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VIBRATIONAL COMMUNICATION OF *ISOPERLA* BANKS FROM CALIFORNIA AND OREGON (PLECOPTERA: PERLODIDAE)

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ABSTRACT

The drumming signals of fourteen species of the stonefly genus *Isoperla* Banks from California and Oregon are reported. Monophasic, varied beat-interval and diphasic signal types were determined by graphing the mean interval pattern. Monophasic signals had a maximum mean interval difference of 10 milliseconds and varied beat-interval signals had greater than 10 millisecond interval differences. The diphasic signal was a continuous signal composed of monophasic, decreasing varied beat-interval and monophasic intervals. Signals are described for the first time for six species: *I. baumanni* Szczytko & Stewart, *I. denningi* Jewett, *I. laucki* Baumann & Lee, *I. marmorata* Needham & Claassen, *I. pinta* Frison and *I. sordida* Banks. Descriptions of new signal characters and signals from additional locations are provided for eight species: *I. acula* Jewett, *I. adunca* Jewett, *I. bifurcata* Szczytko & Stewart, *I. miwok* Bottorff & Szczytko, *I. mormona* Banks, *I. quinquepunctata* (Banks), *I. roguensis* Szczytko & Stewart and *I. sobria* (Hagen).

Keywords: Stonefly, Drumming signals, Mate-finding behavior

INTRODUCTION

Stonefly mate location behavior, or drumming, is thought to be a species-specific vibrational communication system (Stewart 2001; Stewart & Sandberg 2006). Communication is initiated by the male call (♂C) and answered by a receptive and virgin female (♀) in sequenced or overlapped 2-way exchanges. A third signal type in some species, the male response (♂R), follows the female answer in 3-way exchanges. Males produce vibrational signals using three methods: percussion (or tapping the abdomen upon resonant substrates), rubbing (scratching or scraping the abdomen), and tremulation (vibratory signal produced by swift body movements without abdomen-substrate contact). Stewart & Sandberg (2006) summarized the various call types which include monophasic (percussive, rub or tremulation signals with nearly even to variable interbeat intervals), diphasic (percussive calls having two interval phases separated by a transition from long to short interbeat intervals), and grouped (percussive signals with repeating groups of beats with variable numbers of beats/group and groups/call). Members of the genus *Isoperla*, including the western Nearctic species, drum primarily using percussive monophasic signals with males usually possessing a posterior lobe on the eighth sternite (or vesicle).

The genus *Isoperla* includes 61 Nearctic species (Baumann & Lee 2009; Grubs & Szczytko 2010; Stewart & Stark 2002, Szczytko & Stewart 2004) of which 27 have western distributions (Bottorff et al. 1990b; Jewett 1960, 1962; Szczytko & Stewart 1979a, 1984, 2004) and 17 have collection records from California (seven of these are California endemics). The drumming for *Isoperla* is fairly well known with

Table 1. General signal characters of previously published descriptions for twenty western Nearctic *Isoperla* species. Previous descriptions within parentheses when updated by current study (followed by asterisk). Abdomen with vesicle (V), abdomen with no specialized structure (N), male call (♂c), female answer (♀), male response (♂R). Signal and exchange type: monophasic (M), varied beat-interval (VB), diphasic (D), grouped (G), tapping (T), rub (R), sequenced answer (S), and interspersed answer (I). Published species analyzed again in this study listed in gray and their detailed characters listed in Table 3 are provided for comparison to the current study.

