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THE DRUMMING SIGNALS OF THREE WINTER STONEFLY SPECIES (CAPNIIDAE, LEUCTRIDAE: PLECOPTERA); WITH DISCUSSION RESOLVING TWO COMMON INTERVAL PATTERNS

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ABSTRACT

The drumming signals of three winter stonefly species from two intermittent California Coast Range streams are described. *Calileuctra dobryi* male calls have monophasic and decreasing varied beat-interval patterns. *Mesocapnia frisoni* calls have monophasic and increasing varied beat-interval patterns. *Calileuctra ephemera* calls only have decreasing varied beat-interval patterns. There is considerable overlap in the mean interbeat intervals of the two allopatric *Calileuctra* species and only slight differences in mean number of beats/call and call duration. However, the mean interbeat interval pattern provides the most accurate recognition of the species.

From a review of 34 Nearctic descriptive drumming papers (1977 to 2011), the term diphasic was inconsistently used to describe percussive signals in two different ways: the interbeat interval pattern (radically changing rhythm) and the signal pattern (two repeated calls composed of differing beat counts and interbeat intervals). Currently, the term monophasic is used to describe nearly-even or unchanging signal interval patterns. The definitions of 20 drumming variables are provided and four broad descriptive characters are updated, including a generalized example of three interbeat interval patterns with analyses and pattern determinations. The accuracy and precision of three sound analysis programs are compared, and methods for drumming signal recording, digital signal analysis, and experimental research are presented.

Keywords: Plecoptera, *Calileuctra*, *Mesocapnia*, vibrational communication, drumming

INTRODUCTION

Drumming behavior is known in 141 of 144 tested Nearctic stonefly species (Appendix). This mode of intersexual communication contains descriptive signal characters exhibiting a broad range in complexity, determined from enumerated and measured drumming signal variables. Our understanding of these has increased over the last decade (Stewart & Sandberg 2006), leading to more accurate and updated descriptions. In response to these increases, we provide an updated list of 14 signal characters from four categories (Table 1) and an associated example describing the methodology of interbeat interval pattern determination (Fig. 1). However, this fascinating system of vibrational signaling remains poorly understood and untested in relation to the effects of adult age and environmental variables including ambient temperature.

Despite the shortage of experimental research, continued descriptive studies have revealed the need for greater accuracy. Recent descriptions continued to report the mean interbeat interval and introduced a new drumming variable, the interbeat interval pattern. These two signal variables are determined in two very different ways: 1) a single **overall** mean interbeat interval, usually reported in tables, summarizing all interbeat intervals from all analyzed signals; and 2) a partially summarized, continuous and sequential series of **individual** mean interbeat intervals (with standard deviation and range), usually reported graphically, providing the mean interval pattern of the entire signal. The mean interbeat interval pattern was referred to as the drumming signal's "vibrational fingerprint" (Sandberg 2011a).

The drumming signals of 12 Nearctic Capniidae and Leuctridae species have been described (Table 2). The mean interbeat interval patterns for six of these species (1 Capniidae, 5 Leuctridae) have been updated from monophasic to varied beat-interval where the complete interval range was reported. Nearctic Capniidae typically have simple calls with fewer beats/signal and monophasic interval patterns compared to intermediate or complex signals with higher beats/signal and varied beat-interval or diphasic interval patterns. *Bolshecapnia maculata* (Jewett) calls were uniquely complex in that 4-way exchanges lacked male response signals, and each of the two sequential calls and female answers had different mean intervals and mean interval patterns (Sandberg 2011b). Two *Mesocapnia* Raušer species were described with complex grouped signal patterns. Nearctic Leuctridae species interval patterns ranged from simple monophasic and intermediate varied beat-interval to complex grouped signal patterning in *Megaleuctra complicata* Claassen (Sandberg 2011b).

The objective of this study was to describe the drumming signals of *Calileuctra dobryi* Shepard & Baumann, *C. ephemera* Shepard & Baumann, and *Mesocapnia frisoni* Baumann & Gaufin using reared adults with known ages. We had hoped to gain some insight concerning the effects of age upon signal variables. However the current study fell short of this objective and provides preliminary species descriptions based mostly upon adults with estimated ages determined in number of days after collection. In addition to three new descriptions, the accuracy and precision of three computer sound analysis programs are compared, and definitions for all known drumming signal variables are updated.

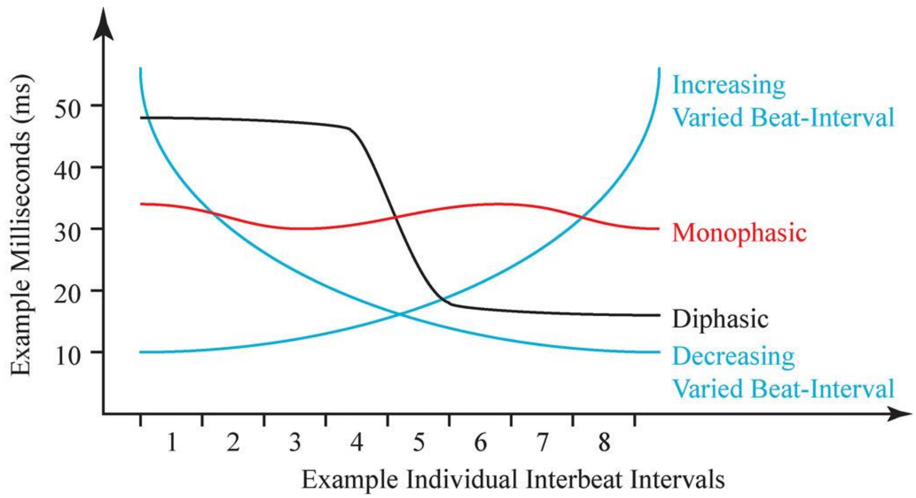
MATERIAL AND METHODS

Collecting & Rearing. In an attempt to obtain reared *Calileuctra* adults with known ages, mature larvae were collected using a dip net and placed inside labeled 250-500 ml Nalgene jars with 3-5 mm thick Styrofoam interior linings and stream water. Because *Calileuctra* larvae were either unavailable or present in low numbers, adults were collected using a beating sheet and held individually in labeled aspirator tubes lined internally with 1 mm thick Styrofoam containing crumpled paper towel for additional habitat. Adults and larvae were transported in ice chests to the laboratory where the larvae were transferred into 12-24 ounce Styrofoam rearing cups containing stream water. Pieces of Styrofoam were added to rearing cups to provide additional habitat. Larvae, adults and additional stream water used to refresh rearing cups were maintained in a refrigerator with a glass door adjusted to ~7°C and placed outdoors

Table 1. Updated stonefly drumming signal character descriptions (Stewart 2001, Stewart & Sandberg 2006 & Sandberg 2009, 2011a, 2011b).

	Character	Description
Signal Types	♂C-♀A-♂R	Male calls (♂C) initiate intersexual exchanges (communication). Female answers (♀A) are the 2^{nd} signal in simple-intermediate exchanges. Male responses (♂R) are the 3^{rd} signal in intermediate-complex exchanges, usually with intervals different from the call.
Signal Methods	Percussion	Simple tapping of the ventro-apical abdomen onto substrates.
	Rub	Complex non-percussive scratching, scraping or rubbing on substrates, involves a short anteriorly directed drag of the ventro-apical portion of the abdomen. Descriptive variables include number of rubs/signal and rub duration but not frequency (Hz).
	Tremulation	Complex vibrational signaling without abdomen to substrate contact, produced by rapid body movements which transmit the percussion-like signal.
Interval and Signal Patterns	Monophasic Interval Pattern (M)	Simple signal with approximately even interbeat intervals without increasing, decreasing or other patterns, determined by a maximum – minimum interval difference (ID) of 10 ms or less (Sandberg 2011b). Interval pattern nearly a horizontal line (Fig. 1).
	Varied Beat-Interval Pattern (VB-I)	Signal of intermediate complexity with varying interbeat interval patterns (decreasing, increasing, or other), determined by a 10 ms or more ID. Interval pattern chart with increasing, decreasing or other curved line (Fig. 1).
	Diphasic Interval Pattern (D)	A single complex continuous signal with two "phases" and 3 distinct interval patterns (monophasic–rapidly decreasing VB-I–monophasic). Interval pattern chart sigmoidal (Fig. 1).
	Diphasic Signal Pattern	An intermediate signal in a few chloroperlid, perlodid, perlid, & peltoperlid species, composed of two successive grouped call signals having monophasic or VB-I interval patterns with slightly different mean intervals and beat counts.
	Grouped Signal Pattern	Complex series of call or answer signals composed of regularly repeating monophasic or varied beat-interval sequences having 2 or more beats.
	Combination Signal Pattern	Complex signal(s) composed of 2 or more interval patterns. Either a single signal composed of monophasic and grouped patterns (Sandberg 2009) or multiple signals composed of varied beat-interval, diphasic or grouped patterns (Sandberg 2011a).
Exchange Patterns	Two way Exchange	Simple intersexual exchange composed of a single ♂ call followed by a single sequenced or overlapped ♀ answer.
	Three way Exchange	Intermediate intersexual exchange composed of a single ♂ call followed by a single sequenced or overlapped ♀ answer, and concluded with a ♂ response signal. 4-way (♂C-♀A-♂C-♀A) and longer exchanges have been documented.
	Symphonic Exchange	Complex intersexual exchange composed of diphasic and/or grouped ♂ calls, with multiple overlapped or interspersed ♀ answers and ♂R either interspersed or at end.
	Female Answers	Simple to intermediate signal following ♂ call (Sequenced), beginning before end of the ♂ call (Overlapped), or multiple signals inserted throughout a ♂ call or between grouped calls (Interspersed).

exposed to indirect sunlight. The adults that emerged were transferred to insulated collecting tubes labeled with site, gender, emergence date and id-number, and corresponding exuviae were preserved individually and labeled using the same unique data.



