CONTINUED STUDIES OF VIBRATIONAL COMMUNICATION (DRUMMING) OF NORTH AMERICAN PLECOPTERA

John B. Sandberg[1] & Kenneth W. Stewart[2]

Department of Biological Sciences, University of North Texas, Denton, TX 76203

[1] E-mail: jbs001@unt.edu
[2] E-mail: stewart@unt.edu

ABSTRACT

The drumming signals of thirteen North American stonefly species are reported. New signals are described for six species (*Isoperla muir*, *I. rainera*, *I. rougensis*, *I. tilasqua*, *Pteronarcys scotti* and the female answer of *Soliperla campanula*). Descriptions of new signal characters and results from additional population locations are provided for seven species (*Perlinella drymo*, *Hydroperla crosbyi*, *I. bifurcata*, *I. sobria*, *I. phalerata*, *I. quinquepunctata* and *Pteronarcys dorsata*).

Keywords: Plecoptera, drumming, Peltoperlidae, Perlidae, Perlodidae, Pteronarcyidae

INTRODUCTION

The typical mating system of the stonefly suborder Arctoperlaria includes vibrational (mostly drumming) signaling between the sexes, with males calling and searching and females conveying their stationary position with answers. This vibrational duetting is a species-specific fixed action behavior, and one of the most diverse and complex known in insects.

The percussion, rubbing and tremulation signals have been described for 121 North American and about 29 European species, respectively. The latest reviews of known species behaviors, and the wider implications of drumming such as its use as a behavioral line of evidence for species delineation and Plecoptera systematics, defining intraspecific variations and dialects, signal information content, related searching and mate finding, and proposed evolutionary paradigms, were by Stewart (2001) and Stewart and Sandberg (2006).

Our objectives in this study were to (1) continue describing new signals of species to expand knowledge at the generic and family levels, (2) to test different populations of given species to determine potential differences that might be attributable to dialects, and (3) to determine how new discoveries fit the evolutionary paradigm of Stewart (2001) and Stewart and Sandberg (2006).

It is now well established that Arctoperlarian stonefly vibrational communication is a species-specific behavior, which along with morphology of genitalia, isolates and defines species. A major complex question that characterization of additional species and population signaling will ultimately help answer is (1) whether populations that become geographically widely separated or isolated undergo selective change, first to minor or non-isolating dialects, then toward behavioral isolation, and (2) how the timing of such selective change might relate to morphological change.

MATERIALS AND METHODS

Virgin adults were reared from mature nymphs and collected as follows:
(1) *Soliperla campanula* (Jewett), Kink Creek, Roadside falls, Hwy 126, 8mi. N. of Belknap Springs, Linn Co., Oregon, 17-V-2001; (2) *Perlinella drymo* (Newman), Rock River, 1.5 mi. E. of Rock Valley, Hwy 9, Sioux Co., Iowa, 13-IV-2000; (3)

Hydroperla crosbyi (Needham & Claassen), Clear Creek, near bridge on Waide Rd., 10 mi. N.W. of Denton, Denton Co., Texas, February & March-2002; (4) *Isoperla bifurcata* Szczytko & Stewart, Oak Burn Creek, Corvallis, Benton Co., Oregon, 28-IV-1999; (5) *Isoperla sobria* (Hagen), Fall River, F.R.C.G., 1.3 mi. E. of springs on S. Century Dr. (Hwy 42), Deschutes Co., Oregon, 16-V-2001 and *Isoperla sobria* (Hagen), Fall River, F.R.C.G., 1.3 mi. E. of springs on S. Century Dr. (Hwy 42), Deschutes Co., Oregon, 27-IV-2004; (6) *Isoperla muir* Szczytko & Stewart, Muir Creek, bridge on Hwy. 220, Douglas Co., Oregon, 12-V-2002; (7) *Isoperla phalerata* (Smith), W. Pass Creek, 2.5 mi. W. of North Pass, Hwy 114 and FR 878, Saguache Co., Colorado, 27-V-1999; (8) *Isoperla quinquepunctata* (Banks), Uncompahgre River, City Park, Montrose, Montrose Co., Colorado, 06-VII-1999; (9) *Isoperla rainera* Jewett, W. Fork Salmon River, 1 mi. S. of Timberline Lodge on E. Timberline Rd., 1.5 mi. N. of Government Camp, Clackamas Co., Oregon, 10-V-2002; (10) *Isoperla rougensis* Szczytko & Stewart, Fall River, F.R.C.G., 1.3 mi. E. of springs on S. Century Dr. (Hwy 42), Deschutes Co., Oregon, 16-V-2001; (11) *Isoperla tilasqua* Szczytko & Stewart, Fall River, F.R.C.G., 1.3 mi. E. of springs on S. Century Dr. (Hwy 42), Deschutes Co., Oregon, 16-V-2001; (12) *Pteronarcys dorsata* (Say), Mill Creek, CR 472, 1 mi. S.W. of Pinola, Simpson Co., Mississippi, 11-II-2000; (13) *Pteronarcys scotti* Ricker, Stony Creek, 2 mi. N. of confluence with Laurel Branch, Hwy 635, Giles Co., Virginia, 24-II-2001.

One thousand three hundred-two drumming signals were recorded following the methods in Sandberg and Stewart (2003), except that Ace of Wave Ver. 2.6 (Polyhedric Software) was used to perform all analyses and the files (708 MB) were stored on DVD+RW media.

