Continued studies of drumming in North American Plecoptera; Evolutionary implications

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Abstract

Previous studies of vibrational communication of over 140 stonefly species, and those of other American and European workers, have led to a proposed paradigm on how the behavior has evolved from non-percussion through degrees of derived complexity of percussive signaling or derived methods of vibration production (Stewart 2001). We report here: 1) newly discovered signals of *Helopicus bogaloosa*, *Isogenoides frontalis, Isoperla sobria*, and *Rickera sorpta*, 2) additional signal characteristics of *Paraperla frontalis* and *I. mormona*, and 3) recording of different populations of *Helopicus nalatus* and *Isoperla fulva*, previously reported. Signaling by these eight species and the substantial results of earlier studies essentially support the paradigm. Study of Southern Hemisphere Antarctoperlaria, particularly the species rich genera *Anacroneuria* in South America, *Neoperla* in Africa, and further testing of Arctoperlaria is critically needed.

Keywords: Plecoptera, stonefly, behavior, vibrational communication, digital recording and analysis.

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Introduction

Drumming of Palearctic and Nearctic Arctoperlarian stoneflies is the most widely varied and complex system of vibrational communication currently known in insects (Stewart, 1997, 2001). The intersexual signaling involves use of low frequency, substrate-borne vibrations produced ancestrally by abdominal percussion, or by derived abdominal scratching, rubbing, or tremulation. The call signals of males are complex and convey species-specific and probably fitness information to conspecific females for up to eight meters in resonant substrates (Stewart and Zeigler 1984). Responsive females become stationary and answer with simple percussive signals that convey her specificity and location. The research on New World Arctoperlaria has been conducted mainly in the laboratory of K.W. Stewart and students, and has resulted in descriptions of male calls or duets of 140 species. Stewart and Maketon (1991) reviewed many of these. Rupprecht (1968, 1969, 1981) has reported the signals of several European species.

In previous symposia we have reported wider implications of this interesting behavioral system including the use of drumming in Plecoptera systematics (Stewart and Zeigler 1984: Toulouse, France), intraspecific variation and information content of signals (Stewart and Maketon 1990; Marysville, Australia), theoretical considerations of mate finding in relation to drumming (Stewart 1994: Tomahawk, Wisconsin, USA), considerations of mate searching behavior and tremulation (Alexander and Stewart 1997: Lausanne, Switzerland), and the most recent evolutionary paradigm of drumming and mate searching (Stewart 2001: Tucumán, Argentina).

Since the earliest quantitative studies of drumming by Rupprecht (1968) and, Zeigler and Stewart (1977), there have been major advances in the technology affecting experimental methodology, ranging from recording and analyzing with cassette recorders and oscilloscopes to the current digital recording on mini disc and computer sound analysis software. This has raised the question whether specific parameters of the signals from older and newer studies are comparably accurate, at least to the point of characterization from an evolutionary perspective. Advancement of our knowledge of this important behavioral communication system requires: 1) continued discovery of the signals of more species representing a broader spectrum of genera and families, and the potential differences (dialects) of different populations of given species, and 2) additional data on species whose signals have been characterized from few individuals to determine the extent of intraspecific variation of the critical informational parameters of signals. Our objective in this paper has been to continue to address these questions by reporting newly discovered signals or duets of species, signals of additional populations of previously reported species, and how they fit the evolutionary paradigm of Stewart (2001).

Material and Methods

Virgin adults of six species were reared from mature larvae and collected as follows: (1) *Isoperla fulva* CLAASSEN, 1937, North Fork John Day River, 19.3 Km S of Ukiah, Umatilla Co., Oregon, 16-V-2001; (2) *I. mormona* BANKS 1920, Uncompahgre River, Montrose City Park, Montrose Co., Colorado, 11-VI-1999; (3) *I. sobria* (HAGEN, 1874), Rio Fernando de Taos, 1.6 Km W of Palo Flechado Pass, Taos Co., New Mexico, 26-V-1999; (4) *Helopicus bogaloosa* STARK & RAY, 1983, Mill Creek, 1.6 Km SW of Pinola, Simpson Co., Mississippi, 11-II-2000; (5) *H. nalatus* (FRISON, 1942) Little Muskegon River, 4.8 Km E of Morley, Mecosta Co., Michigan, 09-IV-1999; (6) *Isogenoides frontalis* (NEWMAN, 1838), Rocky Run Creek, 2.4 Km N of Brule, Douglas Co., Wisconsin, 07-IV-2000, (7) *I. frontalis*, East Fork Cranberry River, 4.8 Km S of Herbster, Bayfield Co., Wisconsin, 08-IV-2000, and (8) *I. frontalis*, Confluence of Fish and Pine Creeks, Intersection of Fish Cr. Rd. & Old US 2, Bayfield, Wisconsin, 09-IV-2000. Wild adults were collected as follows: (9) *Isoperla fulva*, Quartz Creek, Pitkin, Gunnison Co., Colorado, 08-VII-2000; (10) *Rickera sorpta* (NEEDHAM & CLAASSEN, 1925), McKinzie River, 67.6 Km E of Springfield, Lane Co., Oregon, 18-V-2001; (11) *Paraperla frontalis* (BANKS, 1902), San Miguel River, 6.42 Km E of Placerville, San Miguel Co., Colorado, 28-VI-1999.