Ex. 1

Ex. Species	Example $\bar{x}$ Interbeat Intervals (ms) i1	i2	i3	i4	i5	i6	i7	i8	$\bar{x}$ Σ (ms)	$\bar{x}$ # Beats	ID (max-min)	Interval Pattern
A (N=4)	34	32	30	31	32	34	33	30	216	7.7	4	M
B (N=1)	48	48	47	46	25	17	16	16	247	9	32	D
C (N=4)	41	30	23	21	15	13	12	11	151	7.7	30	↓ VB–I
D (N=1)	10	11	12	14	17	21	27	35	147	9	25	↑ VB–I

Ex. 2

Ex. Species A Males	Example Interbeat Intervals (ms) i1	i2	i3	i4	i5	i6	i7	i8	Σ (ms)	# Beats	ID (max-min)	Interval Pattern
1	34	32	30	31	32	34	33	30	256	9	4	M
2	33	32	29	30	31	35	33		220	8	6	M
3	35	30	29	33	34				186	6	6	M
4	32	35	30	31	32	31	33		221	8	5	M
$\bar{x}$ IIP, Σ, #	34	32	30	31	32	34	33	30	216	7.7	4	M

Ex. 3

Ex. Species C Males	Example Interbeat Intervals (ms) i1	i2	i3	i4	i5	i6	i7	i8	Σ (ms)	# Beats	ID (max-min)	Interval Pattern
1	41	30	23	21	15	13	12	11	166	9	30	↓ VB-I
2	40	30	22	20	14	14	12		152	8	28	↓ VB-I
3	42	28	22	23	17				132	6	25	↓ VB-I
4	40	30	23	21	15	11	12		155	8	29	↓ VB-I
$\bar{x}$ IIP, Σ, #	41	30	23	21	15	13	12	11	151	7.7	30	↓ VB-I

Fig. 1. Generalized stonefly drumming interval patterns defined using example data. Ex. 1: Summary data of four species (A-D) illustrating the mean interbeat interval patterns (IIP) in the chart (N = Number of signals, Monophasic = M, Varied Beat-Interval = VB-I, and Diphasic = D). Ex. 2: Species A data determining the mean monophasic interval pattern. Ex. 3: Species-C data determining the mean decreasing

varied beat-interval pattern. Interbeat intervals (i1-i8), Signal duration (Σ), Interval difference (ID). Note the mean IIP is based upon unequal observations and sound analysis programs report measurements in hundredths of milliseconds (seconds^{-5}).

Table 2. Overall ♂ call signal characters and variables of previously published descriptions for 12 Nearctic stonefly species. Previous monophasic interval patterns (M) conforming to the current varied beat–interval (VB–I) definition are marked with an asterisk. Upward and downward arrows indicate increasing and decreasing intervals. G = grouped signal character. ? = not reported. Drumming variables expressed as mean ± standard deviation or range.

Species of Capniidae & Leuctridae	T°C & (Age (d))	Interval & (Signal) Patterns	# Beats/ Signal, Group[A], & Groups/Call[B]	Interbeat, Intragroup[A], Intergroup[B], Interval (ms)	Duration (ms)
Allocapnia granulata[1]	8 (?)	M	2.0 ± 0.0	59.0 ± 27.8	80.7 ± 30.6
Bolshecapnia maculata[2]	16–17 (?)	M	4.6 ± 0.7	33.3 ± 1.7	?
B. maculata[2]	21–22 (?)	M	4.0 ± 0 .3	29.7 ± 1.1	?
B. maculata[2]	18–20 (?)	M	5.2 ± 0.5	7.4 ± 0.6	?
B. maculata[2]	17 (?)	M	4.1 ± 0.3	9.5 ± 0.7	?
B. maculata[3]	19–20 (1)	↑M ♂1st, ↑VB-I ♂2nd	5.2 ± 0.5 6.0 ± 1.1	32.6 ± 1.6 49.8 ± 8.4	138.2 ± 14.8 249.1 ± 58.6
Capnia quadrituberosa[2]	22 (?)	M	3.4 ± 0.5	29.2 ± 2.3	?
Isocapnia grandis[4]	? (?)	?	4.3 ± 0.7	287.0 ± 55.0	?
Mesocapnia lapwae[5]	17–21 (?)	M(G)	3.4 ± 1.0	38.6 ± 2.7	?
Mesocapnia werneri[5]	20 (?)	↓VB–I*	6.4 ± 0.7	94.1–21.9	?
Mesocapnia yoloensis[5]	20–22 (?)	M(G)	2.8 ± 0.5	20.0 ± 3.9	?
Megaleuctra complicata[6]	22–23 (?)	M(G)	2.7 ± 0.5[A] 2–23[B]	30.3 ± 4.4[A] 326.7 ± 43.2[B]	3500–2290
M. complicata[7]	21.7 (8)	M(G)	40.1 ± 4.4 2.8 ± 2.7[A] 17.5 ± 1.5[B]	25.6 ± 2.7[A] 318.0 ± 11.7[B]	4834 ± 675
Zealeuctra arnoldi[8]	23–25 (?)	↓VB–I*	28.8 ± 3.0	~80–51	1818 ± 248
Z. claasseni[8]	23–25 (?)	↓VB – I*	22.9	~112–67	1986 ± 116
Z. claasseni[9]	22 (?)	↓VB – I*	21.4 ± 2.5	~60–25	793 ± 116
Z. hitei[8]	23–25 (?)	↓VB – I*	39 ± 3	~60–33	~2400 ± 100
Z. hitei[9]	22 (?)	M	31.6 ± 4.5	~20–12.5	518 ± 75
Z. warreni[10]	24–25 (?)	↓VB – I*	10.8 ± 3.0	68.5 ± 8.1	?

Citations – State: [1]Graham 1982 - WI, [2]Stewart et al. 1991 - CA, [3]Sandberg 2011b - CA, [4]Stewart & Zeigler 1984 - MT, [5]Abbott & Stewart 1997 - CA, [6]Stewart & Sandberg 2004 - OR, [7]Sandberg 2011b - CA, [8]Zeigler & Stewart 1977 - TX, [9]Snellen & Stewart 1979 - TX, [10]Stewart et al. 1995 - ARK.

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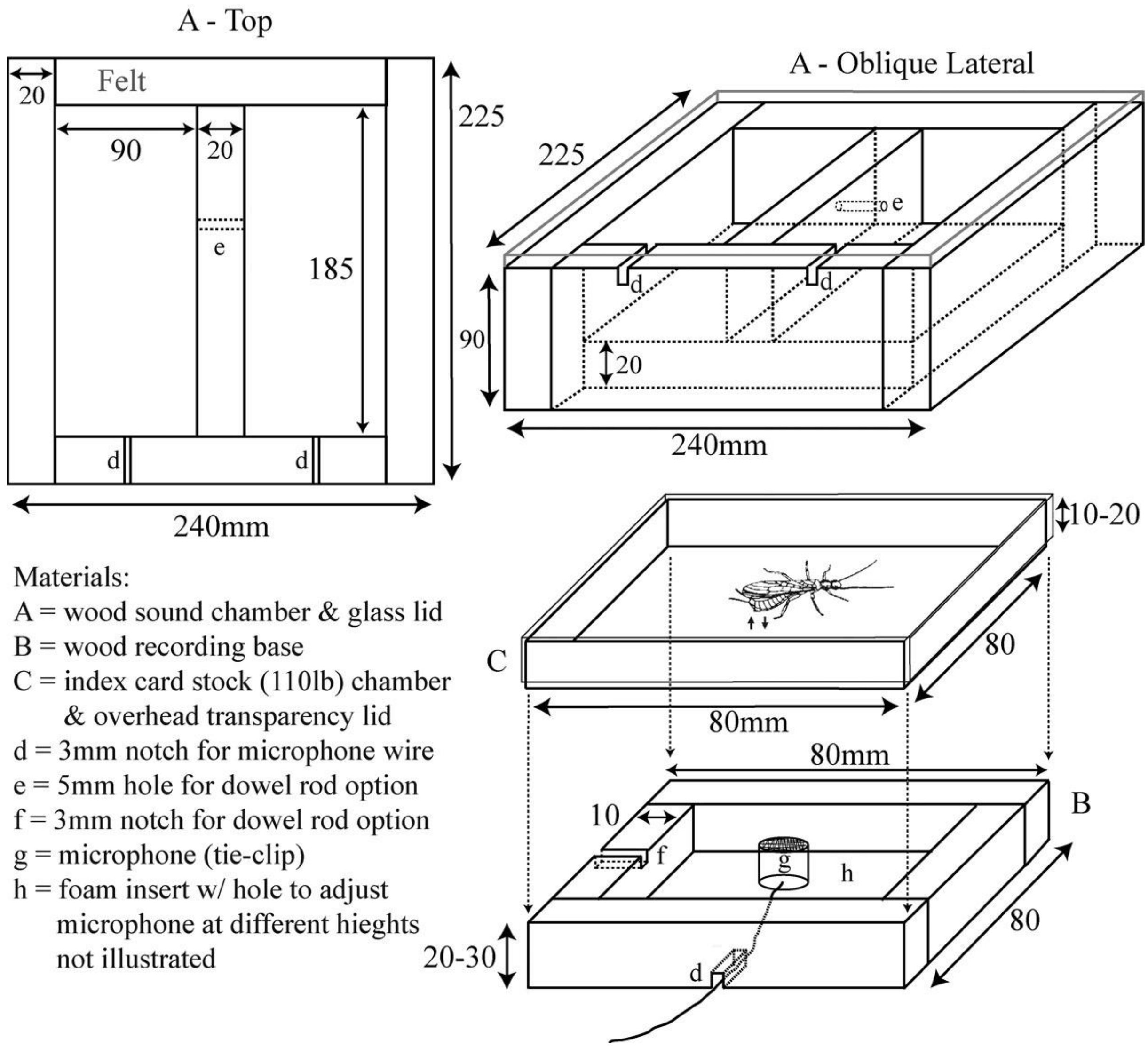


Fig. 2. One sound dampened recording chamber. Isolated left and right sound chambers (A) containing recording bases and chambers (B&C) provide separated stereo recordings (necessary for analysis of ♀ overlapped answers). Smaller stoneflies may require recording chambers (C) to be connected using a thin wooden dowel (not illustrated) taped to the bottom and passing through hole (e).

Collecting Locations. *Calileuctra ephemera*: U.S.A.: California, Mendocino Co., Intermittent tributary to Whitlow Creek, Hollow Tree Rd., 4 km SW Little Penny, 38.91306°N, -123.47111°W, J.B. Sandberg, L.E. Serpa, 16/II/2013. *Calileuctra dobryi* and *Mesocapnia frisoni*: California, Orange Co., Silverado Creek, Silverado Canyon Rd., 2nd concrete low water crossing, 6.8 km E Silverado, 33.75118°N, -117.57162°W, J.B. Sandberg, E.F. Drake, 09-11/II/2014. Mature larvae were absent from small isolated pools at intermittent tributary to Whitlow Creek, and *C. dobryi* larvae were present in low numbers within decaying leaves in shallow pools of Silverado Creek. Mature *M. frisoni* larvae were abundant and widely distributed in Silverado Creek.

Recording & Analysis Materials. Drumming signals were obtained using two, partitioned and sound dampened chambers, each constructed of wood and glass (Fig. 2). Stoneflies were individually held inside small recording chambers constructed of heavy card stock and transparency film which if necessary, could be connected by a thin wood dowel. Two digital audio recorders were used to make stereo 16 bit/44.1 kHz (wav) recordings (Roland models R-09HR and R05), each connected to a pair of omnidirectional electret microphones. Thus, two pairs of individuals could be recorded simultaneously inside two sound dampened chambers placed in close proximity to each other, without sound interference from the opposite pair.