Signals from nine species (*S. campanula*, *P. drymo*, *H. crosbyi*, *I. bifurcata*, *I. ebria* (2004), *I. muir*, *I. rainera*, *P. dorsata*, and *P. scotti*) were recorded at the University of North Texas with ambient temperatures of 23-24°C and 58–84 foot-candles (FTC). The signals of three species (*I. ebria* (2001), *I. rougensis*, and *I. tilasqua*) were recorded at room temperature (23-24°C), with normal incandescent lighting near a window at Redmond, Washington. Two species (*I. phalerata* and *I. quinquepunctata* were recorded at room temperature (23-24°C), with normal incandescent lighting in Pitkin, Colorado.

RESULTS AND DISCUSSION

Unless otherwise stated, all numbers of signal beats and time intervals presented in the following descriptions are expressed as mean ± standard deviation.

New Signals

Peltoperlidae

Soliperla campanula. Sixty-two signals were obtained from two, 3-day old females at 24°C and 60 FTC. Light finger tapping near the recording chamber induced all their answers. The two females produced signals with average individual intervals gradually increasing from 22.4 ms for interval 1 (i1) to 28.4 ms at interval 10 (i10). Total average beat count per answer and overall average intervals were 6.2 ± 2.7 and 25.4 ± 2.5 ms (Fig. 1, Table 1). There were 8 mode beats per signal and average answer duration was 133.3 ± 73.6 ms.

Perlodidae

Isoperla muir. Two hundred thirty-two and two signals were obtained from eight and one, 1–4 day old males and female, respectively, at 24°C and 62 FTC. Males and the female produced 2-way sequenced duets with no female interspersed answers. The eight males called with signals of 9 mode beats (10.5 ± 2.0) with intervals of 48.1 ± 3.2 ms (Figs. 2A–B, Table 1). Their average individual intervals were variable and gradually increased from 46.5 ms (i1) to 56.4 ms (i16) (Table 2). These intervals (i2, i4, i6, i10, i12) decreased slightly from their previous intervals, but overall fit into the gradually increasing pattern. Range and mean number of beats per female answer signal were 6–7 and 6.5 ± 0.7; mean beat interval was 62.8 ± 7.8 ms. The time interval between the last male call beat and the first female answer beat (♂-♀ exchange interval) was 131.6 ± 21.3 ms.

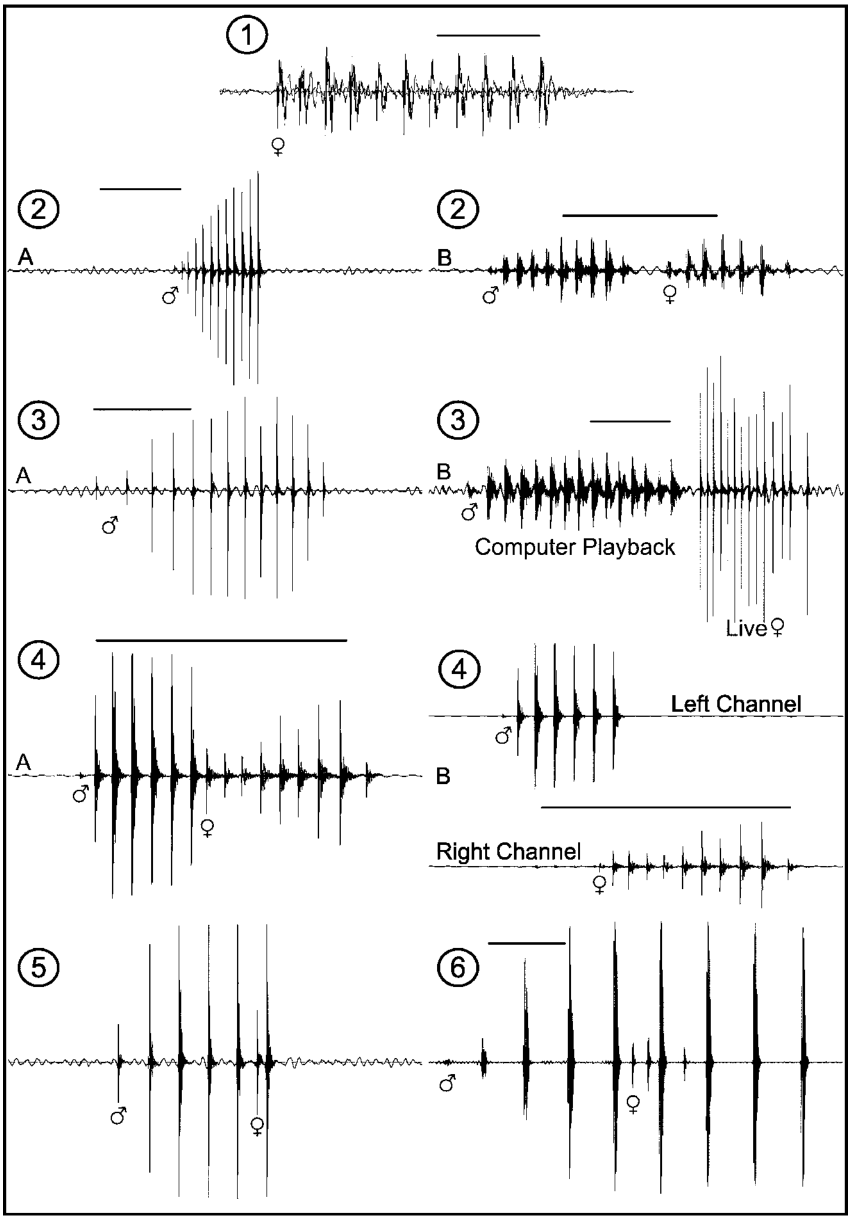
Isoperla rainera. Fifty-five and 32 signals were obtained from four and two, 1–5 day old males and females, respectively, at 24°C and 62 FTC. Males and females produced 2-way sequenced duets with no female interspersed answers. The four males called with signals of 13 mode beats (13.5 ± 2.0); with intervals of 94.0 ± 19.8 ms (Figs. 3A–B, Table 1). Their average individual intervals within calls decreased from 138.7 ms (i1) to 76.2 (i16) (Table 2). Mode and mean number of beats per female answer signal were 9 and 13.8 ± 6.4; mean beat interval was 58.3 ± 25.9 ms. The ♂-♀ exchange interval was 230.9 ± 95.2 ms.