***Isoperla* Species Complex**	**Species**	**Abd**	♂c	♀	♂R	**Exchange**	**Citation - State**
I. quinq.	*I. acula*	V	(M-T)&VB-R*				Bottorff et al. 1990-CA
	I. mormona	V	(M) M&VB*	M		2-way I	Sandberg & Stewart 2003-CO
	I. quinquepunctata	V	(M) VB*	M		2-way I	Sandberg & Stewart 2006-CO
I. phalerata	*I. phalerata*	V	D	M		2-way S	Sandberg & Stewart 2006-CO
	I. pinta	V	D	VB	VB	2-3 way S	
I. sobria	*I. baumanni*[1]	V	VB	M		2-way S, I	
	I. miwok	N	(M) G*	VB*		2-6 way S	Bottorff et al. 1990-CA
	I. sobria	N	(M) M&VB*	M		2-way S, I	Sandberg & Stewart 2006-OR
	I. tilasqua	V	M	M		2-way S, I	Sandberg & Stewart 2006-OR
I. marmorata	*I. fulva*	V	M			2-way S	Sandberg & Stewart 2003 CO-OR
	I. marmorata	V	G		VB		
	I. roguensis	V	(M) G*	M		2-way S, I	Sandberg & Stewart 2006-OR
I. sordida	*I. adunca*	V	(M) VB*				Bottorff et al. 1990-CA
	I. bifurcata	V	(M) VB*	(M) VB*		2-way S, I	Sandberg & Stewart 2006-OR
	I. denningi	V	VB	M		2-way S, I	
	I. petersoni	V	M	M		2-way S, I	Sandberg & Stewart 2001-CO
	I. rainera	V	M	M		2-way S	Sandberg & Stewart 2006-OR
	I. sordida	V	VB				
unassigned	*I. laucki*	V	M				
	I. muir	V	M	M		2-way S	Sandberg & Stewart 2006-OR

I. baumanni[1] tentatively assigned to *I. sobria* complex, requires description of ovum.

35 Nearctic species signals described (Bottorff et al. 1990a; Graham 1982; Maketon & Stewart 1984; Sandberg & Stewart 2001, 2003, 2006; Stewart et al. 1988; Szczytko & Stewart 1979b; Ziminske 1989). In western states, there are 14 species with previously published drumming signal descriptions (Table 1), and of these, eight occur in California.

This study was undertaken to provide additional knowledge of drumming behavior in Nearctic stoneflies by recording and analyzing signals of reared-virgin and field collected *Isoperla* adults from California and Oregon.

MATERIAL AND METHODS

Virgin adult stoneflies were reared from mature nymphs collected with a kick net and adults were collected using a beating sheet and aspirator from the following streams (stream abbreviations in parentheses are used in Table 2 after the species listing and in interval pattern charts).

(1) *Isoperla acula*, El Dorado Co., CA, Deadman Creek (DC), Church Mine Rd. xing, 2.45 mi (3.9 km) SE El Dorado, (10- & 16)-V-2009 (♂♀ reared), 10-V-2009 (♂♀ field collected-teneral). **(2)** *Isoperla adunca*, Butte Co., CA, Campbell Creek & tributaries (CCT), North Table Mountain Wildlife Area, Cherokee Rd., 5 mi (8.0 km) S Cherokee, (17-, 24-, & 30)-III-2008 (♂♀ reared). **(3)** *Isoperla baumanni*, Plumas Co., CA, Domingo Spring (DS), Domingo Springs Campground, 8 mi (12.9 km) NW Chester on Old Red Bluff Rd., 13-VI-2008 (♂♀ reared), (13- & 20)-VI-2008 (♂♀ field collected teneral). **(4)** *Isoperla bifurcata*, Plumas Co., CA, Domingo Spring (DS), Domingo Springs Campground, 8 mi (12.9 km) NW Chester on

