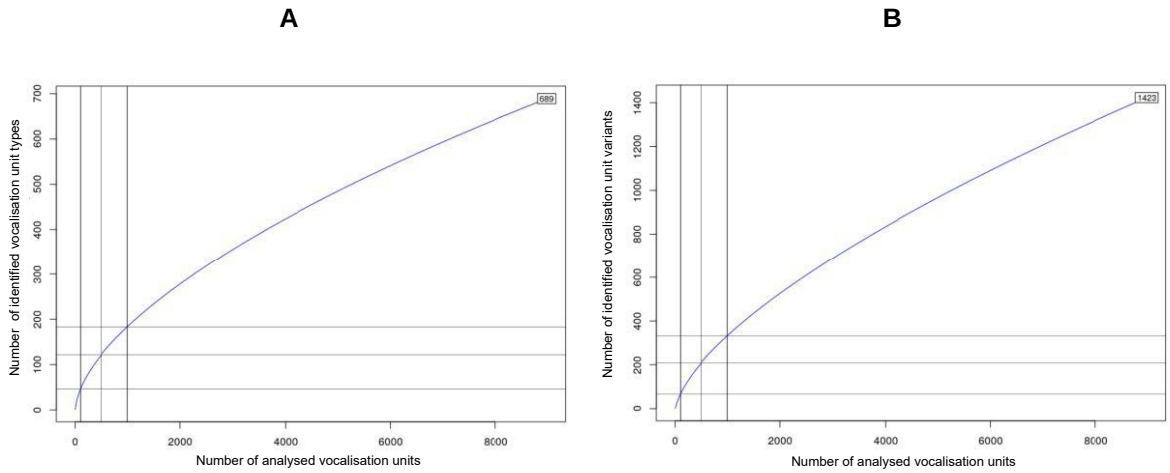
Figure 4



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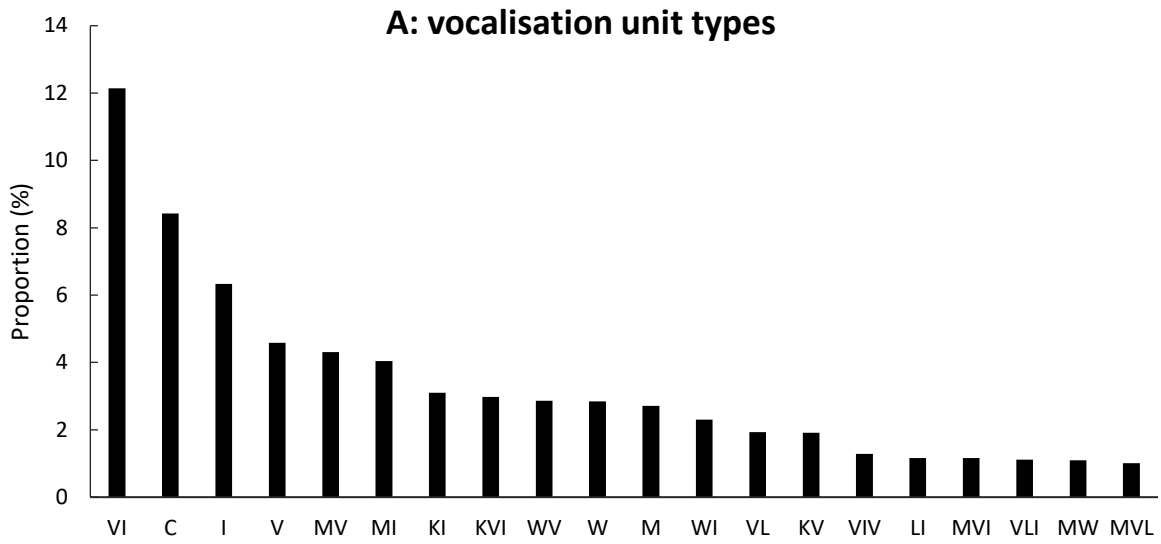