New Descriptions Species-State/Year	No. Signals / No. Individuals ♂	♀	♂	Range (Mode) beats/signal / $\bar{x}$ ± SD beats / signal ♂	♀	♂	Beat intervals (ms) ($\bar{x}$ ± SD) ♂	♀	♂	Exchange intervals (ms) ($\bar{x}$ ± SD) ♂–♀	♀–♂
Soliperla campanula OR 2001		62 / 2			2–11 (8) / 6.2 ± 2.7			25.4± 2.5			
Isoperla muir OR 2002	232 / 8	2 / 1		7–17 (9) / 10.5 ± 2.0	6–7 / 6.5 ± 0.7		48.1 ± 3.2	62.8 ± 7.8		131.6 ± 21.3	
Isoperla rainera OR 2002	55 / 4	32 / 2		9–17 (13) / 13.5 ± 2.0	2-22 (9) / 13.8 ± 6.4		94.0 ± 19.8	58.3 ± 25.9		230.9 ± 95.2	
Isoperla rougensis OR 2001	128 / 1	111 / 1		6–7 (7) / 6.9 ± 0.3	2–11 (7) / 6.5 ± 1.7		37.2 ± 3.2	40.8 ± 7.2		27.9 ± 27.5	
Isoperla tilasqua OR 2001	71 / 1	8 / 1		4–8 (6) / 6.1 ± 1.0	1 (1) / n/a		168.8 ± 8.3	n/a		118.2 ± 4.5	
Pteronarcys scotti VA 2001	51 / 1	6 / 1		2–12 (9) / 8.1 ± 2.2	5–7 (5) / 5.7 ± 1.0		600.9 ± 42.1	198.9 ± 47.5		361.6 ± 189.5	

Table 1 New drumming descriptions of six Plecoptera species. Number of signals and individuals, numbers of beats per signal, and total average beat intervals are provided for male calls and female answers. Exchange intervals are the intervals between male calls and female answers.

New Descriptions																	
Species	Average individual intervals 1-16 (ms)																
State/Year	i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11	i12	i13	i14	i15	i16	
I. muir OR 2002	46.5	45.3	48.1	47.4	48.4	48.3	48.8	49.0	49.6	49.4	50.1	49.9	51.2	51.2	51.3	56.4	**I**
I. rainera OR 2002	138.7	115.3	105.3	95.9	91.6	88.7	86.8	84.8	84.4	81.5	81.8	80.6	81.2	80.0	80.0	76.2	**D**
I. rougensis OR 2001	31.6	35.6	38.4	39.4	39.5	38.9	**I-D**										
I. tilasqua OR 2001	174.6	170.2	166.5	164.9	167.6	167.1	169.9	**D-I**									
P. scotti VA 2001	538.0	586.4	588.6	608.0	613.4	624.0	627.1	636.9	643.2	673.3	655.2	**I**					

Table 2. Average individual male call intervals for six Plecoptera species. Underlined intervals indicate slight changes in general patterns of increasing (I), decreasing (D), or both (I-D or D-I).



Figs. 1–6. **1**. *Soliperla campanula* drumming. Bar = 100-msec, total duration (TD)= 257-msec; **2**. *Isoperla muir* drumming. (A) Male call, TD = 482-msec, (B) 2-way duet, TD = 960-msec. Bars = 500-msec.; **3**. *Isoperla rainera* drumming. (A) Male call, TD = 1172-msec, (B) 2-way duet, female answer to computer playback of male call, TD = 2150-msec. Bars = 500-msec; **4**. *Isoperla rougensis* drumming. (A) 2-way duet with female interspersed answer, (B) Split-channel view reveals previously hidden female first answer beats, TD = 574-msec. Bars = 500-msec; **5**. *Isoperla tilasqua* drumming: 2-way duet with female interspersed answer, TD = 849-msec. Bar = 500 msec; **6**. *Pteronarcys scotti* drumming: 2-way duet with female interspersed answer, TD = 4725-msec. Bar = 1000-msec.