Drumming signals were recorded with a Sony® WALKMAN™ portable MiniDisc recorder (model MZ-R37) and Optimus® model 33-3013 (1000 ohm, 70–1600 Hz) omni-directional microphones, in a 2-compartment, glass covered, field-recording chamber. The field-chamber dimensions were 265-mm long, 265-mm wide, 70-mm high, and the plate glass cover was 6 mm thick. MiniDisc recording media included Sony® model MDW-74 or Memorex® MD-74 digital recordable minidiscs.

Experimental pairs were acclimated and recorded in the field chamber on separate channels in Manila file folder boxes with lids constructed from Xerox® transparencies. The positioning of the microphones varied by the size and drumming intensity of the individual. The smaller sized *Isoperla* species required the microphones to be placed within a few millimeters below the Manila paper box and recording levels maximized.

Recorded signals were encoded to WAV files (Properties: Stereo, 16 bits-96 dB S/N, 44.100 Hz) by feeding source sound into the computer via the sound card Line In stereo-mini port. Because of their extremely large size, WAV files were then archived onto two other computer storage media including Iomega® PC-100 MB zip disks and Memorex® recordable compact discs for digital audio music (CD-R). Computer software used to accomplish both the encoding and signal analysis included Audiowave (Voyetra-Turtle Beach Inc.) and Acid WAV (Polyhedric Software). The later program automatically measures any cursor-selected distance in milliseconds (ms) and allows audio playback of complete duets, signals, or any individual tap or rest interval of a signal. The signals of males and females (left and right channels) are color coded, thus allowing discrete identification of the two sexes when analyzing overlapped duets (Sandberg and Stewart 2001). Accuracy of signal analysis software was tested with a WAV file recorded in Coral Metronome (Coral Acoustics), a computer software program providing a 60 beat/minute measure. The recorded eight-beat, seven-interval WAV file was opened and measured in milliseconds with Acid WAV and 1-second metronome beat intervals had an average of 1003.73 ± 1.11 SD (Range: 1001.7–1004.8 ms, Median: 1003.9 ms, Mode: 1003.9 ms).

Signals from three species (*Isogenoides frontalis*, *Helopicus bogaloosa*, and *H. nalatus*) were recorded at the University of North Texas laboratory with ambient temperatures of 23–24ºC and 70–84 foot-candles (FTC). The signals of five species (*Paraperla frontalis*, *Rickera sorpta*, *Isoperla fulva*, *I. mormona*, and *I. sobria*) were recorded at various indoor settings in Colorado, Oregon and Washington at normal room temperatures of 18–24ºC and normal room lighting or no light.

Results and Discussion

Unless otherwise stated, all numbers of signal beats and time intervals presented in the following descriptions are expressed as $\bar{x}$ ± standard deviation.

New signals

Perlodidae

Helopicus bogaloosa. One hundred twenty and 62 signals were obtained from four and one, 1–5 day old males and female, respectively, at 23ºC, and 80 FTC. Males and the female produced monophasic signals with 2- or 3-way communication. The four males called with signals of 17 mode beats (16.8 ± 1.29) with intervals of 110.2 ± 11.9 ms (Fig. 1, Table 1). Mode and $\bar{x}$ number of beats per female answer signal (Figs. 1B, C) were 6 and 5.1 ± 1.60; mean beat interval was 72.3 ± 6.48 ms. The time interval between the last male call beat and the first female answer beat (Γ-E exchange interval) was variable with a range of 182.8–706.3 ms.

In 3-way communication (Fig. 1C), mode and $\bar{x}$ number of beats per male response signal were 10 and 9.00 ± 1.53; intervals were 63.2 ± 6.54 ms. The time interval between the last female answer beat and the first male response beat (♀-♂ exchange interval) was variable with a range of 666.1–2,211.4 ms. The amplitude increased during the first 3–7 male call beats and remained constant. Female answer beat amplitude was always less than either male call or response beats.