The sound analysis program Ace of Wav 2.6-2.7 (Polyhedric Software) has entered maintenance mode for Windows XP and failed to install in Windows 7. To continue using this program in new or different operating systems we bypassed the installer conflict. The Ace of Wav program folders and files were copied from a Windows XP program directory and pasted (instead of installed) into the root directory of a Windows 7 computer. The executable file (acid.exe) within the Ace of Wav program folder was fully operational in Windows 7.

Beat Counts & Interval Measurements. Analysis was conducted using two computer programs open at once, Ace of Wav and an Excel spreadsheet. When a wav file was opened for analysis, the file name (species, gender, id number, collection or emergence date, recording date, time and sequence-number) was entered along with each measured individual interbeat interval, number of beats/signal, and signal duration. Ace of Wav provided interval and duration measurements in milliseconds to the hundredth place, and Excel calculations provided the beats/signal (COUNT +1) and duration (SUM) of selected intervals.

A second method to measure signal duration was employed as a quality control (QC) measure. While remaining in the same analysis magnification, the elapsed time from the beginning of the first beat to the beginning of the last beat was selected and measured. The QC duration (measured) was then compared to the sum of the multiple individually measured intervals (calculated duration). If the difference between them was equal to 5 ms or less, the intervals were accepted. If the difference was greater than 5 ms, the intervals were deleted, and re-measured. This procedure is recommended for all future drumming analysis.

Table 3. Metronome signal variables for a single signal (10s, 11 beats, 60bpm) measured 10 times each with three computer sound analysis programs (N=300 intervals). Mean interval patterns in Figure 3.

Sound Analysis Program	Avg ± SD / Range		
	Interbeat Interval (ms)	Duration (ms)	Quality Control Duration (ms)
Ace of Wav	999.93 ± 0.01	9,999.22 ± 0.01	10,000.16 ± 0.00
	999.93–999.91	9,999.20–9,999.24	10,0000.16
Audacity	999.96 ± 0.17	9,999.64 ± 0.68	9,999.95 ± 0.16
	999.32–1,000.11	9,998.24–10,000.43	9,999.50–10000.01
Avisoft SASLab Lite	1,000.06 ± 0.06	10,000.58 ± 0.17	10,000.08 ± 0.15
	999.93–1,000.40	10,000.25–10,000.76	10,000.00–10,000.13

Sound Analysis Program Comparison. Three sound analysis programs were tested for interval measurement accuracy and precision using a single metronome test signal (10 seconds, 11 beats, 60 beats/minute). The test signal was generated using the Roland R-09HR metronome function, and recorded using the Roland R05 by connecting the line out and line-in of each (respectively), using a mini 3.5 mm stereo patch cable. The 10-beat test signal was transferred to the computer and measured 10 times, for a total of 100 intervals per program (Ace of Wav, Audacity, and Avisoft SASLab Lite).

Recording & Analysis Methods. Individual recording sessions ranged from 8-10 hours producing a total of 663 recorded signals from 28 males and one female over a total of 208 hours. One male was recorded continuously over a 36 hour period. This method produced too many signals to analyze for the *Calileuctra* species with calls ranging 80-100 beats/signal. The analysis of a single signal could require a maximum of one hour. In order to expedite the analysis of each male, only the first 10 calls from each 8-10 hour recording session were analyzed (a consistent and minimum subsample of the total signals per recording from the earliest part of the recording). To increase the interbeat interval measurement precision and accuracy of *Calileuctra* signals (with high number of beats/signal and short intervals), Ace of Wav horizontal zoom function was increased to 20x and vertical zoom adjusted from 1-10x.

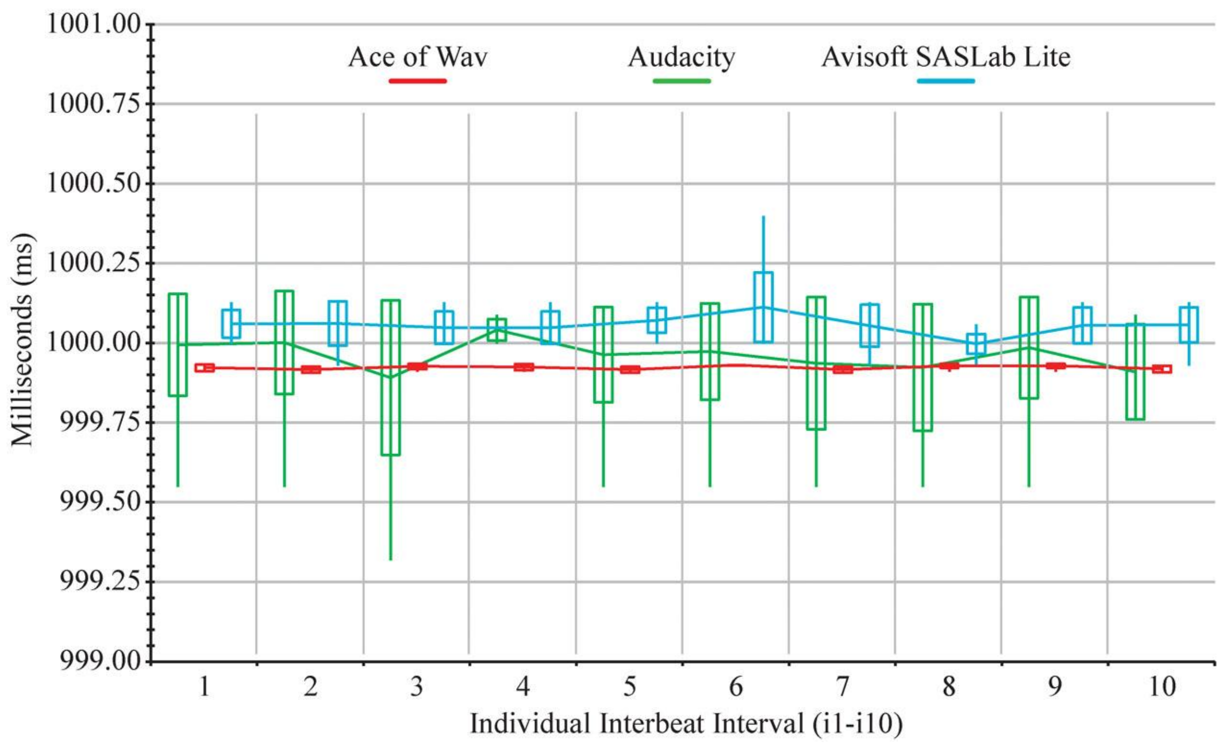


Fig. 3. Performance comparison of three computer sound analysis programs using a single recording from a metronome (10 s, 11 beats, 60 bpm). The monophasic signal was measured 10 times using Ace of Wav (red), Audacity (green), and Avisoft SASLab Lite (blue). Horizontal lines = mean interbeat interval, boxes = standard deviation, and vertical lines = range.

RESULTS

Accuracy & Precision of Sound Analysis Programs

The 300 total test intervals and three categories from three programs were entered into SPSS v21 and Levene's test failed to accept the null hypothesis that measurement variances were equal ($p < .001$). The non-parametric Kruskal-Wallis one-way analysis of variance confirmed that overall mean measurements of the three programs were significantly different from each other (p < .001, CI 95%). The mean interval of each program was used to compare measurement accuracy and standard deviation was used to compare the measurement precision. Audacity and Avisoft mean interbeat intervals were slightly more accurate (Table 3), each mean varying 0.04 ms from perfect (1000.00 ± 0.0 ms). Conversely, these programs had slightly lower precision (higher standard deviation). Although Ace of Wav consistently under measured mean interbeat interval by 0.07 ms (Table 3), its precision was the best (lowest standard deviation) of the three programs (Fig. 3).

Drumming Signal Variables for Descriptive and Experimental Studies

- *Ambient Temperature*. Recorded at the start and end of recording periods. The effects of environmental variables including temperature require further study.

- *Number of Adults (Male, Female)*. Indication of robustness. Rearing mature larvae insures multiple adults are available. Descriptions are complete only when male-female exchanges are analyzed. Lone male call descriptions are preliminary, especially for species with 3-way exchanges or grouped calls that are dependent upon the female's answer signal. Should be fixed in experimental studies between species or test groups.

- *Age of Adults (Male, Female)*. Laboratory reared and collected teneral adults have known ages at the time signals are recorded. Knowing exact age is necessary for accurate species descriptions, comparisons between individuals, additional and successive recordings of the same individual, and for repeated future studies. Collected adult age is estimated by the number of days after collection followed by the + symbol indicating that they are probably older. The effects of age and temperature require continued experimental research to determine the effect upon drumming variables.

- *Number of Signals Analyzed (Call, Answer, & Response)*: Indication of robustness. A statistical minimum observation includes at least 10 signals per male of known age (or 10 exchange signals per pair), and should be repeated daily or every other day over their lifespans.

- *Number of Beats/Signal (Call, Answer, & Response)*. Usually highly variable. Observed by using sound analysis software. Determined by counting the percussive peaks of a drumming signal's audio file, or calculated as a count of the spreadsheet cells containing interval measurements, plus one (Fig. 1).

- *Interbeat Interval (Call, Answer, & Response)*. The elapsed time between two consecutive beats. Amount of observed variability depends upon the signal interval pattern, age, and environmental variables including temperature. Observed and measured using sound analysis software. Entered in a spreadsheet and labeled sequentially. The first interbeat interval is expressed as i1, and the range 1 to 10 as i1-i10.

- *Mean Interbeat Interval (Call, Answer, & Response)*. Usually highly variable. The calculated mean, standard deviation and range <u>summarizing all measured interbeat intervals from all signals</u>. Usually reported in tables for all individuals, for each individual, & for each individual on each successive day with 10 or more signals (minimum statistical subsample).

- *Interval Difference (Call, Answer, & Response)*. Interval difference (ID) is the mathematic difference between the maximum and minimum interbeat intervals within a signal (Sandberg 2011c). Provides the result determining monophasic patterns (≤10 ms) and varied beat interval patterns (>10 ms). Monophasic interval patterns with "even" interval variation typically have less than a 10 ms interval difference representing natural and random variation (nearly flat interval pattern). Varied beat-interval patterns typically have either an increasing, decreasing or other type of interval pattern, usually with a greater than 10 ms interval difference. Applies to all species (with possible exceptions, *B. maculata*), reporting the "evenness" or "unevenness" (flat interval pattern or a curved interval pattern) of continuous, sequential interbeat intervals regardless of mean interbeat interval. Calculated for individual signals to determine the ratio of monophasic to varied beat-interval signals, and for

Table 4. Male call signal variables for *Calileuctra dobryi*, *C. ephemera*, and *Mesocapnia frisoni*. *Calileuctra dobryi* had 23 calls with monophasic interval patterns and 137 with decreasing varied beat-interval patterns. *Mesocapnia frisoni* had three calls with monophasic interval patterns and 31 with increasing varied beat-interval patterns. *Calileuctra ephemera* calls had only decreasing varied beat-interval patterns. The ages of collected males were estimated as the number days held in captivity before recordings and followed by the plus symbol (+) indicating they were probably older.