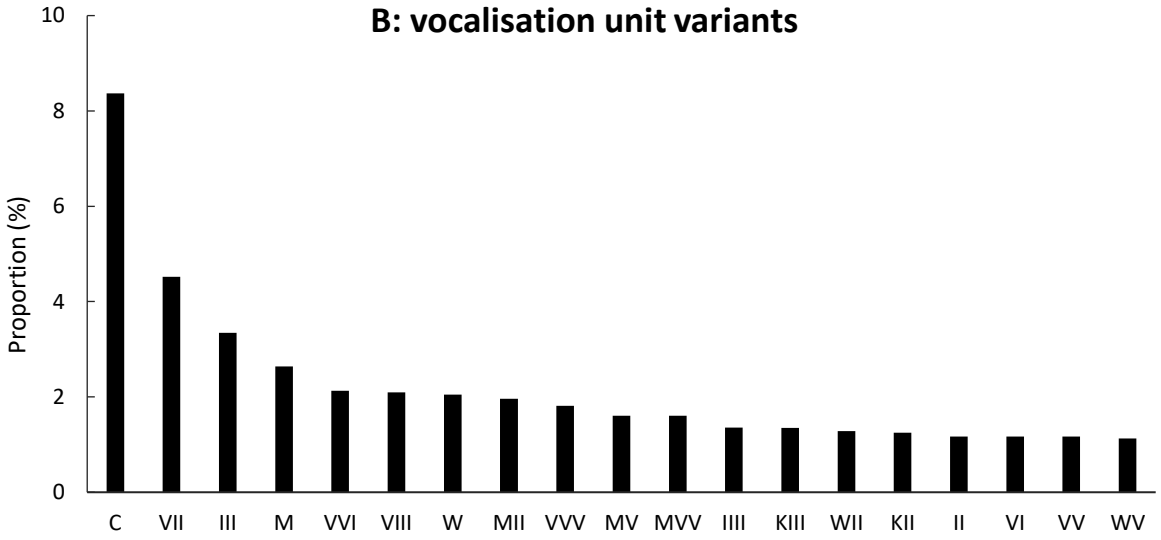

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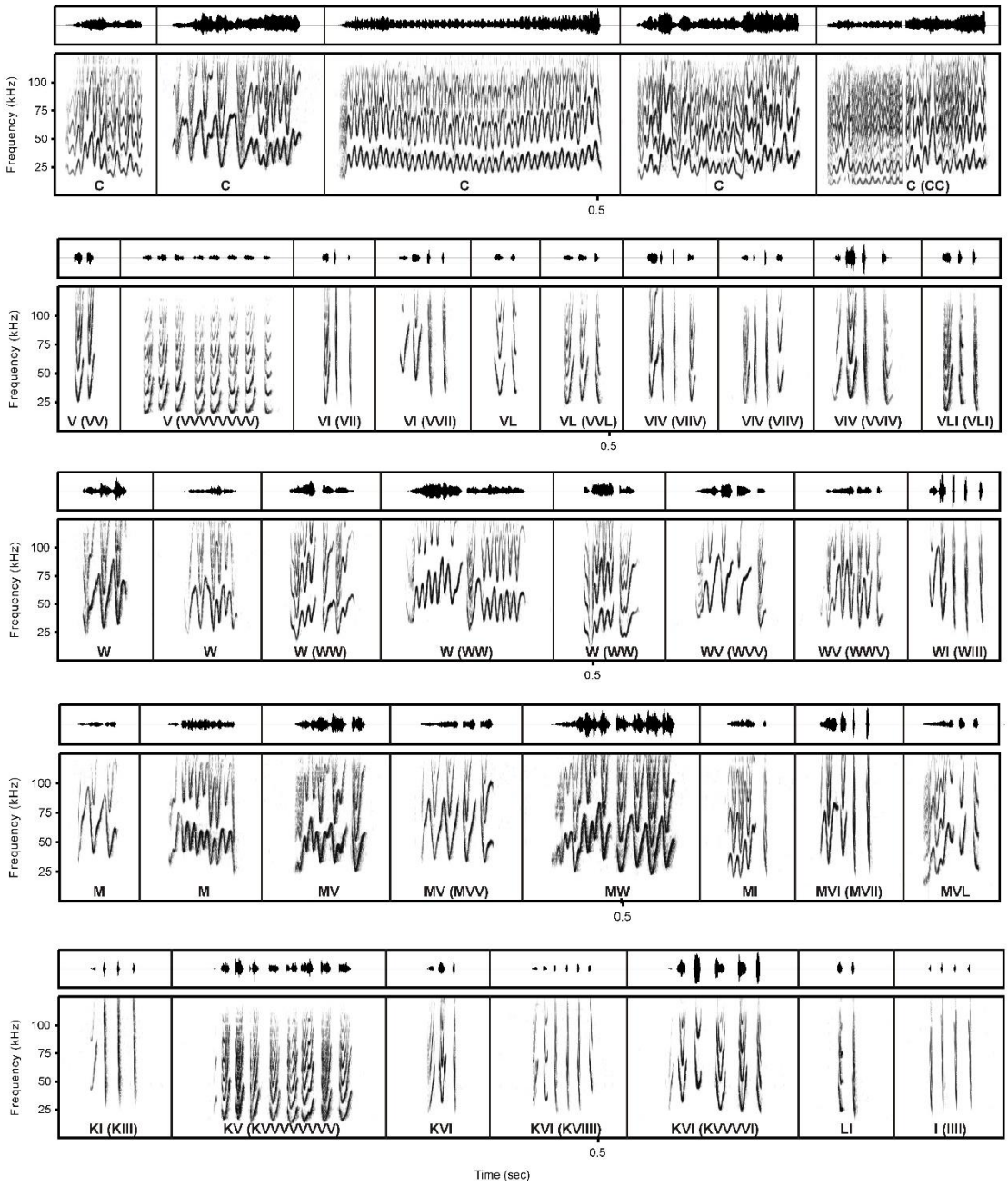
Figure 6