Isoperla rougensis. One hundred twenty-eight and 111 signals were obtained from one, 1-day old male and female, respectively, at room temperature and normal incandescent light near a window. The male and the female produced 2-way duets either with the female answer following the call (N=78) or with interspersed answer beats during the male's 3rd (N=1), 5th (N=5) or 6th (N=27) beat intervals. The male called with signals of 7 mode beats (6.9 ± 0.3); with intervals of 37.2 ± 3.2 ms (Fig. 3 –B, Table 1). The male's average individual intervals gradually increased from 31.6 ms (i1) to 39.5 (i5), the last interval decreased to 38.9 ms (N=117) (Table 2). Mode and mean number of beats per female answer signal were 7 and 6.5 ± 1.7; mean beat interval was 40.8 ± 7.2 ms for sequenced and overlapped duets. The ♂-♀ exchange interval was 27.9 ± 27.5 ms. A split-channel view (Fig. 3B), revealed overlapped and interspersed female beats during the 5th and 6th call intervals.

Isoperla tilasqua. Seventy-one and eight signals were obtained from one, 1-day old male and female, respectively, at room temperature and normal incandescent light near a window. The male and the female produced 2-way duets either with the female answer following the call (N=3) or with interspersed answer beats during the male's 5th (N=2) or 6th (N=3) beat intervals. The male called with signals of 6 mode beats (6.1 ± 1.0); with intervals of 168.8 ± 8.3 ms (Fig. 5, Table 1). The male's average individual intervals gradually decreased from 174.6 ms (i1) to 164.5 ms (i4) and then gradually increased to 169.9 ms (i7) (Table 2). The beat count of female answer signals was always 1 and the ♂-♀ exchange interval was 118.2 ± 4.5 ms for sequenced and overlapped duets.

Pteronarcys scotti. Fifty-one and six signals were obtained from one, 6–11 day old male and female, respectively, at 24°C and 70 FTC. The male and the female produced 2-way duets either with the female answer following the call (N=3) or with interspersed answer beats during the male's 2nd (N=1), 3rd (N=1), or 5th (N=1) beat intervals. The male called with signals of 9 mode beats (8.1 ± 2.2); with intervals of 600.9 ± 42.1 ms (Fig. 6, Table 1). The male's average individual intervals gradually increased from 538.0 ms (i1) to 655.2 ms (i11) (Table 2). Mode and mean number of beats per female answer signal were 5 and 5.7 ± 1.0; mean beat interval was 198.9 ± 47.5 ms. The ♂-♀ exchange interval was 361.6 ± 189.5 ms for sequenced and overlapped duets.

New Signal Character

Perlinella drymo. Forty-seven and 37 signals were obtained from one, 1-day old male and female, respectively, at 24°C and 70 FTC. The male and female produced 2-way duets (N=36) and a new 3-way exchange (N=1), consisting of a male call, female answer, and male response following the answer. Previously, Zeigler and Stewart (1977) reported this species with only a 2-way vibrational communication. Males consistently called with 3-beat signals containing a long 1st interval (92.3 ± 1.4 ms) and a short 2nd interval (26.9 ± 3.2 ms) (Fig. 7, Tables 3–4). The female answer was a single beat and followed the last male call beat by 138.0 ± 5.1 ms. The male response signal followed the female answer (♀-♂ exchange interval) by 181.9 ms and contained 10 beats with intervals of 28.3 ± 2.3 ms.

Additional Populations

Perlodidae

Hydroperla crosbyi. Eighty-four and 60 signals were obtained from four and three, 1–5 day old males and females, respectively, at 23°C and 58 FTC. Males and the females produced 2-way (N=56) and 3-way exchanges (N=4). The four males consistently called with two grouped (Bi-grouped) signals. The first group's range in beat count from 2–4 contains one less and more than previously described by Zeigler & Stewart (1985). Treating the two call-groups separately, the first contained 3 mode beats (3.0 ± 0.4); with intervals of 45.8 ± 16.6 ms and the second group had 4 mode beats (3.6 ± 0.5); with intervals of 47.4 ± 5.0 ms. The intergroup interval between these groups was 157.7 ± 29.8 ms Overall, males called with two groups containing 7 mode beats (6.6 ± 0.7), with overall intervals of 46.7 ± 11.5 ms (Fig. 8, Table 3). The individual average call intervals of groups 1 and 2 gradually decreased from 47.4 ms (i1) to 40.2 (i3) and from 49.6 ms (i5) to 45.1 ms (i7) respectively (Table 4). Mode and mean number of beats per female answer signal were 4 and 5.0 ± 1.8; mean beat interval was 64.0 ± 10.4 ms. The ♂-♀ exchange interval was 246.8 ms ± 84.4 ms and the male response contained 6 mode beats (4.7 ± 1.5); with intervals of 84.9 ± 19.2 ms. The ♀-♂ exchange interval was 39.4.3 ± 48.3 ms.