Species, # of Males Temperature, Age	# Signals # Intervals	# Call Beats/ Signal	Avg ± SD / Range Interbeat Interval (ms)	Duration (ms)	Quality Control Duration (ms)
Calileuctra dobryi, N=18	160	117.8 ± 23.7	31.9 ± 6.9	3724.9 ± 984.2	3729.1 ± 983.6
20–20.5°C, 2–4+d	18,693	57–157	22.5–123.0	1813.3–6140.6	1812.2–6145.3
Calileuctra ephemera, N=5	50	87.5 ± 5.3	38.1 ± 13.6	3298.1 ± 584.9	3300.8 ± 587.2
20–20.5°C, 1+–3+d	4,324	75–103	21.7–123.5	2271.0–4612.5	2268.8–4615.1
Mesocapnia frisoni, N=5	34	5.9 ± 1.4	100.1 ± 15.2	494.5 ± 174.1	494.6 ± 174.1
20.5–21°C, 2–4d	168	3–10	70.1–174.5	155.8–1076.1	156.5–1075.9

the mean interbeat interval pattern (Table 1 & Fig. 1).

- *Mean Interbeat Interval Pattern (Call, Answer, & Response)*. Inherently less variable than mean interbeat interval. The most informative and accurate drumming signal description. The calculated mean, standard deviation and range for each individual and successive interbeat interval from all signals (usually reported in box and whisker charts for all individuals, for each individual on each successive day with 10 or more signals (minimum statistical subsample). Note: two signals may have the exact same mean interbeat interval, number of beats/signal, and signal duration, but have different interval patterns (Table 1, Fig. 1).

- *Signal Duration (Call, Answer, & Response)*. Usually highly variable. Dependent upon number of beats/signal and individual interbeat intervals. The calculated sum of the measured interbeat intervals. For quality control, the signal duration is measured between the first and last beats (single measurement) and compared to the sum of the interbeat intervals (multiple measurements). A maximum threshold for error can be set (example: 5 ms), and if exceeded, the signal's individual intervals should be re-measured.

- *Call-Answer Exchange Interval*. Usually highly variable. The duration between the last male call beat and the first female answer beat in sequenced exchanges.

-*Answer-Response Exchange Interval*. Usually highly variable. The duration between the last female answer beat and the first male response beat in 3-way sequenced exchanges.

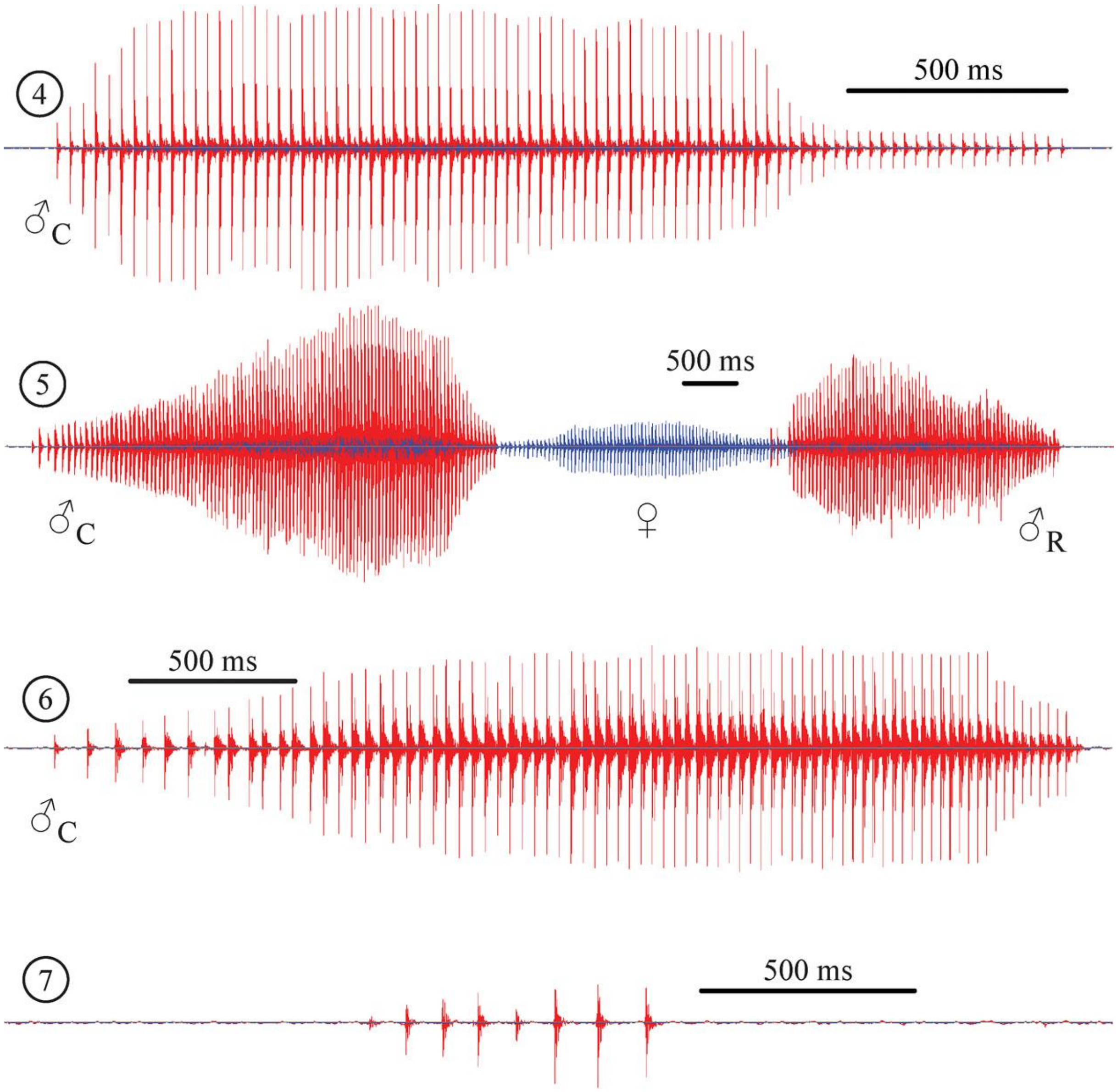
- *Exchange Duration*. Usually highly variable. The sum of the signal durations (call, answer, & response) and exchange intervals (call-call, call-answer, answer-response, or other).

- *Number of Groups/Call*. Usually highly variable. Grouped calls are difficult to differentiate from irregularly repeated calls without repeated female answers. A count of the regularly repeated call groups/call.

- *Number of Beats/Group*: Usually less variable than the number of beats per non-grouped call. A count of call beats from each individual call group.

-*Total Number of Beats/Grouped Call*. The total number of beats from all individual groups of a grouped call.

- *Intergroup Interval*. Usually highly variable despite that grouped signals patterns are described



Figs. 4-7. Sonograms of stonefly drumming signals (Ace of Wav). 4. *Calileuctra dobryi* monophasic interval call (6.1 ms ID). 5. *Calileuctra dobryi* overlapped, decreasing varied beat-interval, 3-way exchange. 6. *Calileuctra ephemera* decreasing varied beat-interval call (68.5 ms ID). 7. *Mesocapnia frisoni* increasing varied beat-interval call (30.5 ms ID).

as regularly repeating. Alternatively expressed as the ♂-♂ (or call-call) exchange interval in the absence of an interspersed female answer. Determined by measuring the duration between the last grouped call beat within the first call group, and the first grouped call beat of the second call group, and repeated for each successive group.

- *Intragroup Interval*. Usually less variable than the interbeat call intervals of 2-way and 3-way exchanges. Measured in the same way as interbeat intervals, except the intervals are within regularly repeated groups of beats.

- *Call Interval containing 1st Overlapped Female Answer Beat*. Usually highly variable. A record of the sequentially numbered call interval that contains the first female answer beat. The elapsed time between the preceding call beat and first answer beat is measured and labeled as the overlapped male-female exchange interval.

- *Intergroup Intervals containing multiple Interspersed Female Answer Signals*. Usually highly variable. Records of sequentially numbered intergroup intervals containing repeated female answers. Additionally, the interspersed male-female exchange interval is measured.

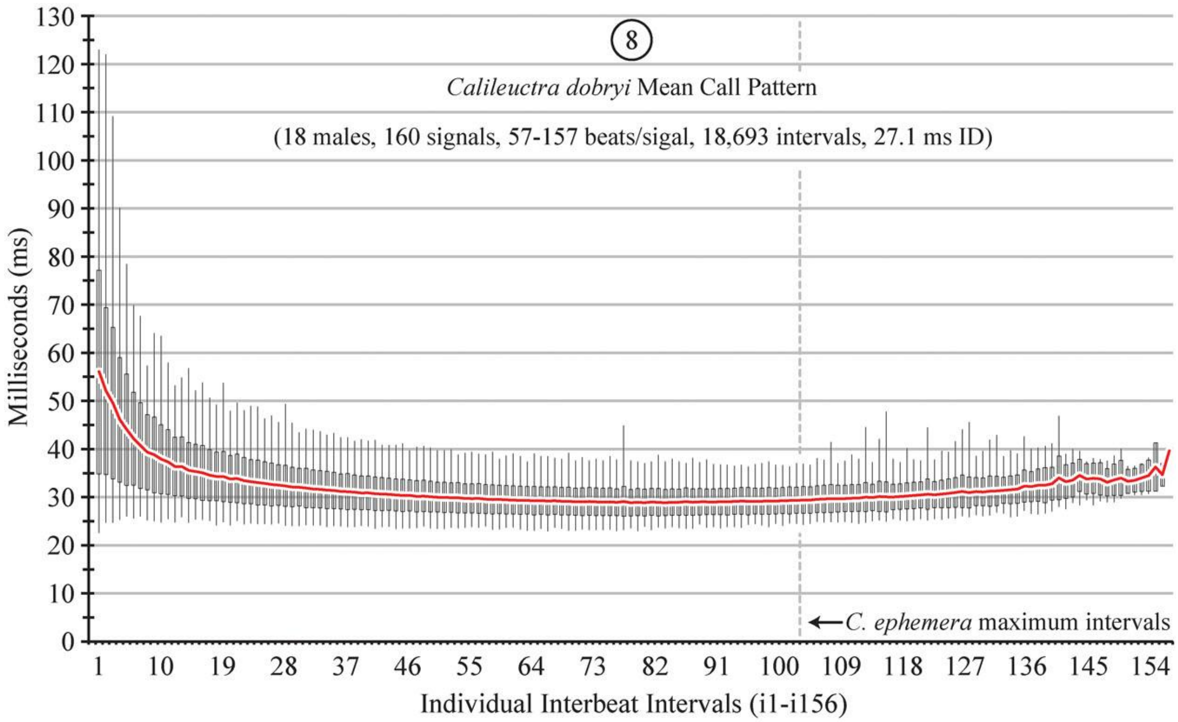
Calileuctra dobryi. This species was a prolific drummer with a total of 405 drumming signals recorded from 18 males and one female at 20-20.5°C. The estimated age of 15 collected males ranged from 1+ to 5+ d and the actual age of three