Old Red Bluff Rd., 01-X-2006 (♂♀ reared), 20-VI-2008 (♂♀ field collected); Mosquito Spring creek (MS), 0.4 mi (0.6 km) E of Domingo Spring Campground, 7.4 mi (11.9 km) W of Chester, (19- & 28)-V-2007 (♂♀ reared); Tehama Co., CA, Spring Tributary of Gurnsey Creek, (STGC) Gurnsey Creek Campground, Hwy 36, 2.3 mi (3.7 km) N Hwy 32 intersection, 26-IV-2010, 15-V-2010 (♂♀ reared). **(5)** *Isoperla denningi*, San Diego Co., CA, De Luz Creek (DLC), De Luz Murrieta Rd., 2.9 mi (4.7 km) NE De Luz, 17-IV-2010 (♂♀ field collected teneral). **(6)** *Isoperla laucki*, Humboldt Co., CA, Dragsaw Spring (DSS), FR 13N01 xing (Six Rivers NF), 6.1 mi (9.8 km) E Hwy 96 nr Aikens Creek Campground and 11.1 mi (17.9 km) NE Weitchpec, 12-VII-2009 (♂♀ reared). **(7)** *Isoperla marmorata*, Butte Co., CA, Big Chico Creek (BCC), CSU-Chico, near Biology Building (Holt Hall), 08-IV-2008 (♂ field collected); El Dorado Co., CA, North Fork Cosumnes River (NFCR), Hwy 49 cattle corral, 1.7 mi (2.7 km) S Nashville, nr confluence MF Cosumnes River, (05- & 11)-IV-2009 (♂♀ reared). **(8)** *Isoperla miwok*, Butte Co., CA, Campbell Creek & tributaries (CCT), North Table Mountain Wildlife Area, Cherokee Rd., 5 mi (8.0 km) S Cherokee, (17- & 30)-III-2008 (♂♀ reared), 06-IV-2008 (♂ field collected); El Dorado Co., CA, Tributary of North Fork Cosumnes River (TNFCR), Union Mine Rd., 3.4 mi (5.5 km) N Nashville at McNulty Mine Rd. xing, 25-IV-2009 (♂♀ reared). **(9)** *Isoperla mormona*, El Dorado Co., CA, Greenwood Creek (GC), Greenwood Creek Park, Hwy 49, 4 mi (6.4 km) E Pilot Hill, 16-V-2009 (♂♀ reared). **(10)** *Isoperla pinta*, Butte Co., CA, Butte Creek (BC), Butte Creek Ecological Preserve, Honey Run Rd, 2.9 mi (4.7 km) E intersec w/Skyway, 04-III-2007, (07- & 13)-IV-2007 (♂♀ reared). **(11)** *Isoperla quinquepunctata*, Yuba Co., Yuba River (YR), Hwy 22 bridge xing, 16.4 mi (26.4 km) NE Marysville, (02- & 07)-V-2010 (♂♀ reared). **(12)** *Isoperla roguensis*, Butte Co., Butte Creek (BC), Butte Creek Ecological Preserve, Honey Run Rd, 2.9 mi (4.7 km) E intersec w/Skyway, 30-III-2008 (♂♀ field collected), (11- & 14)-III-2010 (♂♀ reared); Curry Co., OR, Rogue River (RR), Orchard Bar, Cty Hwy 595 (Agness Rd), 8.9 mi (14.3 km) NE Hwy 101 at Gold Beach, 20-III-2010 (♂♀ reared). **(13)** *Isoperla sobria*, Butte Co., CA, Butte Creek (BCCH), Cherry Hill Campground, Humboldt Rd, 9 mi (14.4 km) NE Lomo (Hwy 32), 26-IV-2010 (♂ reared); Plumas Co., CA, Spring Tributary of Lake Davis (STLD), Threemile Valley Rd, at corral, 06-VI-2010 (♂♀ reared); Mosquito Spring creek (MS), 0.4 mi (0.6 km) E Domingo Spring Campground, 7.4 mi (11.9 km) W Chester, 05-VI-2010 (♂♀ reared). **(14)** *Isoperla sordida*, Deschutes Co., OR, Fall River (FR), Fall River Campground, Hwy 42 (S Century Dr), 13 mi (20.9 km) E Hwy 97, 28-V-2008 (♂♀ reared); Mono Co., CA, Cold Water Creek (CWC), Cold Water Campground, Inyo NF, 4.7 mi (7.6 km) S Mammoth Lakes (Hwy 203), 26-VII-2010 (♂ reared).

One thousand sixteen drumming signals were obtained from stonefly adults held in laboratory recording chambers using the methods of Sandberg & Stewart (2003, 2006). Recordings were made at temperatures between 20.0–26.7°C and under incandescent light. In several recordings, females answered the playback of previously recorded male calls through speakers approximately 3.5 m from the recording chamber or answered live males held in Styrofoam cups outside the recording chamber. Most of these recordings only permitted analysis of the signal produced within the chamber.