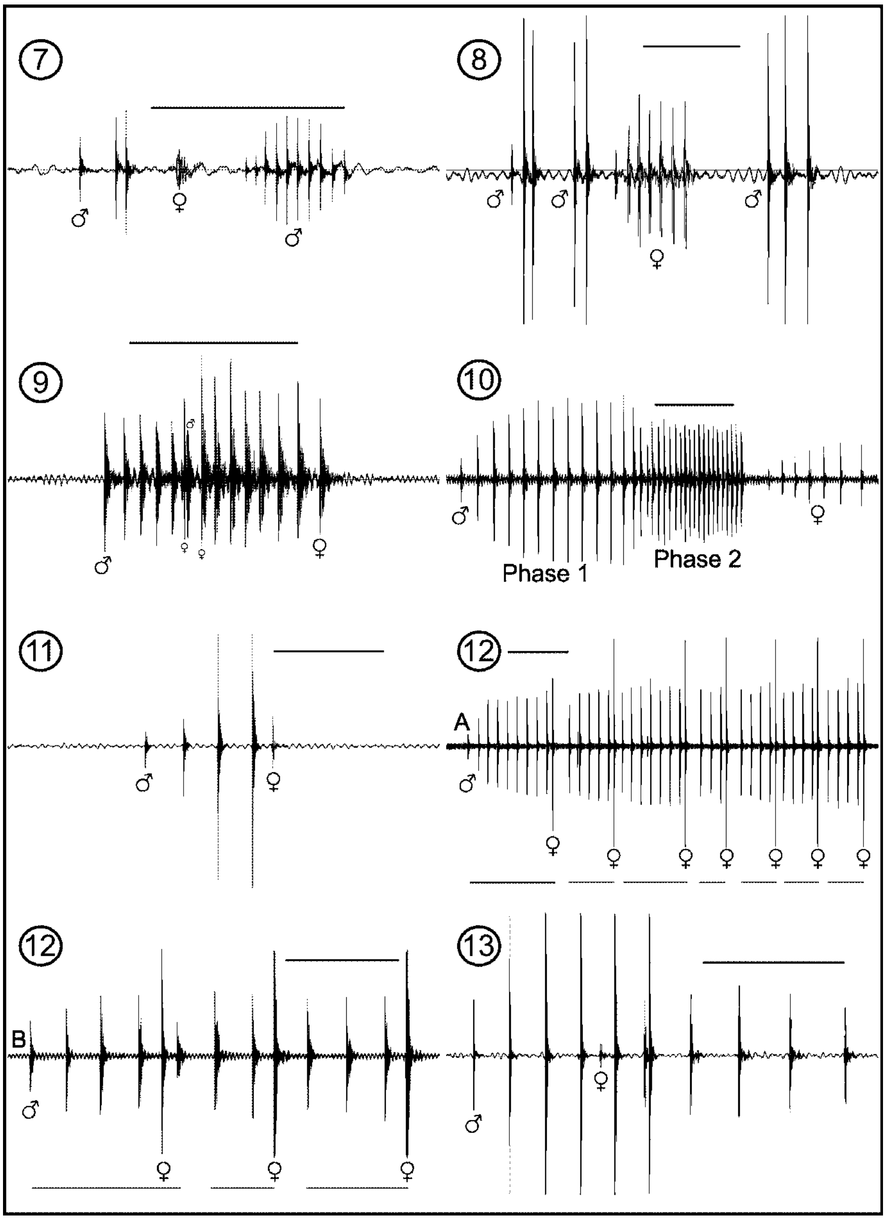
Isoperla bifurcata. One hundred thirty-six and 130 signals were obtained from two and one, 2–8 day old males and female, respectively, at 23°C and 65 FTC. Males and females produced 2-way

Species-State/Year	No. Signals / No. Individuals			Range (Mode) beats / signal / $\bar{x}$ ± SD beats / signal			Beat intervals (ms) ($\bar{x}$ ± SD)			Exchange intervals (ms) ($\bar{x}$ ± SD)	
	♂	♀	♂	♂	♀	♂	♂	♀	♂	♂–♀	♀–♂
NEW CHARACTER											
Perlinella drymo	47	37	1	3 (3)	1 (1)	10 (10)	1st 92.3± 1.4	n/a	28.3 ± 2.3	138.0 ± 5.1	181.9 (N=1)
IA 2000	1	1	1	n/a	n/a	n/a	2nd 26.9 ± 3.2				
ADDITIONAL POPULATIONS											
Hydroperla crosbyi	84	60	4	5–8 (7)	2–9 (4)	3–6 (6)	46.7 ± 11.5	64.0± 10.4	84.9 ± 19.2	246.8 ± 84.4	394.3 ± 48.3
TX 2002	1	3	3	6.6 ± 0.7	5.0 ± 1.8	4.7 ± 1.5					
Isoperla bifurcata	136	130		4–10 (6)	1–14 (3)		50.2 ± 5.7	50.0 ± 10.0		44.3 ± 18.3	
OR 1999	2	1		6.2 ± 0.8	3.9 ± 2.5						
Isoperla phalerata	50	28		10–15 (13)	3–7 (5)		96.6 ± 16.6	109.9 ± 27.7		301.0 ± 124.0	
CO 1999	1	1		12.8 ± 0.9	5.0 ± 1.0						
♂ 2nd phase	50			19–25 (22)			34.6 ± 5.7				
	1			22.2 ± 1.6							
Isoperla sobria	44	16		2–5 (4)	1–2 (1)		159.1 ± 7.2	62.9 (N=1)		99.8 ± 5.6	
OR 2001	1	1		3.7 ± 0.8	1.1 ± 0.2						
Isoperla sobria	50	4		3–7 (6)	1 (1)		151.1 ± 5.8	n/a		112.8 ± 4.0	
OR 2004	1	1		5.2 ± 1.0	n/a						
I. quinquepunctata	107	78		1–21 (7)	1–2 (1)		173.6 ± 11.4	924.5 ± 254.0		98.0 ± 5.2	
CO 1999	1	1		8.6 ± 5.7	1.0 ± 0.2						
Pteronarcys dorsata	35	35		6–8 (6)	3–6 (5)		251.9 ± 9.6	359.7 ± 45.9		141.1 ± 85.5	
MS 2000	1	1		6.6 ± 0.6	4.9 ± 0.8						

Table 3. New signal characters and additional population measurements of eight Plecoptera species. Number of signals and individuals, numbers of beats per signal, and total average beat intervals are provided for male calls, female answers and male response signals. Exchange intervals are the intervals between male calls and female answers or female answers and male response signals.