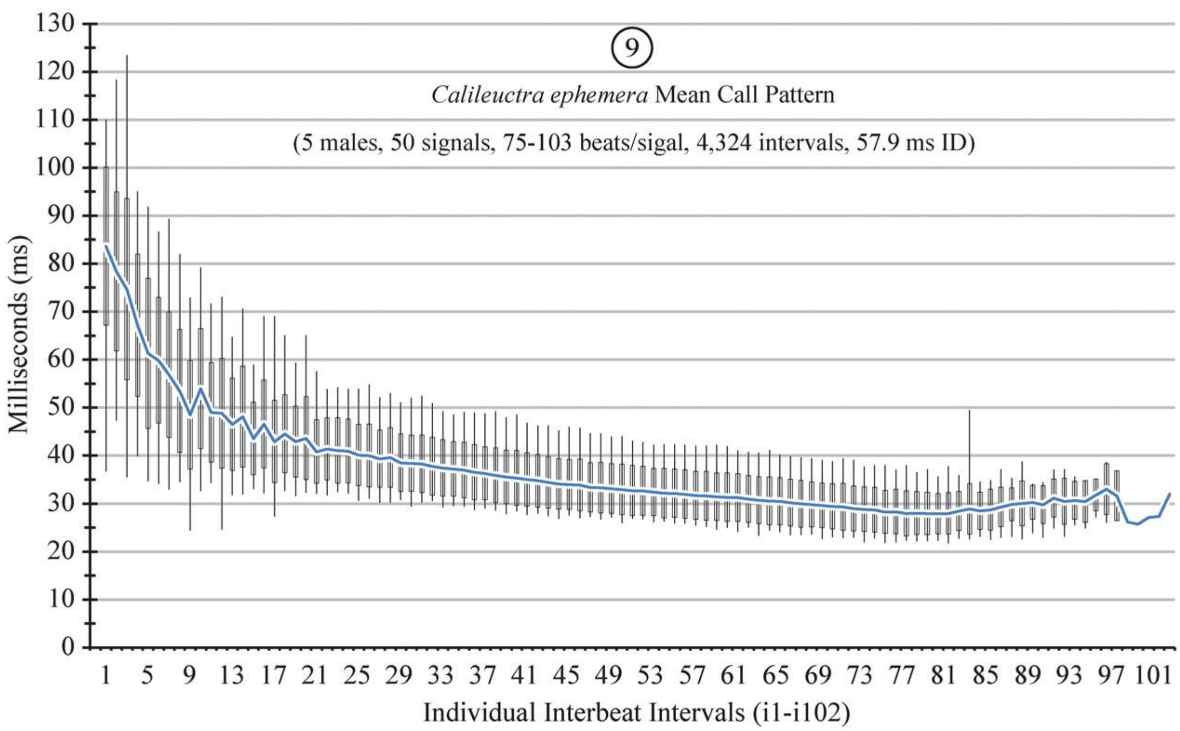
Table 5. *Calileuctra dobryi* ♂ call signal variables, mean interval patterns, and mean interval differences for individuals with at least 8-10 signals (N=138). Male 06R was recorded for 36 hours, the first 10 signals were analyzed from the beginning of 3 consecutive 12 hour periods from midnight 2/18/2014 to 5 PM 2/19/2014. Mean interval patterns in Figure 10.

Individual	Age (d)	# Signals	# Interbeat Intervals	Mean Interval Pattern*	# Beats/ Signal	Avg ± SD / Range Interbeat Interval (ms)	Duration (ms)
♂01 C	2+	8	1180	↓VB-I / 65.6	148.5 ± 4.2 / 144–156	39.2 ± 9.6 / 31.2–123.0	5778.4 ± 168.1 / 5614.0–6140.6
♂03 F	1+	10	1259	↓VB-I / 33.3	126.9 ± 8.5 / 113–137	32.7 ± 6.8 / 27.3–86.8	4116.8 ± 241.4 / 3545.7–4410.3
♂06 R	3–4	30	2556	↓VB-I&M / 7.3	86.2 ± 8.0 / 67–98	28.5 ± 3.0 / 22.5–51.4	2427.1 ± 323.1 / 1813.5–2949.9
♂07 C	4+	10	719	↓VB-I&M / 6.5	72.9 ± 6.5 / 57–80	31.2 ± 1.9 / 27.8–44.9	2240.1 ± 184.1 / 1813.3–2490.4
♂08 C	2–3+	10	1366	↓VB-I / 24.9	137.6 ± 4.4 / 132–144	29.3 ± 4.8 / 23.8–73.4	3997.0 ± 267.9 / 3571.3–4525.6
♂09 C	2+	10	1318	↓VB-I / 37.5	132.8 ± 4.4 / 125–139	29.3 ± 6.2 / 24.9–81.1	3863.4 ± 147.6 / 3674.4–4177.6
♂11 C	3–4+	10	1352	↓VB-I / 25.5	136.2 ± 9.3 / 123–154	32.1 ± 4.5 / 26.9–81.4	4340.0 ± 376.1 / 3789.9–5005.3
♂12 C	3+	10	1413	↓VB-I / 42.9	142.3 ± 8.3 / 129–157	31.6 ± 7.0 / 26.3–86.9	4466.9 ± 266.5 / 4067.8–4891.7
♂13 C	3+	10	1374	↓VB-I / 38.0	138.4 ± 5.9 / 127–148	31.8 ± 6.5 / 26.2–106.4	4357.1 ± 224.0 / 4134.1–4932.1
♂14 C	4+	10	1162	↓VB-I / 24.2	117.2 ± 4.4 / 111–127	31.9 ± 4.8 / 28.0–75.2	3704.2 ± 174.3 / 3460.6–4093.4
♂16 R	4	10	1059	↓VB-I / 26.2	106.9 ± 5.3 / 99–116	33.5 ± 6.2 / 24.6–66.3	3544.8 ± 457.1 / 2910–4198.7
♂17 R	2	10	1188	↓VB-I / 21.6	119.8 ± 3.8 / 113–126	28.0 ± 3.9 / 22.9–71.2	3318.2 ± 235.8 / 2906.8–3645.2

C= collected, F= field, R= reared, *- interval pattern / mean interval difference (ms), ↓ = decreasing.

Sandberg, J.B., L.E. Serpa, and E.F. Drake. 2015. The drumming signals of three winter stonefly species (Capniidae, Leuctridae: Plecoptera); with discussion resolving two common interval patterns.
Illiesia, 11(06):51-74. Available online: http://illiesia.speciesfile.org/papers/Illiesia11-06.pdf





Figs. 8-9. *Calileuctra* mean interbeat interval patterns. 8. *Calileuctra dobryi* mean (red line) decreasing varied beat-interval call pattern. 9. *Calileuctra ephemera* mean (blue line) decreasing varied beat-interval call pattern. Mean interval pattern (colored lines), standard deviation (boxes), and range (vertical lines). Note: x-axis scales unequal.

Sandberg, J.B., L.E. Serpa, and E.F. Drake. 2015. The drumming signals of three winter stonefly species (Capniidae, Leuctridae: Plecoptera); with discussion resolving two common interval patterns.
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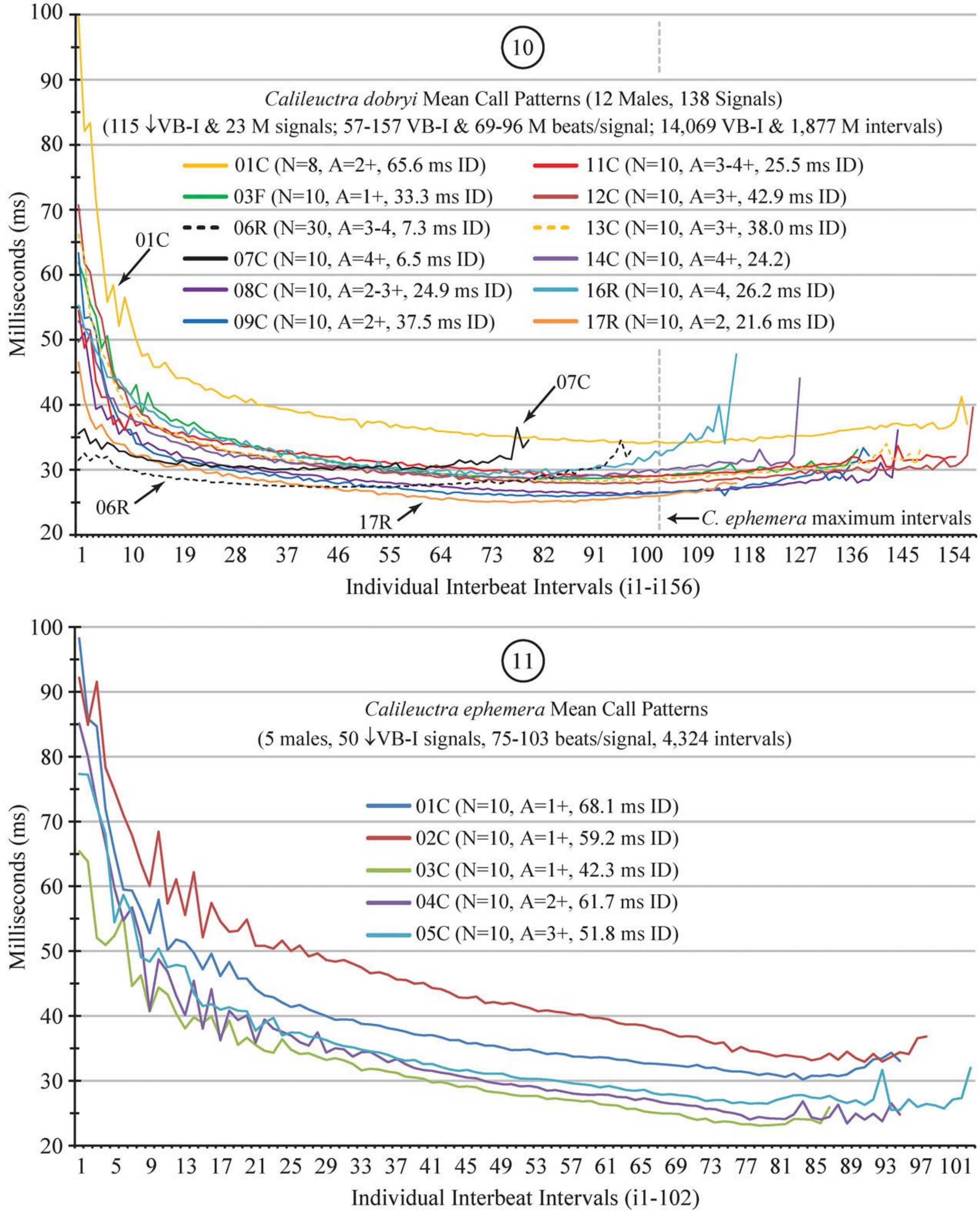


Figs. 10-11. Individual mean interval patterns. 10. *Calileuctra dobryi* decreasing varied beat-interval & monophasic (males 06R, 07C) mean call interval patterns of individuals with at least 8-10 signals. 11. *Calileuctra ephemera* decreasing varied beat-interval mean call patterns. Note: x-axis scales unequal.

reared males ranged from 2-4 d (Table 4). Three of the 18 collected males were recorded at Silverado Creek (N=16 signals). One reared male (♂06R) was recorded continuously over a 36 hour period. For this male, a subsample of the first 10 signals from the beginning of each successive 12 hour period were first analyzed as a group (N=30), and then re-analyzed in three separate groups of 10 signals per 12 hour period to examine the possible effect of increased age.