Isogenoides frontalis. One hundred thirty-five duets were obtained from ten, 1–2 day old males and four females, respectively, at 23–24ºC, and 84 FTC. Their exchanges were complex, ranging from 3-way call-answer-response sequences (Fig. 2B), to grouped calls with grouped, interspersed female answers (Fig. 2A). Typically these grouped exchanges involved a short symphony of about three ♂-♀ signals, terminated by a slow (wider-interval) male signal (Fig. 2A, Table 1). Females did not always intersperse an answer between every male call group and three duets lacked the slow male response signal. The male call groups and sequenced calls consisted of 4 mode beats (4.1 ± 0.72) with intervals of 61.2 ± 11.3 ms (Fig. 2, Table 1). Only one symphony possessed a male group with six beats; all other male call groups ranged 2–5 beats. The number of call groups ranged from one (3-way duets) to six. The $\bar{x}$ intra-group intervals (beat intervals within groups) increased slightly in approximate 10 ms increments, beginning roughly at 50 ms and ending at 80 ms. The second call group conformed to this generalization except for the above mentioned six-beat second call group. Mode and $\bar{x}$ number of beats per interspersed female answer signals were 2 and 1.6 ± 0.58. Intervals were 93.8 ± 29.27 ms. In symphonies, female answers followed each male call group (♂-♀ exchange interval) by 581.5 ± 76.33 ms and the terminal male response signal was different from call groups with a mode beat count of 3 (3.5 ± 1.55), range 1–8; and intervals of 288.8 ± 129.4 (Table 1). Intervals of this response increased from 251.8 ± 114 ms to 446.2 ms. The last (♀-♂) exchange interval following the last beat of the last female interspersed answer was 427.7 ± 147.4 ms; the last call group signaled the end of the duet.

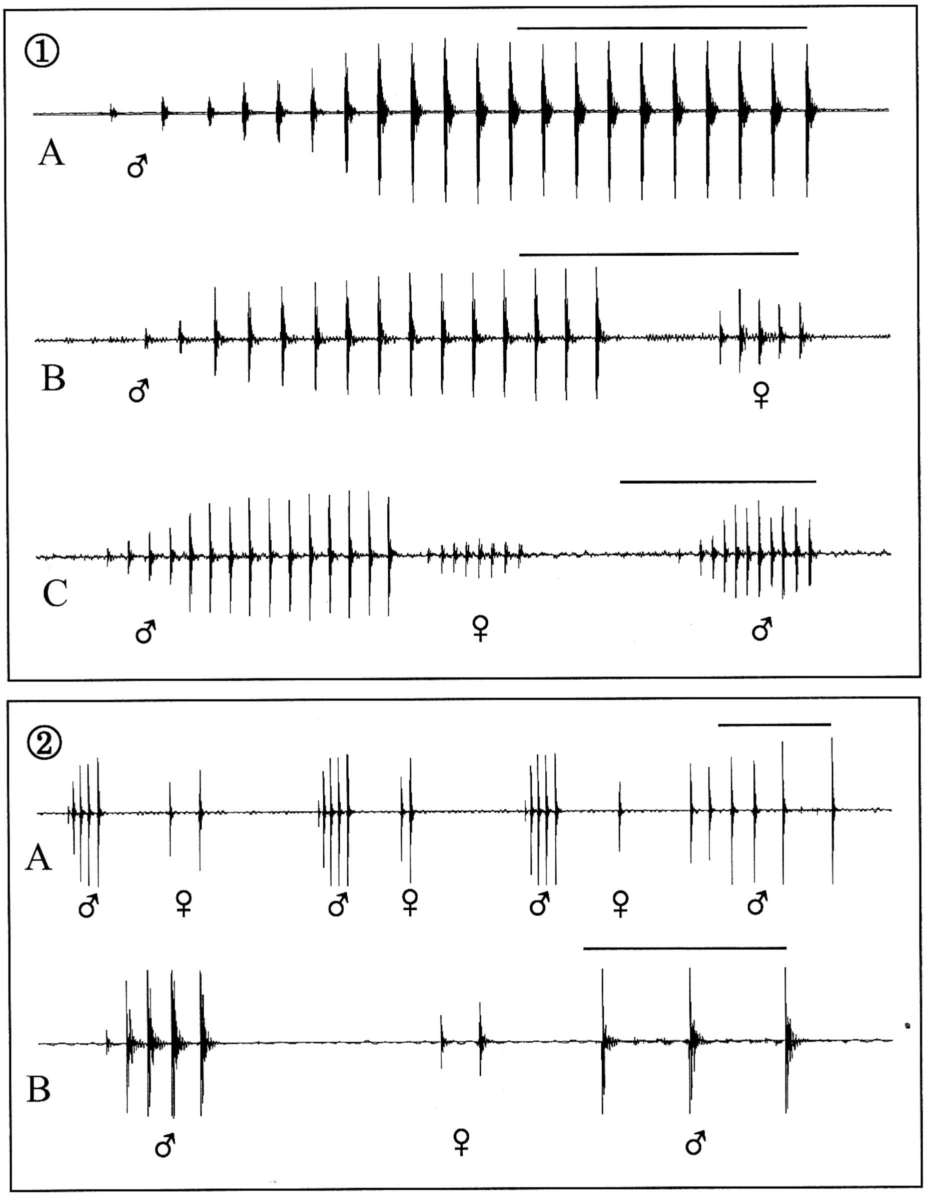
These signals from our Wisconsin population differed slightly from the Minnesota population (approximately 190 Km NE) reported by Graham (1982). Minnesota males called with up to three grouped signals with the same range in beats per group, but with slightly greater $\bar{x}$ and mode (4.9 ± 4.14 and 5 respectively) beats per group. The $\bar{x}$ intra-group interval of Minnesota males was 49.9 ± 9.08 ms, therefore less than our Wisconsin population.