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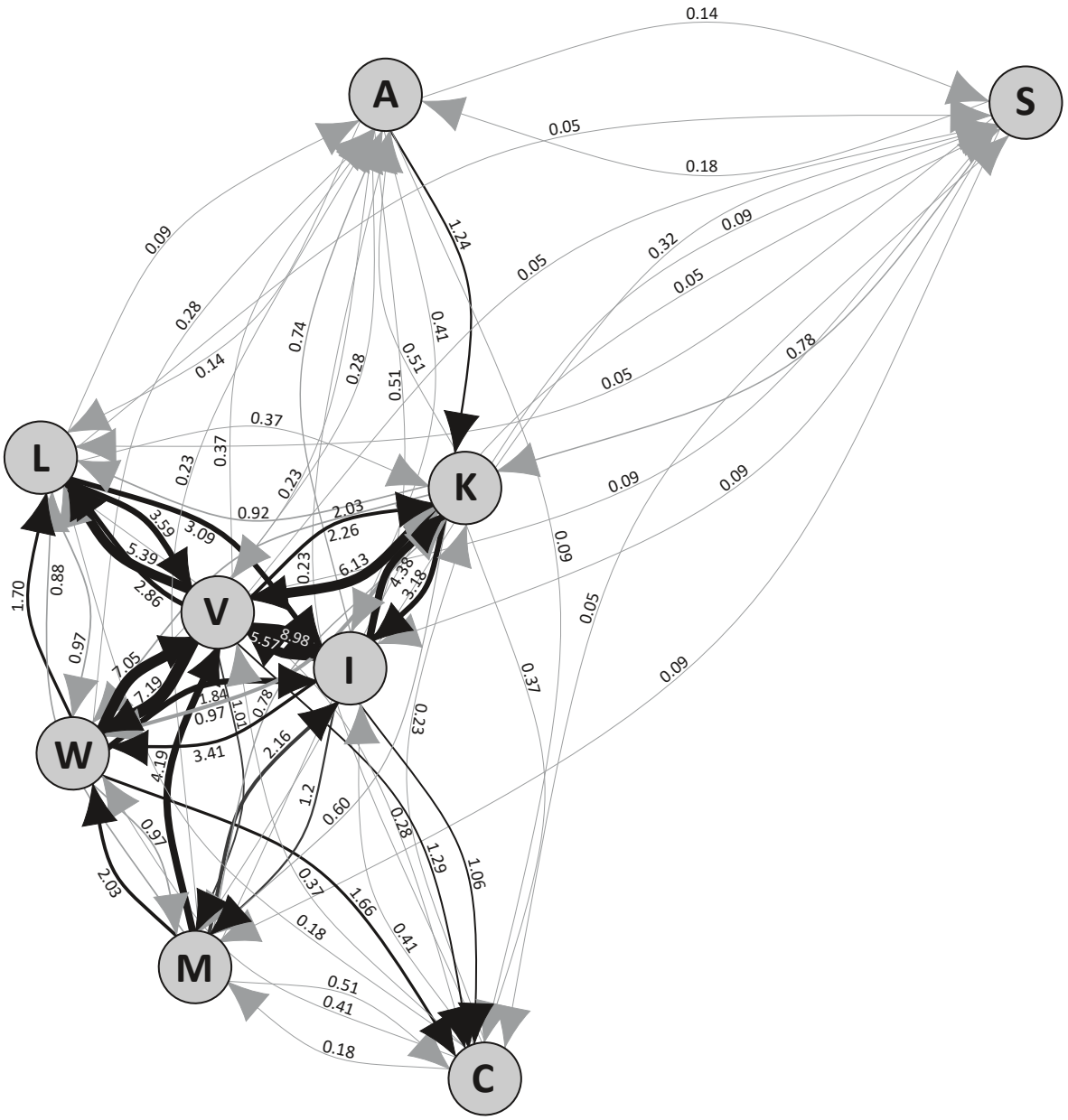