During recording sessions, the *Isoperla* adult males were rarely prolific drummers and females seldom answered male calls (*I. denningi* was one exception, producing nearly 70 calls and 11 duets in two days of recording). Most species in this study required several individuals to be recorded over several days in order to obtain an adequate sample for signal description. Field collected adults were also recorded to increase sample size. Recording signals over multiple days to weeks, or from individuals without known ages, is not suggested because of the possible effect that increased age (or other physiological and environmental variables) have upon signal rate, beat interval and beats per signal.

The entire signal interval pattern or the consecutive change in beat or group intervals over time was described using box and whisker charts graphing the mean, standard deviation, and range. These charts display time intervals in milliseconds between (1) the beats of monophasic, varied beat-interval and diphasic signals (interbeat intervals), (2) the beats of grouped signals (intra-group intervals), and (3) groups (inter-group intervals). Written descriptions of interval patterns were based upon the

Table 2. Detailed signal characters for fourteen California and Oregon *Isoperla* species recorded in 2006-2010. Male call (♂C), female answer (♀), male response (♂R) and varied beat-interval (VB). Total number of male rubs, intra-group interval (ms), rub duration (ms), and inter-rub interval (ms) indicated by superscript[1-4], respectively. *Isoperla baumanni*, *I. denningi*, *I. laucki*, *I. marmorata*, *I. pinta*, and *I. sordida* are reported for the first time.