Isoperla sobria. Two hundred seventy-eight and sixty-five signals were obtained from eight, 1–11 day old males and four females, respectively, at 18–21ºC, and normal incandescent room lighting at Pitkin, Colorado. Males and females of this species exhibited monophasic signals as simple 2-way duets. Female answers either began after the male call (10 duets, Fig. 3A) or within the last two intervals of the male call (55 duets, Fig. 3B). Males called with signals of 5 mode beats (5.7 ± 1.47) with intervals of 168.0 ± 35.2 ms (Fig. 3, Table 1). Intervals decreased gradually from 182.5 ± 39.53 ms (1st) to 148.9 ± 60.14 ms (7th), then increased during intervals 8–9 to 204.3 ± 0.71 ms.

Mode and $\bar{x}$ number of beats per female answer signal were 1 and 1.01 ± 0.24. Intervals were 107.8 ± 74.19 ms. The ♂-♀ exchange interval for simple and interspersed duets was 104.6 ± 12.64 ms. The $\bar{x}$ call beat interval was analyzed by sorting all duet measurements into like groups by beat count. This resulted in five data sets (male call beats 5–9) that indicated that the male call pattern was slightly different from the above comparison of all duets together. The sorted male 5- and 6-beat call data produced a similar call pattern of decreasing intervals from 1–3 or 4 and a gradual increase in intervals four or five. However, sorted 7–9 beat male call duets followed similar decreasing and increasing patterns, except that in each, the last intervals were substantially less than the previous interval. The last two intervals were, 1) 163.2 ± 8.01 and

85.4 ± 43.93 ms, 2) 166.6 ± 12.13 and 78.2 ± 26.56 ms, and 3) 167.9 ± 7.99 and 71.1 ± 5.69 ms for 7- to 9-beat male call duets respectively. The call of *I. sobria* is most similar in $\overline{x}$ number of beats to that of *I. miwoc* (Bottorff *et al.*, 1990), but differs by having larger intervals and does not call with grouped signals. The $\overline{x}$ inter-beat interval is most similar to that of *I. montana* (Stewart *et al.*, 1988), but differs in $\overline{x}$ number of beats.