Manuscript body

Download source file (279 kB)

Tables

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Figures

Figure 1 - Download source file (306.12 kB)
Fig. 1. Study sites of M. blythii: 1 – GRK-K mine complex, 2 – ZGN-K mine, 3 – R-20 et al. mine complex (Ak-Monayski mines), 4 – R-21 to R-24 mine complex (Petrovski mines), 5 – R-7 mine (one of the Bulganakski mines).

Figure 2 - Download source file (687.98 kB)
Fig. 2. Examples of the division of the vocalisation units into syllables and phrases, and their classification into vocalisation types and variants.

Figure 3 - Download source file (230.69 kB)
Fig 3. Syllable types and their variations identified in courtship vocalisations of M. blythii.

Figure 4 - Download source file (227.82 kB)
Fig. 4. Relationship between the number of vocalisations analysed and number of identified vocalisation types (A) and vocalisation variants (B) based on rarefraction analysis. Horizontal lines indicate three rarefaction sample sizes (100, 500, and 1000 vocalisations). Vertical lines show the expected numbers of vocalisation types and variants at these sample sizes.

Figure 5 - Download source file (157.62 kB)
Fig. 5. Proportion of the most frequent vocalisation types (A) and vocalisation variants (B) (>1% of the analysed vocal repertoire).

Figure 6 - Download source file (360.26 kB)
Fig. 6. Examples of the most frequently produced vocalisation types (phrase ordering). Corresponding vocalisation variants (syllable ordering) are given in parentheses.

Figure 7 - Download source file (32.26 kB)
Fig. 7. Network of phrase transition showing the ordering of phrases within vocalisations. Nodes represent phrase types and arrows indicate transitions between them. Arrow thickness is proportional to transition frequency, and proportions of individual transitions are given indicated along the connecting lines.

Supplementary Online Material

File 1 - Download source file (17.15 MB)
Appendix 1. Example video recordings of mating aggregations of M. blythii:
Mov 1a_Site 3_copulating pairs

File 2 - Download source file (26.41 MB)
Appendix 1. Example video recordings of mating aggregations of M. blythii:
Mov 1a_Site 3_copulating pairs

File 3 - Download source file (23.37 MB)
Appendix 1. Example video recordings of mating aggregations of M. blythii:
Mov 1c_Site 3_group of three individuals

File 4 - Download source file (21.5 MB)
Appendix 1. Example video recordings of mating aggregations of M. blythii:
Mov 2_Site 5_aggregation of individuals (some silent and some vocalising); vocalisations of summer aggregation of approximately 100 individuals can be heard in the background

File 5 - Download source file (26.18 MB)
Appendix 1. Example video recordings of mating aggregations of M. blythii: Mov 3_Site 5a_aggregation of individuals and copulating pair

File 6 - Download source file (25.4 MB)
Appendix 1. Example video recordings of mating aggregations of M. blythii: Mov 4_Site 5a_aggregation of individuals and copulating pair

File 7 - Download source file (23.53 MB)
Appendix 1. Example video recordings of mating aggregations of M. blythii: Mov 5_Site 5a_copulating pairs

File 8 - Download source file (16.74 kB)
Appendix 2. Description of identified syllable types in courtship vocalisations of M. blythii.

File 9 - Download source file (1.58 MB)
Appendix 3. Sound files with examples of syllable types found in courtship vocalisations of M. blythii showed in Fig. 3.

File 10 - Download source file (25.39 MB)
Appendix 4. Sound files with examples of courtship vocalisations of M. blythii showed in Fig. 6.

File 11 - Download source file (135.77 kB)
Appendix 5. A complete list of all identified vocalisation types (phrase ordering) and vocalisation variants (variable syllable repetitions within phrases) in courtship vocal display of M. blythii. Vocalisation types are highlighted in bold and grey. Each vocalisation type represents a unique sequence of phrases, whereas vocalisation variants correspond to different numbers of syllable repetitions within the same phrase sequence.