Species	Average individual intervals 1-24 (ms)																								
State/Year	i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11	i12	i13	i14	i15	i16	i17	i18	i19	i20	i21	i22	i23	i24	
NEW CHARACTER																									
P. drymo	92.3	26.9																							
IA 2000																									
ADDITIONAL POPULATIONS																									
H. crosbyi	47.4	44.4	40.2	157.7	49.6	46.6	45.1	**D**																	
TX 2002																									
I. bifurcata	54.5	52.0	48.7	47.0	46.3	45.4	49.5	60.0	58.2	**D-I**															
OR 1999																									
I. phalerata	124.4	109.2	104.4	100.3	99.3	<u>97.0</u>	97.2	95.2	92.3	87.3	78.0	<u>71.1</u>	71.2	62.6	**D**										
2^{nd} Phase	51.3	41.6	40.0	38.1	38.1	36.5	35.8	33.9	33.0	32.3	31.9	31.4	<u>31.5</u>	31.0	31.0	31.0	31.3	<u>31.2</u>	31.4	<u>31.0</u>	31.7	<u>33.2</u>	33.0	35.1	**D-I**
CO 1999																									
I. sobria	162.4	156.1	157.7	163.1	**D-I**																				
OR 2001																									
I. sobria	152.4	147.7	150.9	152.2	153.8	154.6	**D-I**																		
OR 2004																									
I. quinque.	179.9	174.5	<u>171.2</u>	171.3	<u>171.6</u>	171.0	171.6	171.7	173.9	172.1	171.7	173.4	174.4	173.5	173.6	176.9	179.8	<u>174.5</u>	180.5	190.8	**D-I**				
CO 1999																									
P. dorsata	258.3	257.9	253.2	248.8	246.8	241.6	245.6	**D**																	
MS 2000																									

Table 4. Average individual male call intervals for eight Plecoptera species. Underlined intervals indicate slight changes in general patterns of increasing (I), decreasing (D), or both (I-D or D-I).



Figs. 7–13. **7**. *Perlinella drymo* drumming: 3-way exchange, TD = 689-msec. Bar = 500-msec; **8**. *Hydroperla crosbyi* drumming: 3-way exchange, TD = 1491-msec. Bar = 500-msec; **9**. *Isoperla bifurcata* drumming: 2-way duet with female interspersed answer, TD = 647-msec. Bar = 500-msec; **10**. *Isoperla phalerata* 2-way duet, diphasic male call, TD = 2579-msec. Bar = 500-msec; **11**. *Isoperla sobria* drumming: 2-way duet, female interspersed answer not shown, TD = 589-msec. Bar = 500-msec; **12**. *Isoperla quinquepunctata* drumming. (A) Typical "multiple" 2-way duets, indicated by lines below, TD = 6727-msec. Bar = 1000-msec, (B) "Multiple" 2-way duets with female interspersed answer beat in first duet, TD = 1688-msec. Bar = 500-msec; **13**. *Pteronarcys dorsata* drumming: 2-way duet with female interspersed answer, TD = 2652-msec. Bar = 1000-msec.

sequenced signals with female answer signals either following the male call (N=48) or with interspersed answer beats beginning during the male's 4th (N=15), 5th (N=42), 6th (N=24) and 7th (N=1) interval. The two males called with signals of 6 mode beats (6.2 ± 0.8); with intervals of 50.2 ± 5.7 ms (Fig. 9, Table 3). Their average individual intervals gradually decreased from 54.5 ms (i1) to 45.4 ms (i6), then increased to 58.2 ms (i9) (Table 4). Mode and mean number of beats per female answer signal were 3 and 3.9 ± 2.5; mean beat interval was 50.0 ± 10.0 ms. The ♂-♀ exchange interval was 131.6 ± 21.3 ms for sequenced and overlapped duets.

Isoperla phalerata. Fifty and 28 signals were obtained from one, 1–2 day old male and female, respectively, at room temperature and normal incandescent light. The male and female produced 2-way sequenced signals and the male called with diphasic signals. The male called with 13 mode beats (12.8 ± 0.9); with intervals of 96.6 ± 16.6 ms during first phase and with 22 mode beats (22.2 ± 1.6); with 34.6 ± 5.7 ms during the second phase (Fig. 10, Table 3). The first phase average individual intervals decreased from 124.4 ms (i1) to 62.6 ms (i14) and the second phase gradually decreased from 51.3 ms (i1) to 31.0 (i16), then increased to 35.2 ms (i24) (Table 4). Mode and mean number of beats per female signal were 5 and 5.0 ± 1.0; average beat interval was 109.9 ± 27.7 ms. The ♂-♀ exchange interval was 301.0 ± 124.0 ms.