Of the 405 total recorded signals, a subsample of 160 calls (18,693 intervals) including one 85-beat female answer and one 78-beat male response signal were analyzed. Male calls were variable with 137 signals having varied beat-interval patterns and 23 with monophasic patterns. Only one 3-way intersexual exchange was analyzed. The female overlapped answer (ID=19.2 ms) and male response (ID=30.3 ms) signals had varied beat-interval patterns. The highly variable male call had 57-157 beats/signal, interbeat intervals ranging from 22.5-123.0 ms, and 1813-6140 ms signal durations (Table 4, Fig. 4).

The single 3-way, varied beat-interval intersexual exchange consisted of a 115-beat call (50.5 ms ID), followed by an overlapped female answer beginning after the 113th call beat (19.23 ms ID), and concluded with an overlapped male response (30.3 ms ID) beginning after the 77th answer beat (Fig. 5). The mean interbeat interval call pattern for 18 male's initially decreased (i1-i50), held approximately even (i51-i125), and finally increased irregularly from i126-i156 (Fig. 8). The mean interval difference was 27.1 ms (N=18 males and 160 signals), fitting the varied beat-interval pattern definition.

Twelve of the 18 total males with at least 8-10 signals (N=138) were re-analyzed individually in an attempt to provide evidence of the suspected effect that age may have upon drumming variables (Table 5). Collected male 01C (2+ d) was suspected to have the greatest actual age with calls (N=8) having the most mean beats/signal (148.5 ± 4.2) and longest mean intervals of 39.2 ± 9.6 ms (Fig. 10). Reared male 06R (3-4 d) and collected male 07C (4+ d) were suspected to be among the youngest individuals and called with signals (N=40) having varied beat-interval (N=17) and monophasic patterns (N=23). Curiously, they had the fewest mean number of beats/signal (86.2 ± 8 & 72.9 ± 6) respectively (Fig. 10), and their mean intervals were only slightly less than other males. Male 17R had more beats/signal than males 06R and 07C, but may also be another of the youngest individuals with the third shortest mean interval 28.0 ± 3.9 ms (Fig. 10).

Table 6. *Calileuctra ephemera* ♂ call signal variables, mean interval patterns, and mean interval differences for individual males (N=50 signals). Mean interval patterns in Figure 11.

Individual	Age (d)	# Signals	# Interbeat Intervals	Mean Interval Pattern*	Avg ± SD / Range #Beats/ Signal	Avg ± SD / Range Interbeat Interval (ms)	Avg ± SD / Range Duration (ms)
♂**01 C**	1+	10	886	↓VB-I / 68.1	89.6 ± 4.1 / 81-95	40.5 ± 13.6 / 26.8-108.3	3593.6 ± 373.9 / 3604.53-4136.35
♂**02 C**	1+	10	886	↓VB-I / 59.2	89.6 ± 5.0 / 82-98	46.7 ± 13.6 / 28.5-106.5	4137.0 ± 271.0 / 3680.6-4612.5
♂**03 C**	1+	10	828	↓VB-I / 42.3	83.8 ± 2.6 / 78-87	32.4 ± 9.9 / 21.7-75.3	2680.7 ± 176.7 / 2271.0-2910.1
♂**04 C**	2+	10	874	↓VB-I / 61.7	88.4 ± 3.8 / 83-95	34.6 ± 13.3 / 22.3-118.4	3022.9 ± 222.2 / 2776.3-3525.8
♂**05 C**	3+	10	850	↓VB-I / 51.8	86.0 ± 7.2 / 75-103	36.0 ± 12.2 / 24.2-123.5	3062.1 ± 344.2 / 2644.6-3785.6

C= collected, *= interval pattern / mean interval difference (ms), ↓ = decreasing.

Two *C. dobryi* typical drumming variables from Table 5 and a third less informative calculation were plotted in three-dimensional space (Fig. 12). These included the number of beats/signal, signal duration, and a calculated variable not previously included in typical descriptions (average interbeat interval/signal). Average interbeat interval/signal is stripped of individual interbeat interval variation over the course of the signal and simplified into a single value. It would have some value if all drumming signals had perfectly monophasic interval patterns. The plot only illustrates the mean signal data trends from Table 5 (high beats/signal and duration variation), but does not describe the decreasing mean interbeat interval patterns (Fig. 10). Furthermore, if Figure 12 was used to provide behavioral evidence in support of a proposed new species, and because of the outlying individual groupings, one might be tempted to postulate that male 1C and males 6R and 7C might be two additional species separated from the majority of overlapping individuals in the center, instead of recognizing the high variation of a single species.

Monophasic signal patterns were not prevalent in *C. dobryi* signal analysis. Only two suspected-youngest males (06R & 07C) had signals with both monophasic patterns (N=23) and varied beat-interval patterns (N=17). Additionally, these individuals had the fewest number of beats/signal (Fig. 10). We hypothesize that the calls of these and other suspected-younger males had at least some monophasic patterns, possibly fewer mean beats/signal, shorter mean interbeat intervals, and mean interval patterns composed of shorter intervals (males 06R, 07C, 16R, and 17R).

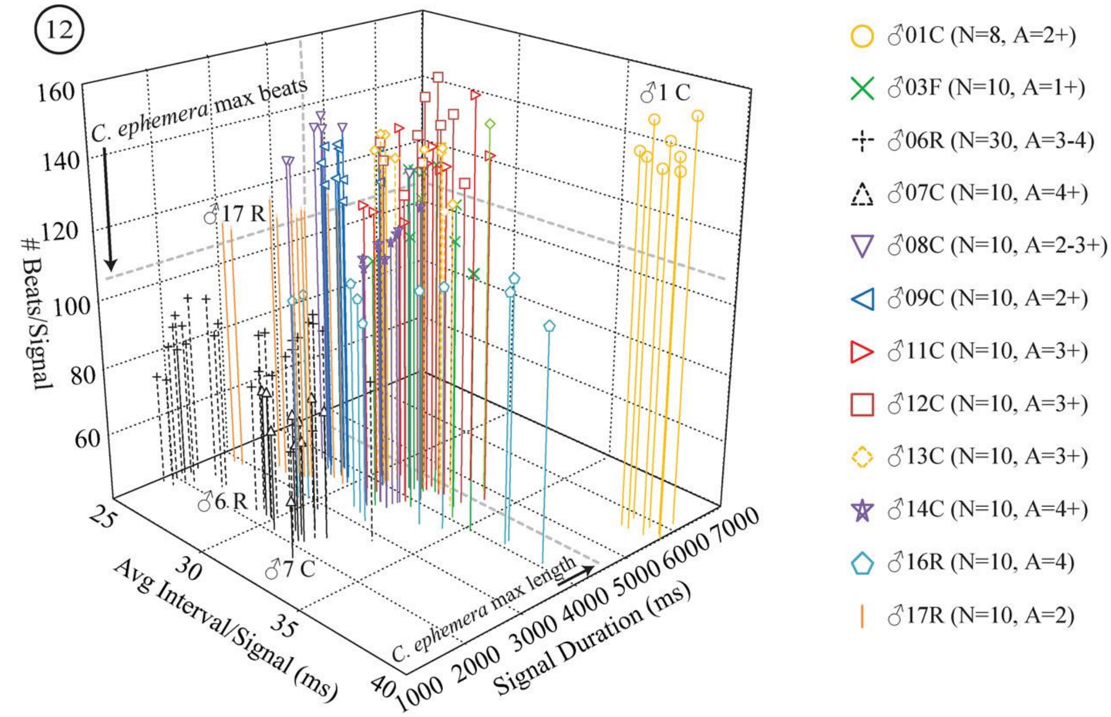
In an attempt to detect if signal variables changed over a brief observation period, one reared male was recorded continuously for 36 hours. Of the male 06R total call signals (N=30) recorded over three consecutive 12 hour periods, half had monophasic patterns (Fig. 10). The occurrence of monophasic interval patterns decreased from 7 (hour 1-12), to 5 (hour 13-24), and 3 (hour 25-36) (Fig. 14). Male 07C (age 4+ d), had eight of 10 signals with monophasic interval patterns. Males 06R and 07C mean beats/signal were less than other males (Table 5). Perhaps the youngest males of this species call with shorter signals that gradually increase over time.