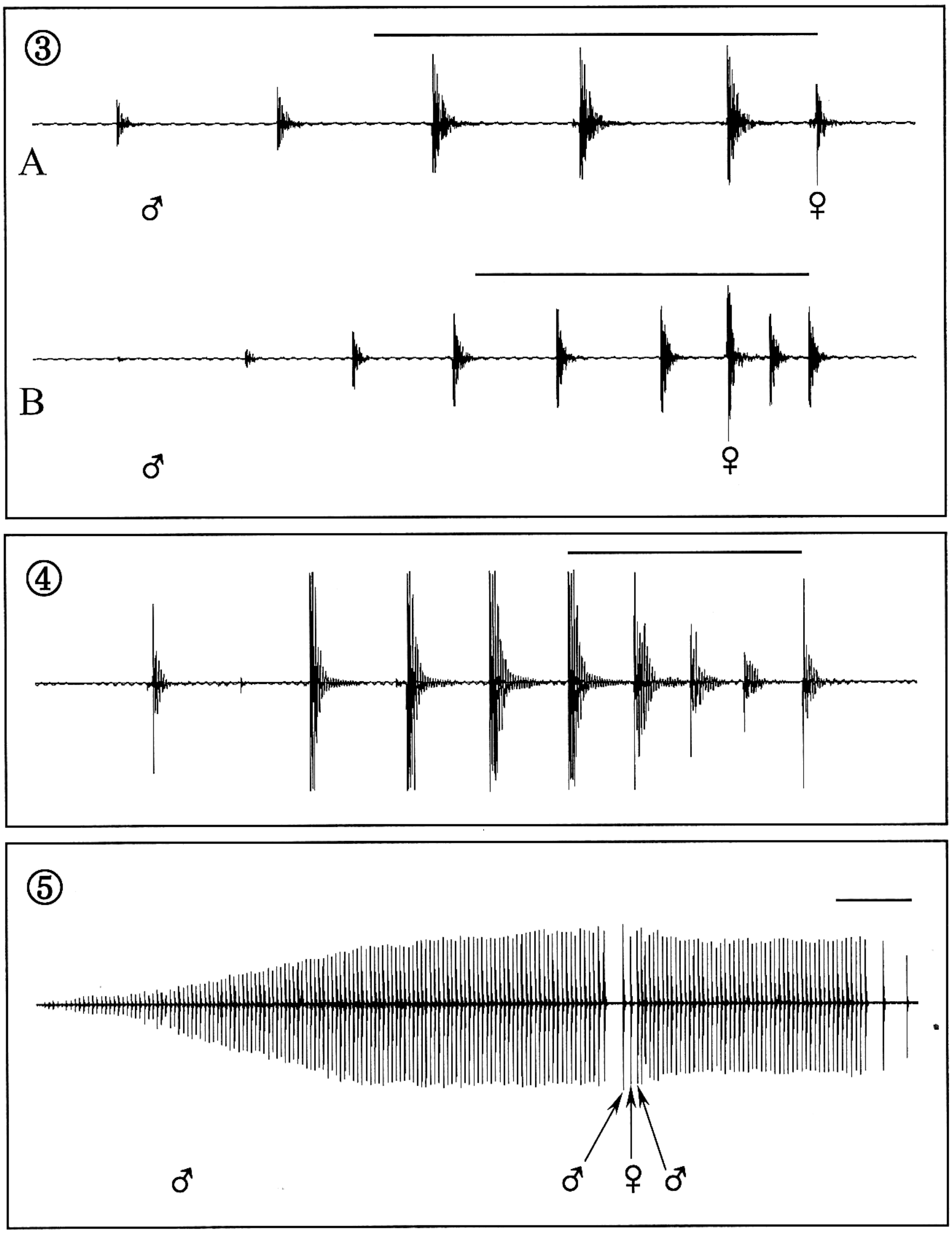
Rickera sorpta. Three signals were obtained from one wild 2 day old or more male, at 23ºC and normal incandescent room lighting, near a window at Redmond, Washington. He called alone, without a female, with variable monophasic signals having 8.0 ± 1.00 beats and intervals of 222.9 ± 96.07 ms (Fig. 4, Table 1). The call beat intervals were irregular, decreasing sharpest at first, between the first three beats (396.7 ± 101.73 and 262.8 ± 73.84 ms), decreasing gradually between beats 4–6 (208.5 ± 43.56, 193.9 ± 25.65, and 159.4 ± 48.53 ms), followed then by a gradual increase to beat 7 (188.6 ± 62.39 ms), and ending with a gradual decrease between beats 8–9 (164.4 ± 70.92 and 125.1 ms). The total time duration of calls ranged from 1312.4–1978.2 ms.



Figs. 1-2. 1. *Helopicus bogaloosa* drumming: (A) Male call, (B) Two-way duet, (C) Three-way communication (Bars = 1000 ms); 2. *Isogenoides frontalis* drumming: (A) Grouped seven-way male-female duet (Bar = 1000-ms), (B) Three-way sequenced communication (Bars = 500-ms).

Table 1 - New descriptions, signal characters and population measurements for eight North American Plecoptera species.

Species, (Location Code)	No. Signals / No. Individuals ♂	No. Signals / No. Individuals ♀	No. Signals / No. Individuals ♂	Range beats / signal or group / x̄ ± SD beats / signal or group ♂	Range beats / signal or group / x̄ ± SD beats / signal or group ♀	Range beats / signal or group / x̄ ± SD beats / signal or group ♂	Beat intervals (ms) (x̄ ± SD) ♂	Beat intervals (ms) (x̄ ± SD) ♀	Beat intervals (ms) (x̄ ± SD) ♂	Exchange intervals (ms) (x̄ ± SD) ♂–♀	Exchange intervals (ms) (x̄ ± SD) ♀–♂	Exchange intervals (ms) (x̄ ± SD) Last ♀–♂
1. New Descriptions												
Helopicus bogaloosa (4)4♂ 1♀	120 / 4	62 / 1	13 / 3	13–21 / 16.8 ± 1.3	2–9 / 5.1 ± 1.6	6–11 / 9.0 ± 1.5	110.2 ± 11.9	72.3 ± 6.5	63.2 ± 6.54	419.0 ± 118.5	1146.3 ± 547.3	N/A
Isogenoides frontalis (1)3♂ 2♀, (2)7♂ 1♀, (3)1♀	135 / 10	135 / 4	132 / 10	2–6 / 4.1 ± 0.7	1–3 / 1.6 ± 0.6	1–8 / 3.5 ± 1.6	61.2 ± 11.3	93.8 ± 29.3	288.8 ± 129.4	581.5 ± 76.3	1466.5 ± 414.8	427.7 ± 147.7
Isoperla sobria (5)8♂ 4♀	278 / 8	4 / 65		2–10 / 5.7 ± 1.5	1–2 / 1.1 ± 0.2		168.0 ± 35.2	107.5 ± 74.2		104.6 ± 12.6		
Rickera sorpta (7)1♂	3 / 1			7–9 / 8.0 ± 1.0			222.9 ± 96.1					
2. New Signal Character												
Paraperla frontalis (6)1♂ 1♀	5 / 1	5 / 1		♂ Phase 1 91–181 / 135.0 ± 35.7 ♂ Phase 2 2–6 / 3.8 ± 1.8	1–4 / 1.6 ± 1.3		♂ Phase 1 56.0 ± 5.29 ♂ Phase 2 160.2 ± 122.4	915.9 ± 1464.2		74.4 ± 40.3		
3. New Locations												
Helopicus nalatus (11)2♂	42 / 2			1–51 18.8 ± 9.9			72.1 ± 23.3					
Isoperla fulva												
(8)1♂	19 / 1			6–8 / 6.9 ± 0.6			46.7 ± 5.1					
(9)2♂	11 / 2			6–9 / 7.8 ± 0.9			42.3 ± 2.9					
Isoperla mormona (10)1♂ 1♀	9 / 1	2 / 1		6–14 / 10.4 ± 2.8	1–2 / 1.5 ± 0.7		232.1 ± 25.7	279.9 (N=1)		119.9 ± 2.26		