These results for *I. phalerata* (Table 3) and those from Sandberg and Stewart (2003) for *I. fulva* and *I. mormona* (Table 6) differ considerably in overall average intervals for the same three species reported by Szczytko and Stewart (1979) (Table 5). We propose here that their consistently smaller intervals for these three species and those of *I. quinquepunctata* are probably in large part due to calibration inconsistency in their oscilloscope compared with the probably more accurate calibration of our computer (Sandberg and Stewart 2003).

Isoperla sobria. This species from a new location was analyzed individually during 2001 and 2004. A total of 99 and 20 signals were obtained from two 3-11 day old males and females, respectively. Recording occurred at room temperature and normal incandescent light in 2001 and 23–24°C and 84 FTC in 2004. In both years, males and females produced 2-way sequenced signals with either the female answer signal following the call (N=12), or with the beginning answer beats interspersed within the males 2nd (N=1), 3rd (N=3), 4th (N=3) and 5th (N=1) interval. In 2001, the male called with 4 mode beats (3.7 ±0.8); with intervals of 159.1 ± 7.2 ms and in 2004, with 6 mode beats (5.2 ± 1.0); with intervals of 151.1 ± 5.8 ms (Fig 11, Table 3). The 2001 average individual intervals gradually decreased from 162.4 ms (i1) to 156.1 ms (i2), then increased to 163.1 ms (i4) (Table 4). The 2004 average individual intervals gradually decreased from 152.4 ms (i1) to 147.7 ms (i2), then increased to 154.6 ms (i6) (Table 4). The 2001 mode and mean number of beats per female answer signal were 1 and 1.1 ± 0.2; beat interval was 62.9 ms (N=1). The 2001 ♂-♀ exchange interval was 99.8 ± 5.6 ms for sequenced and overlapped duets. The 2004 female answer signals contained only a single interspersed beat and the ♂-♀ exchange interval was 112.8 ± 4.0 ms. These results agree well within reasonable expected variation, with those of Sandberg and Stewart (2003) and do not suggest a new dialect.

Isoperla quinquepunctata. One hundred seven and seventy-eight signals were obtained from one, 1-day old male and female respectively, at 21°C and normal incandescent lighting. The male and female produced long signals or "symphonies" (Szczytko and Stewart 1979) of repeating 2-way sequences (Range: 2–9), with either the typical female single answer beat following the call (N=69) (Fig. 12A), or with her answer beat(s) interspersed within the 1st, 3rd, 4th, 6th, 8th, 11th, 13th or 15th (N=2) male interval (Fig. 12B, first underlined duet). The male called with signals of 7 mode beats; with intervals of 173.6 ± 11.4 ms (Table 3). The average individual call intervals gradually decreased from 179.9 ms (i1) to 171.0 ms (i6), remained fairly uniform until (i15), then increased to 190.8 ms (i20) (Table 4). Mode and mean beats per female signal were 1 and 1.0 ± 0.2; mean beat interval was 924.5 ± 254.0. The ♂-♀ exchange interval was 98.0 ± 5.2 ms for sequenced and overlapped duets.

In our analyses, we treated the multiple 2-way sequences and overlapped duets individually, instead of the entire "symphony" (underlined duets, Figs. 12A–B). These duets were separated from one another by consistently longer intervals (279.5 ± 62.4 ms) than typical interbeat call intervals (173.6 ± 11.4 ms).

These results are consistent with Szczytko and Stewart (1979) in terms of general signal description and beats, but differ considerably in beat intervals (Table 5). We propose that our consistently larger overall-mean-interval differences were due to the inconsistencies between

Previously Reported Species-State/Year	No. Signals / No. Individuals ♂	♀	Range (Mode) beats / signal / $\bar{x}$ ± SD beats / signal ♂	♀	♂	Beat intervals (ms) ($\bar{x}$ ± SD) ♂	♀	♂	Exchange intervals (ms) ($\bar{x}$ ± SD) ♂–♀
I. fulva	352	63	5–6 (6)	3–6 (5)		25.9 ± 4.2	16.3 ± 4.7		13.5 ± 8.5
CO, NM 1979	10	2	5.6 ± 0.5	5.3 ± 3.8					
I. mormona	58		6–16 (12)						
UT 1979	2		11.5 ± 5.3						
I. phalerata	298	139	11–15 (13)	6–12 (8)		24.6 ± 3.7			90.8 ± 10.5
CO 1979	6	2	13.1 ± 0.9	7.9 ± 1.7					
♂ 2nd phase	298		14–26 (22)			6.4 ± 1.2			
	6		22.1 ± 3.7						
I. quinquepunctata	502	161	3–17 (9)	1–4 (2)		43.3 ± 5.3	214.2 ± 3.9		
CO, NM, UT 1979	23	7	9.2 ± 2.8	2.1 ± 2.6					

Table 5. Drumming descriptions of four *Isoperla* species from Szczytko and Stewart (1979). Number of signals and individuals, numbers of beats per signal, and total average beat intervals are provided for male calls and female answers. Exchange intervals are the intervals between male calls and female answers.