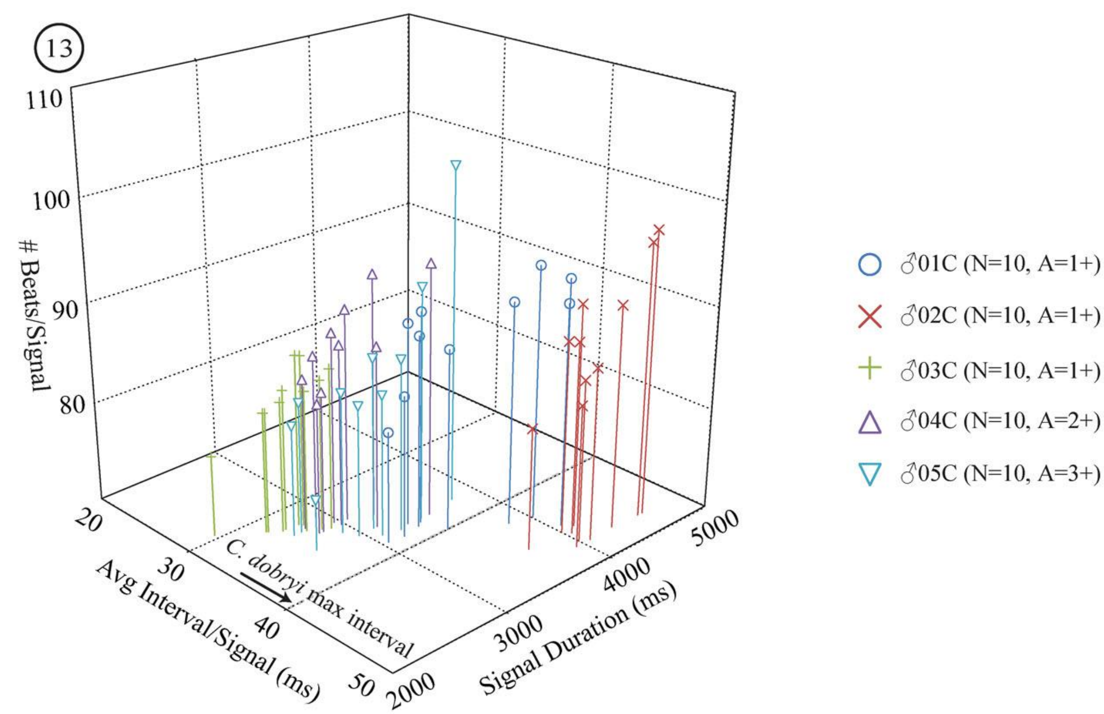
Unexpectedly, the mean interval of male 06R decreased from 29.5 ± 2.6 ms (age 3 d) to 25.6 ± 1.8 ms (age 3.5 d), and increased to 30.2 ± 2.1 ms (age 4 d), ending slightly higher than the first 12 hour observation (Fig. 14). One might have expected from the abundance of other suspected-older individuals with longer intervals (Fig. 10), for a steady increase in mean interval patterns over time. We can't explain this erratic (decrease-increase) interval trend other than from natural variation and too short of an observation period.

Calileuctra ephemera. A total of 224 drumming signals were recorded from five collected males at 20-20.5°C. The estimated age of males ranged from 1+ to 3+ days on recording dates. Similar to *C. dobryi*, only the first 10 signals were analyzed from each male's recording periods in order to expedite analyses.

Of the 224 recorded signals, only 50 calls (4,324 intervals) were analyzed (equivalent effort in comparison to *E. dobryi*). Male calls were consistent having only decreasing varied beat-interval patterns (ID=57.9 ms). The highly variable male call had 75-103 beats/signal, a mean interval of 38.1 ± 13.6 ms, and mean signal duration of 3,298.1 ± 584.9 ms, all overlapping with *C. dobryi* (Table 4, Fig. 6). The mean interbeat interval call pattern for five males decreased irregularly (i1-i21), continued decreasing at a slower rate (i22-i81), and finally increased irregularly from (i82-i102). Although considerable overlap exists between the congeners, the mean interbeat interval patterns (Figs. 8-9) and mean interval differences, best describe the numeric and trend differences between them.

Individually, the five *C. ephemera* males had similar mean number of beats/signal (Table 6) but none had known exact ages. The males estimated age in days after capture that recordings were made (1+ to 3+ d) may be contrary to their actual age. We postulate that the slower (larger) mean individual interbeat intervals patterns at higher graph positions (red and dark blue lines in Fig. 11), and longer overall mean intervals (Table 6) of males 01C-02C, suggest that they may be older than males 03C-05C. This ambiguity between age





Figs. 12-13. Scatterplots of two drumming signal variables from Tables 5 & 6 (# beats/signal, signal duration) and atypical drumming variable (average interval/signal). 12. *Calileuctra dobryi* signals (12 males, 138 signals, 15,946 intervals). 13. *Calileuctra ephemera* signals (5 males, 50 signals, 4,324 intervals). Note: x, y & z-axis scales unequal.

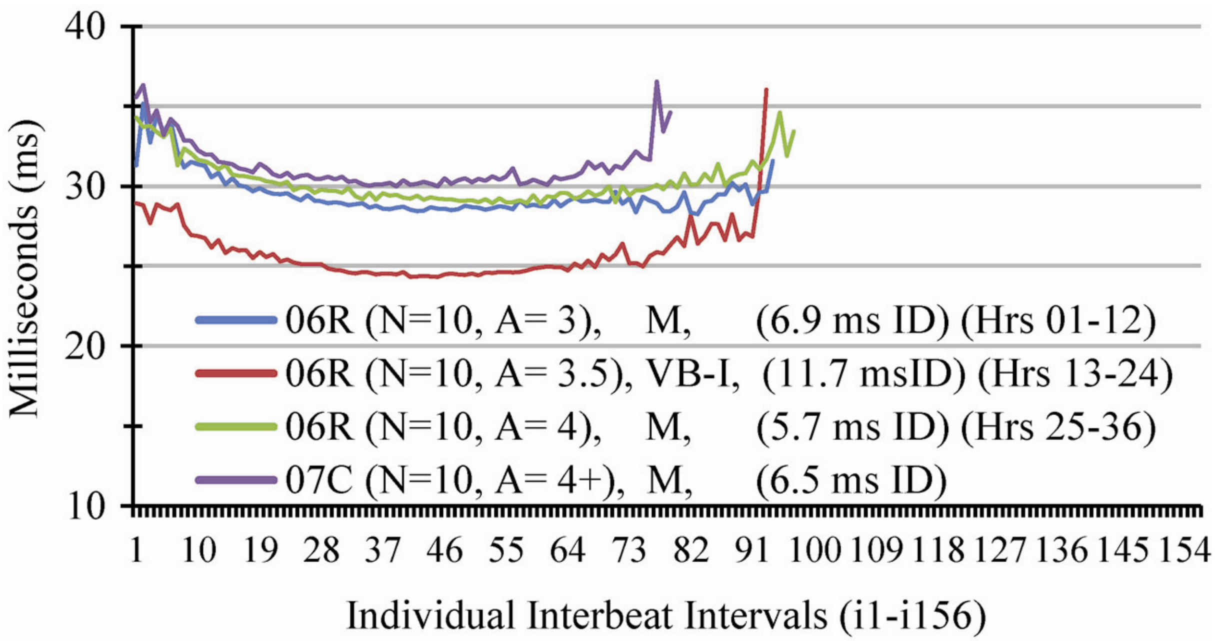


Fig. 14. *Calileuctra dobryi* (2 males, 40 signals) mean individual monophasic (males 06R, 07C) and varied beat-interval (♂ 06R) call patterns. The three ♂ 06R interval patterns were recorded during three consecutive 12 hour periods. The ratio of monophasic to varied beat-interval call patterns for 06R (blue) = 7:3, 06R (red) = 5:5, 06R (green) = 3:7, and 07C (purple) = 8:2.

and drumming variable trends could be readily solved by recording individuals with known ages, and an alternate explanation that *Calileuctra* spp. drumming signals are inherently variable is equally probable. A scatterplot of three drumming variables graphed in three-dimensional space (Fig. 13) does not reveal additional information already described in Tables 4 & 6. It also (with the use of atypical variable: average interval (ms)/signal) subtracts relevant information from the mean interval pattern (Fig. 11), by simplifying the individual intervals (N=102) over time.

Mesocapnia frisoni. A total of 34 signals (168 intervals) were recorded and analyzed from five, 2-4 d reared males at 20.5-21.0°C. The five males called with increasing varied beat-interval patterns (81.3 ms ID) of 3-10 beats/signal (5.9 ± 1.4), mean intervals of 100.1 ± 15.2 ms, and 155.8-1076.1 ms durations (Table 4, Fig. 7). Two males (♂04R, ♂05R) had only three calls with monophasic interval patterns with mean interval differences of 7.8 ms and 9.4 ms respectively (Table 7). Call durations were variable (155.8-1,076), 495 ± 174.1 ms, and dependent upon the number of beats/signal. The mean interbeat interval call pattern of five males (Fig. 15) gradually increased (i1-i6), and held approximately even (i7). The last intervals from a single call, continued to increase irregularly (i8-i9).

Four of the reared *M. frisoni* males, with more than one signal analyzed, had variable and overlapping mean beats/signal, interbeat intervals, and signal durations (Table 7, Fig. 16), indicating no trends concerning the effect of age (2-4 d) among individuals. Each male was only recorded once during an eight hour period. Perhaps if additional recordings could have been made over several successive days, later in life spans reported here, a consistent change in one of the variables may have been detected.

Table 7. *Mesocapnia frisoni* ♂ call signal variables, mean interval patterns, and mean interval differences for individual males with at least two signals (N=33). Males 04R and 05R had 2 and 1 monophasic signals respectively. Mean interval patterns in Figure 15.

Individual	Age (d)	# Signals	# Interbeat Intervals	Mean Interval Pattern*	# Beats/ Signal	Avg ± SD / Range Interbeat Interval (ms)	Duration (ms)
♂02 R	4	2	10	↑VB-I	6.0 ± 0	92.4 ± 14.1	461.9 ± 8.6
				35.8	6–6	78.3–119.1	455.7–468.0
♂03 R	2	13	74	↑VB-I	6.7 ± 1.4	105.8 ± 13.1	602.2 ± 177.0
				27.7	5–10	88.4–174.5	402.7–1076.1
♂04 R	2	15	67	↑VB-I&M	5.5 ± 1.1	97.1 ± 15.5	433.6 ± 133.5
				28.8	4–7	70.1–165.9	262.1–664.5
♂05 R	2	3	10	↑VB-I&M	4.3 ± 1.1	90.8 ± 17.6	302.6 ± 127.3
				32.3	3–5	72.3–121.5	156.5–381.5

R= reared, *= interval pattern / mean interval difference (ms), ↑ = increasing.