Figs. 3-5. 3. *Isoperla sobria* drumming: (A) Monophasic call with female answer, (B) Monophasic call with female interspersed answer (Bars = 500-ms); 4. *Rickera sorpta* drumming: Irregular monophasic male call (Bar = 500-ms); 5. *Paraperla frontalis* drumming: Three-way duet with diphasic call, female answer and diphasic male response (Bar = 1000-ms).

New signal characters and populations

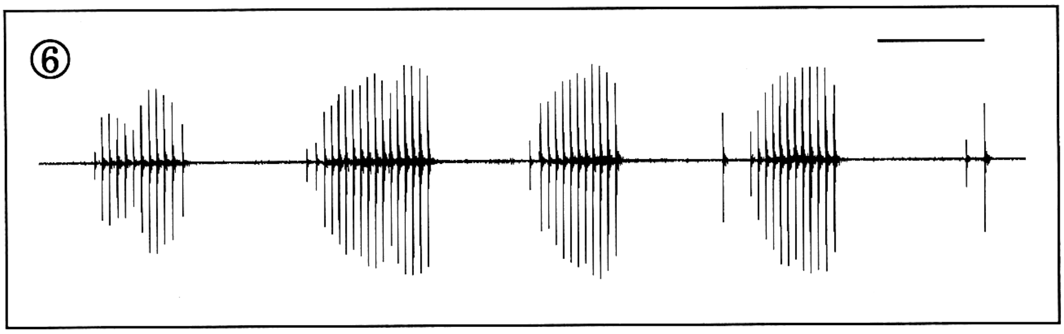
The following results provide additional signal characters for female *Paraperla frontalis* and *Isoperla mormona*, and analyses for different populations of the previously reported species *Helopicus nalatus* and *Isoperla fulva*. Comparisons of new data are primarily made with the original descriptive reports of 1) Stewart and Zeigler (1984) - *Paraperla frontalis* and *Helopicus nalatus*, male call descriptions; and 2) Szczytko and Stewart (1979) - *Isoperla fulva* duet description, and *I. mormona* male call description.