Species–Waterbody (Temp, Age)	# Individuals / # Signals ♂C	♀	♂R	#Groups/ Call Range / (Avg ±SD) ♂C	#Beats/ Group ♂C	Total # Beats-Rubs[1] / Signal Range / (Avg±SD) ♂C	♀	♂R	Interbeat, Intra-group[2] Intervals or Rub Duration[3] (Avg±SD) / Range (ms) ♂C	♀	♂R	Inter-group/rub[4] Intervals (ms) (Avg±SD)/Range ♂-♂	Exchange Intervals (ms) (Avg±SD)/Range ♂C-♀
I. acula DC	6					3-13[1]			30.3±10.3[3]			413.8±55.2[4]	
(20.8-21.2°C, 1-6d)	66					6.1±2.3[1]			10.6-65.8[3]			276.1-590.5[4]	
I. adunca CCT	8					7-22			151.5±8.6				
(20.0°C, 1-6d)	149					11.7±2.8			121.8-187.1				
I. baumanni DS	9	1				3-8	1		206.3±29.3				153.1±4.3
(21.1°C, 1-5d)	83	4				4.8±1.0	1.0±0.0		119.5-263.6				146.9-156.5
I. bifurcata MS	6					4-8			43.6±4.8				
(20.5-21.1°C, 1-3d)	38					6.3±1.1			32.7-58.0				
I. bifurcata DS	3					5-8			52.6±6.1				
(20-22°C, 1-7d)	16					6.6±1.0			43.4-70.9				
I. bifurcata STGC	2	1				4-7	2-12		58.5±6.9	67.5±15.5			
(21-22°C, 5-8d)	42	15				5.7±0.7	6.7±2.3		43.0-77.7	33.8-120.1			
I. denningi DLC	2	1				4-6	1		163.3±9.9				131.3±10.5
(21.1-22.8°C, 3-4d)	68	14				5.0±0.6	1.0±0.0		130.9-197.3				116.5-150.2
I. laucki DSS	2					10-22			21.6±3.0				
(22.2°C, 2-3d)	4					17.5±5.2			9.5-33.6				
I. marmorata BCC	2		1	7-15	1-9	61-102		70(n=1)	20.3±2.4[2]		172.6±29.7	347.9±77.9	
(21.7°C, 3d)	22		1	11.8±1.8	7.5±1.2	88.5±14.6			13.8-20.3[2]		144.4-275.2	210.2-907.1	
I. marmorata NFCR	3			4-13	1-8	21-70			21.9±3.5[2]			383.06±116.3	
(21.1-21.7°C, 4-10d)	10			8.8±2.5	5.7±1.7	50.5±15.2			12.3-39.5[2]			232.7-840.3	
I. miwok CC ♂1	4			1-3	2-10	5-32			27.9±4.7[2]			1143.4±197.4	
(21.1-21.7°C, 1-7d)	38			2.0±0.7	6.8±1.6	17.5±7.5			19.2-46.6[2]			938.1-1787.6	
♂ 2nd Group	3				6-13				28.3±4.1[2]			1073.1±174.1	
	30				10.4±1.6				21.0-48.1[2]			944.6-1499.5	
♂ 3rd Group	1				4-12				28.2±3.8[2]				
	10				9.8±2.7				20.0-39.8[2]				
I. miwok TNFCR ♂1	1	2		1-2	2-8	4-17	13-16		22.7±2.9[2]	54.0±12.6		1049.7±263.0	255.4±68.1
(20.5-21.5°C, 2-5d)	15	6		1.8±0.4	5.4±1.6	12.1±3.6	14.3±1.5		17.7-35.6[2]	33.6-85.9		860.5-1611.6	183.1-384.4
♂ 2nd Group	1				7-11				23.9±4.7[2]				
	12				8.3±1.4				17.8-45.1[2]				
I. mormona GC	2					6-15			248.7±13.5				
(21.2°C, 3-8d)	35					9.6±1.9			213.1-297.9				
I. mormona GC	1					6-9			174.4±7.7				
(26°C, 4d)	20					7.6±0.9			152.3-214.1				
I. pinta BC Overall	7	3	1			27-47	29-62	32-50	53.5±32.2	92.4±23.2	124.0±31.4		902.5±430.7
(16.6-22.2°C, 1-10d)	99	45	5			37.0±3.3	38.8±8.4	44.0±7.2	17.5-156.4	58.1-258.4	69.6-240.3		98.4-2271.4
Monophasic phase-1	7								95.8±14.9				
	99								72.6-156.4				
VB Transition	7								63.3±26.7				
	99								23.4-124.6				
Monophasic phase-2	7								27.2±6.1				
	99								17.5-70.2				
I. quinquepunctata YR	6	1				11-37	2		191.2±21.9	1300.2			157.3±8.8
(21.1-22.8°C, 2-7d)	25	1				23.0±7.0	(n=1)		144.3-281.6	(n=1)			149.6-164.9
I. roguensis BC	6			1-6	3-9	3-36			38.1±3.2[2]			2284.0±405.7	
(19.4-20.0°C, 3-8d)	36			1.9±1.2	6.0±1.2	11.5±7.2			28.3-47.3[2]			1713.6-3341.8	
I. roguensis RR	1			1-4	3-6	5-19			34.7±3.9[2]			2512.4±959.6	
(20.5-21.1°C, 8-9d)	5			2.4±1.1	4.8±0.7	11.6±5.1			23.8-41.6[2]			1340.0-3747.4	
I. sobria BCCH	1					3-8			195.6±15.8				
(21.1-21.7°C, 5-8d)	8					5.9±1.5			151.2-226.5				
I. sobria MS	4					3-7			179.7±15.8				
(20.0-23.8°C, 1-5d)	28					4.9±1.1			149.7-233.0				
I. sobria STLD	2					3-6			174.0±18.2				
(20.0-23.8°C, 3-5d)	44					4.7±1.0			139.0-231.2				
I. sordida FR	1					6-8			194.4±15.6				
(21.1-26.7°C, 4-6d)	68					7.4±0.9			148.0-285.8				
I. sordida CWC	1					5-8			153.3±9.4				
(22.2-24.4°C, 2-3d)	21					6.6±0.8			132.0-182.2				

Table 3. Detailed signal characters of previously published descriptions for ten *Isoperla* species of California and Oregon from Table 1. Male call (♂C), female answer (♀), male response (♂R), mode (number in parentheses), ? = data unavailable.