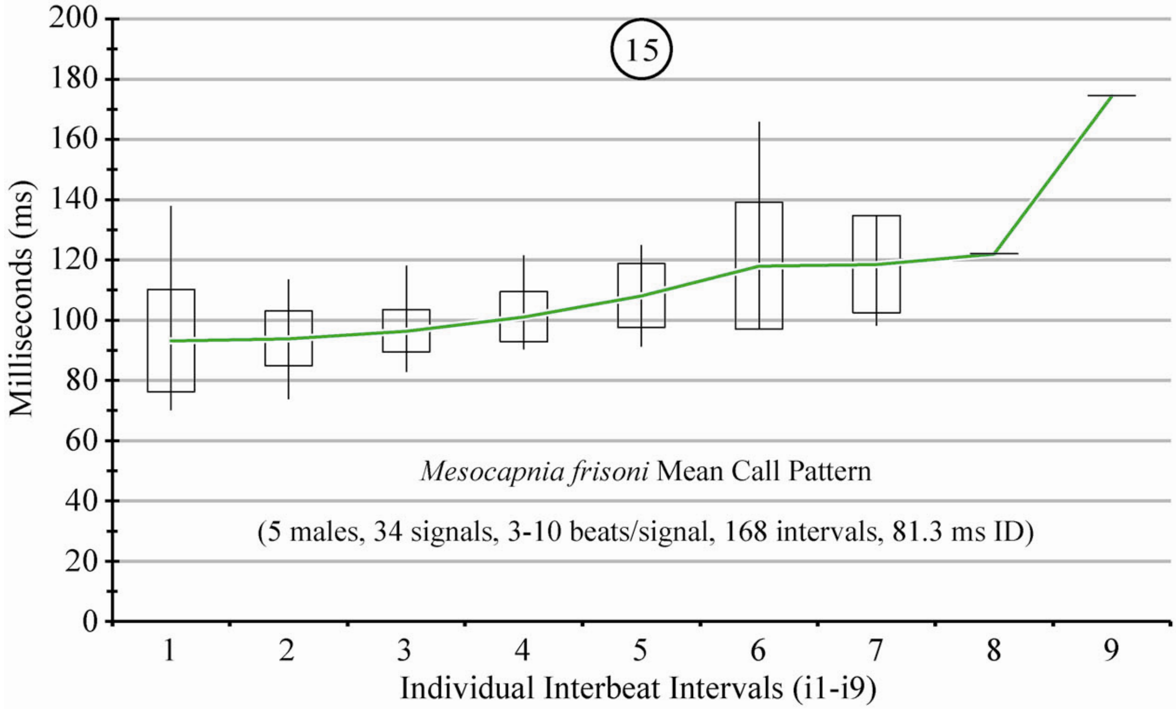
DISCUSSION

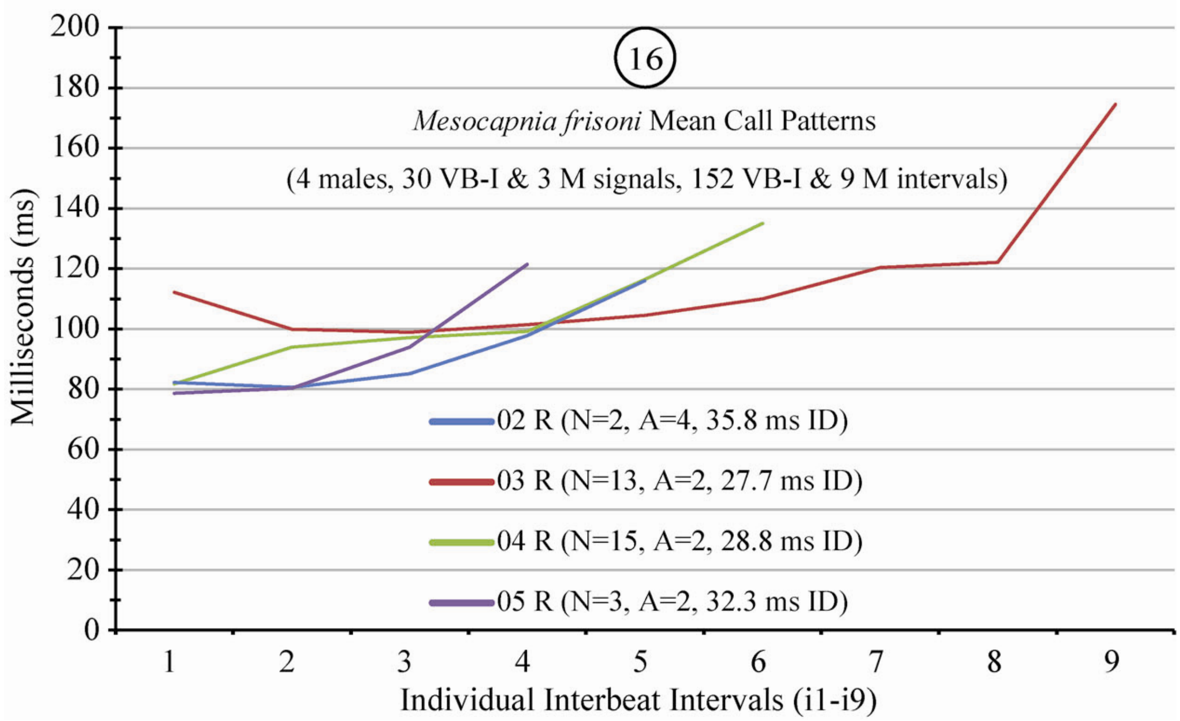
The number of Nearctic Capniidae species with increasing varied beat-interval call patterns increases to two (*M. frisoni* and *B. maculata*). The family ranges from simple monophasic to intermediate increasing or decreasing varied beat-interval interval patterns, complex grouped call patterns, and 2-way to 4-way exchange patterns (Table 2). The call signal variables of *M. frisoni* (Tables 4 & 7) were closest to *M. werneri* (Table 2) except that the latter had calls with decreasing varied beat-intervals (Abbott & Stewart 1997). The original *M. werneri* monophasic call pattern was updated because it was described as having decreasing mean intervals from 94.1 ms (i1) to 21.9 ms (i7). This pattern of consistent change over most of the signal (individual intervals) is consistent with varied beat-interval (mean ID > 10 ms).

Monophasic and decreasing varied beat-interval patterns were observed in the calls of *C. dobryi*. This is not surprising considering the increased precision of interval measurements and the refinement of drumming signal character definitions. The call variables and decreasing varied beat-interval call patterns of *C. dobryi* and *C. ephemera* (Tables 4-6 & Figs. 10-11) were somewhat similar to those of four *Zealeuctra* species (Table 2). *Calileuctra* species had long signals composed of many beats (intermediate complexity), somewhat similar to the long, grouped, tri-beat calls of *Megaleuctra complicata* (higher complexity). *Calileuctra dobryi* and *C. ephemera* calls have intermediate complexity, slightly more complex than *Zealeuctra*, but slightly less complex than *M. complicata*. *Agnetina capitata* (Pictet) from Pennsylvania (Zeigler 1989), *Paraperla frontalis* (Banks) from Colorado (Sandberg & Stewart 2003) and *C. dobryi* are the only Nearctic stoneflies having at least some calls with more than 150 beats per call signal.

During this study, we found no direct evidence to support the hypothesis that age affects drumming signal variables, especially interbeat intervals. However, from the ranges and outliers in mean interval patterns expressed by *C. dobryi* and *C. ephemera* (Figs. 10-11), and range in number of beats/signal (*C. dobryi*), the suspected effects of various unknown ages are implied. Experiments involving individual males with known ages and groups of recorded signals from increasing consecutive days over the life span should be tested for significant differences.

Recent descriptions of common drumming interval and signal patterns have been inconsistent





Figs. 15-16. *Mesocapnia frisoni* overall and individual interval patterns. 15. Overall increasing varied beat-interval mean call pattern. 16. Individual increasing varied beat-interval mean call patterns for males with more than one signal recorded. Mean interval patterns (colored lines), standard deviation (boxes), and range (vertical lines).

even though our current knowledge of the range in signal characters (interval, signal, and exchange patterns) has increased (Table 1). Several examples are found in the primary author's previous studies. Stewart & Sandberg (2006) provided a list of definitions of the then known call signal patterns. In their list, the term "varied beat-interval" was omitted, but its definition was provided. The term was then listed and illustrated for *Capnia quadrituberosa* Hitchcock in diagrams of stonefly duet patterns (Stewart & Sandberg 2006, Figure 12.2). However, their monophasic definition "calls with approximately even interbeat intervals", and their varied beat-interval definition "calls of slightly changed and intermediate complexity having variable length, number of beats, and rhythm of interbeat time intervals", were too vague. These original definitions allow opportunity for overlap, misunderstanding, and lack numeric limits of interval variation for monophasic and varied beat-interval patterns. A second weakness included in this book chapter was the definition of diphasic signaling (Stewart & Sandberg 2006, page 181 & Figs. 12.4-12.5). In the original usage, the term was applied to a grouped signal composed of two successive calls having different beat counts and intervals. A second more recent usage applies the term to a single continuous signal with a sigmoid interval pattern (Table 1, Fig. 1). Therefore, the term "diphasic" applies to both interbeat interval patterns and signal patterns (Table 1).

Sandberg (2009) described the call pattern of *Hesperoperla hoguei* Baumann & Stark as monophasic, despite fitting the original varied beat-interval definition. The *H. hoguei* mean call patterns were illustrated for three different groups indicating two very different interval patterns with > 100 ms mean interval differences, and the suspected increased age of collected males was suggested as the cause. This observation documented large mean interval and interval pattern variation from within a single population. It also illustrated how misrepresentative the use of only the mean interbeat interval and number of beats has been in previous species descriptions, and the critical importance of known adult age. The three *H. hoguei* populations also fit the Sandberg (2011a, 2011c) updated varied beat-interval definition. In that study, monophasic signals were further defined to have nearly even intervals limited to a mean interval difference of 10 ms or less and varied beat-interval signals with an mean interval difference greater than 10 ms. The *H. pacifica* (Banks) combination call was also described as having initial monophasic beats immediately followed by 5-15 grouped signals; the initial beats actually had a varied beat-interval pattern (Sandberg 2009, Figure 6). Only the following grouped signals had monophasic intragroup interval patterns.

Sandberg (2011b) described two of three *Cosumnoperla hypocrena* Szczytko & Bottorff populations from Cooper Canyon and Deadman Creeks, El Dorado Co., California, as having varied beat-interval patterns. This interpretation was based only upon examining the interval pattern charts, without numeric limits. Based upon the most current definitions for monophasic and varied beat-interval patterns (Sandberg 2011a, 2011c), these populations fit the monophasic definition having mean interval differences of 6.5 and 3.5 respectively. The third population from a tributary of the North Fork Cosumnes River had a mean interval difference of 17.2 and remains having varied beat-intervals.

Recently, additional criteria were added to improve the monophasic and varied beat-interval pattern definitions included within the complex 4-way exchange description of *B. maculata* (Sandberg 2011c). The most important was, that if the majority of individual signals possess a consistent interval pattern (increasing, decreasing or other), but had a mean interval difference of less than 10 ms (the general monophasic condition or random variation), than as an exception, the interval pattern should be described as varied beat-interval with a less than 10 ms mean interval difference. The ratio of the described *B. maculata* monophasic first calls that had varied beat-intervals vs. calls with monophasic intervals was 30:72 (not a clear majority).

Computer based sound analysis has increased the efficiency, accuracy (measurements to 10^{-5}

second), and precision (horizontal and vertical zoom) of percussive drumming interval measurements (interbeat, intragroup, and intergroup). Our ability to observe slight, non-random interval changes throughout a signal has improved the definitions for the known interval patterns: monophasic, varied beat-interval and diphasic (Table 1, Fig. 1). Early monophasic signal descriptions are unclear whether they were describing the signal or interval pattern, and many with large interbeat interval ranges are now thought to have varied beat-interval patterns, and should be reanalyzed.

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APPENDIX
33 DRUMMING DESCRIPTION PAPERS FOR 141 NEARCTIC SPECIES (INCLUDING ALL REFERENCES EXCEPT STEWART (2001))

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