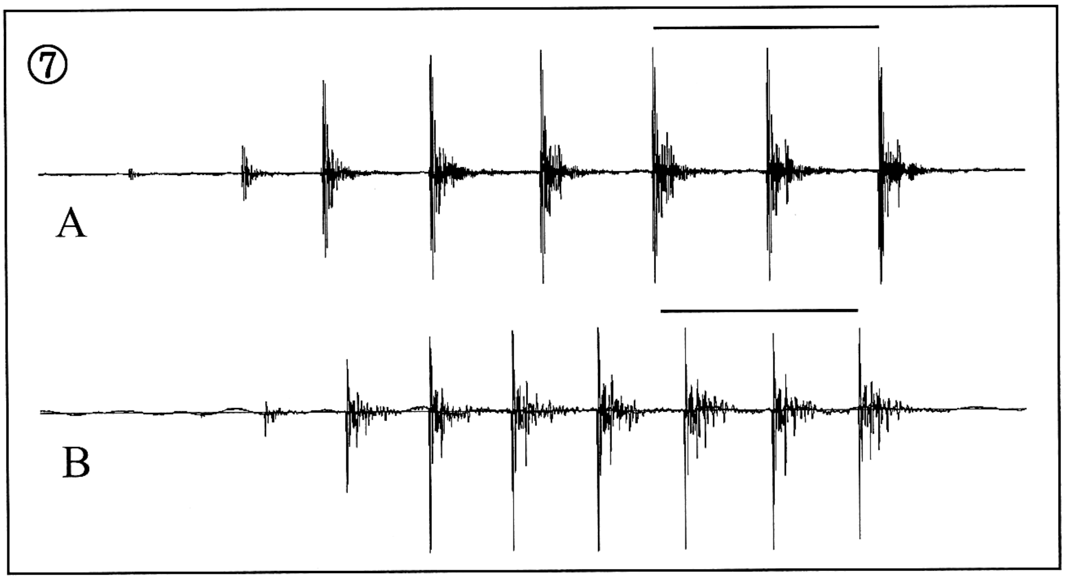
Chloroperlidae

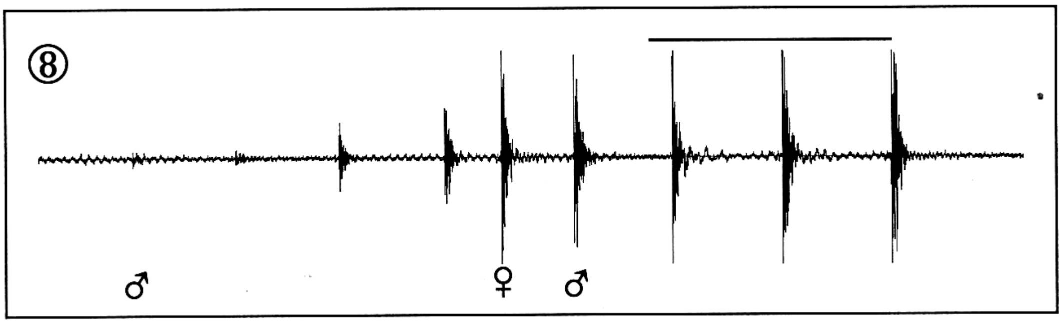
Paraperla frontalis. Five signals were obtained from one wild 2 day old or more male and one female, respectively, at 18–21°C, and normal incandescent room lighting at Pitkin, Colorado. The exchange was 3-way (male-female-male). The male call was long and diphasic as reported by Stewart and Zeigler (1984), with median beat counts of 141 and 4 in the first and second phases respectively. The $\bar{x}$ beat intervals in the first phase were approximately even at 56.0 ± 5.29 ms and ranged 49.0–119.2 ms. The second male phase intervals were 160.2 ± 122.4 ms and were variable (range 19.1–369.8 ms). The interval between phases was 231.8 ± 15.92 ms (Fig. 5).

The single female usually began answering by interspersing a beat within the last male call interval (Fig. 5). The range in male beat intervals where she began answers were intervals 16–154 and the range in number of male beats following her first answer beat was 17–155 beats. The single multi-beat female answer had intervals of 915.9 ± 1464 ms and was highly variable. The variable male response (Fig. 5) usually followed the female answer.

Our Colorado population males (Fig. 5, Table 1) differed from the Montana males (Stewart and Zeigler, 1984) by having larger $\bar{x}$ first phase beat counts and were similar in $\bar{x}$ second phase beat counts. The first phase $\bar{x}$ beat intervals were similar in both populations, but second phase intervals of our Colorado population were much shorter (160.2 ± 122.4 ms) compared to the Montana population (285 ± 26 ms).







Figs. 6-8. 6. *Helopicus nalatus* drumming: Grouped male call (Bar = 1000-ms); 7. *Isoperla fulva* drumming: (A) Monophasic call, Gunnison County, Colorado, (B) Monophasic call, Umatilla County, Oregon (Bars = 100-ms); 8. *Isoperla mormona* drumming: Monophasic male call with female answer inserted early in the call (Bar = 500-ms).

Perlodidae

Helopicus nalatus. Forty-two signals were obtained from two, 2–9 day old, males at 24ºC and 70 FTC. They called with simple to complex grouped signals of 1–5 beats per group, which occasionally ended with a response-like beat or short group with intervals different from the earlier call groups. Total call duration ranged from 942.0 to 7,778.9 ms, with total beats ranging 14–91. Males called with grouped signals that averaged 18.8 ± 9.98 beats per group, with intra-group intervals of 72.1 ± 23.27 ms (Fig. 6, Table 1). The $\bar{x}$ interval between groups was 1,027.8 ± 434.60 ms and ranged from 243.5–2,218.3 ms.

The $\bar{x}$ intra-group interval was analyzed by sorting all signal data into like sets by number of grouped calls per signal. This resulted in five data sets that indicated that the $\bar{x}$ intra-group interval was slightly different from the above comparison of all signals together. The sorted single, two-group, three-group and four-group signals ranged in $\bar{x}$ intra-group interval from 69.78 to 71.70 ms; however the last, or fifth group (N=3 signals) had a $\bar{x}$ intra-group interval of 84.4 ms. These Michigan population $\bar{x}$ call beats per group differed from the Arkansas population (35.7 ± 7.5 ms) reported by Stewart and Zeigler (1984) approximately 1000 Km SE, but were similar in that the $\bar{x}$ beat intervals overlapped slightly.