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Previously Reported / **Species-State/Year**	No. Signals / No. Individuals			Range (Mode) beats / signal / $\overline{x}$ ± SD beats / signal			Beat intervals (ms) ($\overline{x}$ ± SD)			Exchange intervals (ms) ($\overline{x}$ ± SD)
	♂	♀	♂	♂	♀	♂	♂	♀	♂	♂–♀
I. fulva CO 2003	19 / 1			6–8 (7) / 6.9 ± 0.6			46.7 ± 5.1			
OR 2003	11 / 2			6–9 (8) / 7.8 ± 0.9			42.3 ± 2.9			
I. mormona CO 2003	9 / 1	2 / 1		6–14 (12) / 10.4 ± 2.8			232.1 ± 25.7	279.9 N=1		119.9 ± 2.3

Table 6. Drumming descriptions of two *Isoperla* species from Sandberg and Stewart (2003). Number of signals and individuals, numbers of beats per signal, and total average beat intervals are provided for male calls and female answers. Exchange intervals are the intervals between male calls and female answers.

their oscilloscope calibration and our computer, explained above under *I. phalerata*.

Pteronarcyidae

Pteronarcys dorsata. Fifty-one and six signals were obtained from one, 2–3-day old male and female, respectively, at 24°C and 65 FTC. The male and female of this species produced 2-way sequenced signals with either the female answer following the call (N=13), or with the answer beats interspersed within the call, beginning during the male's 4th (N=3), 5th (N= 13) and 6th (N=6) interval. The male called with signals of 6 mode beats; with intervals of 251.9 ± 9.6 ms (Fig. 13, Table 3). His average individual intervals gradually decreased from 258.3 ms (i1) to 241.6 ms (i6), the last interval increased to 245.6 ms (N=2) (Table 4). Mode and mean beats per female signal were 5 and 4.9 ± 0.8; with intervals of 359.7 ± 45.9 ms. The ♂-♀ exchange interval was 141.1 ± 85.5 ms for sequenced and overlapped duets.

The results here coincide well with those of Stewart et al. (1982), with slight differences probably attributed to variation in environmental inputs rather than a new dialect. We add the *interspersed female answer signal to the description of this species signaling.*

GENERAL DISCUSSION

The new signals of female *Soliperla campanula* and new duet descriptions of *Isoperla muir*, *I. rainera*, *I. rougensis*, *I. tilasqua* and *Pteronarcys scotti* continue to reinforce the species specificity of drumming in Plecoptera, and generally fit previously characterized family patterns of signaling and the evolutionary paradigm of Stewart (2001) and Stewart and Sandberg (2006). The first recording of a male response signal, and therefore 3-way exchange, of *Perlinella drymo* probably reflects a variation in that species not detected in previous study due to low numbers of individuals or signals recorded. Such additional variations should be expected as numbers of signals in given species increase.

The recording of additional populations of *Hydroperla crosbyi*, *Isoperla bifurcata*, *I. phalerata*, *I. sobria*, *I. quinquepunctata* and *Pteronarcys dorsata* indicate that there are not substantial differences with previously recorded populations in terms of type of duetting signals. But some variations in numbers of call and answer beats and intervals are evident. These are difficult to attribute to dialectual population differences because of the change and possible calibration inconsistencies between older oscilloscope and newer computer signal measurement technologies and reasonably expected variations in beat numbers. Stewart and Maketon (1990) showed in three stonefly species that females recognize and answer with maximum response to a minimum threshold of male call beat number, despite the fact that those calls contain more and variable numbers of additional beats. They also showed that intervals, probably within the first call beats, are recognized by females as critical and only within a restricted time window. Such an analysis, determining the informational content of male calls recognized by females of each studied population, is probably crucial to determining whether two separate populations of a species actually have developed isolating dialects.

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REFERENCES

Sandberg, J.B. and K.W. Stewart. 2003. Continued studies of drumming in North American Plecoptera; Evolutionary implication, pp. 73–81. *In* E. Gaino (ed.), Research update on Ephemeroptera and Plecoptera. University of Perugia, Perugia, Italy.

Stewart, K.W. 2001. Vibrational communication (drumming) and mate-searching behavior in stoneflies; Evolutionary considerations, pp. 217–226. *In*: E. Dominguez (ed.). Trends in research in Ephemeroptera and Plecoptera. Kluwer Academic/Plenum Publishers, NY.

Stewart, K.W. and M. Maketon. 1990. Intraspecific variation and information content of drumming in three Plecoptera species, pp. 259–268. *In*: I.C. Campbell (ed.). Mayflies and Stoneflies: Life histories and biology. Kluwer Academic Publishers, Dordrecht/Boston/London.

Stewart, K.W. and J.B. Sandberg. 2006. Vibrational communication and mate searching behavior in stoneflies, pp. 179–186. *In*: S. Drosopoulos and M. Claridge (eds.). Insect sounds and communication: physiology, behavior, ecology and evolution. CRC Press, Boca Raton/London/New York.

Stewart, K.W., Szczytko, S.W. and B.P. Stark. 1982. Drumming behavior of four species of North American Pteronarcyidae (Plecoptera): dialects in Colorado and Alaska *Pteronarcella badia*. Annals Entomological Society of America 75: 530–533.

Szczytko, S.W. and K.W. Stewart. 1979. Drumming behavior of four Western Nearctic *Isoperla* (Plecoptera) species. Annals Entomological Society of America 72: 781–786.

Zeigler, D.D. and K.W. Stewart. 1977. Drumming behavior of eleven Nearctic stonefly (Plecoptera) species. Annals Entomological Society of America 70: 495–505.

Zeigler, D.D. and K.W. Stewart. 1985. Drumming behavior of five stonefly (Plecoptera) species from Central and Western North America. Annals Entomological Society of America 78: 717–722.

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