Isoperla fulva. Three males from two new populations were analyzed. Nineteen signals were obtained from one six or more day old wild male from Gunnison County, Colorado at 21ºC and normal incandescent room lighting during the day. He signaled with 7 mode beats (6.9 ± 0.52) that had intervals of 46.7 ± 5.1 ms (Fig. 7A, Table 1). Intervals gradually increased from 43.4 ± 9.90 ms (interval one) to 49.3 ± 1.55 ms (interval 5), and then gradually decreased to 46.3 ± 5.02 ms (interval 7), and call beats ranged from 6–8. The $\bar{x}$ total signal duration was 291.0 ± 65.56 ms.

Two one day old reared and associated males from Umatilla County, Oregon, at 21ºC and no light during the night, signaled with 8 mode beats (7.82 ± 0.87) with intervals of 42.3 ± 2.9 ms (Fig 7B, Table 1). The $\bar{x}$ call beat interval increased gradually throughout the call from 37.2 ± 3.08 ms (interval one) to 44.6 ± 1.48 ms (interval 8), and call beats ranged from 6–9. The $\bar{x}$ total signal duration was 288.2 ± 33.80 ms. This site was approximately 1100 Km NW of the Colorado site.

These few Colorado and Oregon *I. fulva* data agree fairly well with one another in terms of $\bar{x}$ beat counts, intervals and total call duration. The previously reported Colorado, New Mexico, and Utah *I. fulva* populations (Szczytko and Stewart 1979), were different and had a smaller $\bar{x}$ beat count (5.6 ± 0.5), and a greatly different $\bar{x}$ inter-beat interval (25.9 ± 4.2 ms). This suggests substantial population dialects within this widely distributed species or behaviorally different but morphologically cryptic species, and lastly, our analysis did not include *I. fulva* females, which may have influenced male call characters.

Isoperla mormona. Nine and two signals were obtained from one, 8–12 day old, male and female, respectively, at 21ºC and normal incandescent room lighting from Gunnison County, Colorado. We have interpreted the duets (Fig. 8, Table 1) as being a monophasic male call with one or two female answers inserted early in his call. The male called with 12 mode beats (10.4 ± 2.83) with intervals of 232.1 ± 25.7 ms (Fig. 8, Table 1). The $\bar{x}$ inter-beat interval was variable, with a range from 216.4 ± 7.08 ms (interval eight) to 248.3 ± 33.52 ms (interval four) with a range in beat count from 6–14.

Median and $\bar{x}$ number of beats for the two female answers were 1.5 and 1.5 ± 0.71 respectively, and the interval of the single 2-beat answer was 279.9 ms. The $\bar{x}$ time interval between the male beat just before the first female answer beat was 119.9 ± 2.26 ms. The range and $\bar{x}$ for male call and duet duration was (1,462.9–2,990.3 ms) and 2192.3 ± 558.66 ms, respectively.

The $\bar{x}$ beat count of this Colorado population was similar to that reported by Szczytko and Stewart (1979) for a Utah population (11.5 ± 5.3 beats) approximately 420 Km E. The $\bar{x}$ male call interval of the Utah population (45.9 ± 9.3 ms) was greatly different from our Colorado population, indicating a substantial dialectual difference or potentially behaviorally cryptic species.

Discussion

The consistency of signal types of our recordings of additional populations of *P. frontalis*, *I. mormona*, *H. nalatus* and *I. fulva* compared with previously reported populations of these species. This suggests that the old and new recording and analysis technologies have arrived at descriptions for species that are sufficient for evolutionary considerations. Exact duplication over time of a species can not be expected due to the many sources of error such as temperature and light conditions at recording, instrument calibration integrity, population (dialect) variation, age of adults recorded (Zeigler and Stewart, 1985a), and variation in the number of signals and individual males and females successfully recorded. We feel that signal variations between populations can be attributed to such possible error, or may, if the changing technology is not a factor, be due to population behavioral differences (dialects) or particularly in the cases of widely distributed adaptable species indicate behaviorally definable, morphologically cryptic sibling species. This is particularly true if signal type or major rhythm differences are indicated. Minor variations of male call beats are not as important in light of the work of Zeigler and Stewart (1985b) and Stewart and Maketon (1990). This dilemma is similar to the classic question of whether, and to what extent, morphological differences indicate either variation within a species or different sibling species. It is probable that behavioral and morphological "speciation" may occur at different rates of time. The signals characterized for these eight species continue to support the evolutionary paradigm of stonefly drumming proposed by Stewart (2001).

Arctoperlaria continue to produce the most advanced signals known in the Insecta and the Antarctoperlaria need additional testing. This report increases the known drumming signals for the perlodid tribe Diploperlini to five and there are now 10 published descriptions for the perlodid tribe Perlodini with a range of signal type from ancestral to derived patterns including, simple monophasic calls, 3-way communication, grouped calls, bi-beat and bi-grouped male calls. No new call patterns were found for these tribes in this study. This study reported two new female answers in the subfamilies Isoperlinae and Chloroperlinae and also several variable male call signal characters.

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