Species - State	# Individuals / # Signals			Total # Beats / Signal Range / (Avg±SD)			Interbeat Interval (ms) (Avg±SD) / Range		Exchange Interval (ms) (Avg±SD) / Range
Citation (Temp, Age)	♂C	♀	♂R	♂C	♀	♂R	♂C	♀	♂C-♀
***Isoperla acula* CA**	1	1		2-6	4		356.8±32.6	352.6±42.0	496.6±?
Bottorff et al. 1990 (24-25°C, ?d)	44	2		4.1±0.9	4.0±0.0		198.6-486.6	297-437.0	?
***Isoperla adunca* CA**	2			2-9			137.8±18.2		
Bottorff et al. 1990 (22-24°C, ?d)	56			6.1±1.5			31.5-259.3		
***Isoperla bifurcata* CA**	2	1		3-8	1-8		47.2±6.6	57.4±24.4	132.6±49.8
Bottorff et al. 1990 (23-24°C, ?d)	103	19		6.4±1.1	4.5±1.8		27.5-91.7	32.6-146.7	73.3-243.0
***I. bifurcata* OR**	2	1		4-10	1-14		50.2±5.7	5-.0±10.0	44.3±18.3
Sandberg & Stewart 2006 (23°C, 2-8d)	136	130		6.2±0.8	3.9±2.5		?	?	?
Isoperla fulva OR	2			6-8			46.7±5.1		
Sandberg & Stewart 2003 (21°C, 1d)	11			6.9±0.6			?		
***I. fulva* CO**	1			6-9			42.3±2.9		
Sandberg & Stewart 2003 (21°C, 6d)	19			7.8±0.9			?		
***Isoperla miwok* CA**	6	2		2-10	3-18		25.3±9.0	68.6±17.0	413.0±146.0
Bottorff et al. 1990 (20-21°C, ?d) Call 1	133	39		5.7±2.2	10.6±3.6		10.0-140.5	20.1-146.7	40.2-762.7
	3	3		(4)	(6)		24.5±4.0	65.8±19.9	398.1±130.7
Call 2	4	1		5.0±1.2	7.3±1.9		20.1-30.1	20.1-100.4	220.8-531.9
	1	1		7	8		26.7±4.7	80.3±22.0	913.3
Call 3	1	1		--	--		20.1-35.1	60.2-130.5	?
***Isoperla mormona* CO**	1	1		6-14	1-2		232.1±25.7	279.9 (n=1)	119.9±2.3
Sandberg & Stewart 2003 (21°C, 8-12d)	9	2		10.4±2.8	1.5±0.7		?		?
***Isoperla phalerata* CO** Phase 1	1	1		10-15	3-7		96.6±16.6	109.9±27.7	301.0±124.0
Sandberg & Stewart 2006 (?°C, 1-2d)	50	28		12.8±0.9	5.0±1.0		?	?	?
Phase 2				19-25			34.6±5.7		
				22.2±1.6			?		
***Isoperla quinquepunctata* CO**	1	1		1-21	1-2		173.6±11.4	924.5±254.0	98.0±5.2
Sandberg & Stewart 2006 (21°C, 1d)	107	78		8.6±5.7	1.0±0.2		?	?	?
***Isoperla roguensis* OR**	1	1		6-7	2-11		37.2±3.2	40.8+7.2	27.9±27.5
Sandberg & Stewart 2006 (?°C, 1d)	128	111		6.9±0.3	6.5±1.7		?	?	?
***Isoperla sobria* NM**	8	4		2-10	1-2		168.0±35.2	107.5±74.2	104.6±12.6
Sandberg & Stewart 2003 (18-21°C, 1-11d)	278	65		5.7±1.5	1.1±0.2		?	?	?
***I. sobria* OR 2001**	1	1		2-5	1-2		159.1±7.2	69.9	99.8±5.6
Sandberg & Stewart 2006 (?°C, 3-11d)	44	16		3.7±0.8	1.1±0.2		?	(n=1)	?
***I. sobria* OR 2004**	1	1		3-7	1		151.1±5.8	--	112.8±4.0
Sandberg & Stewart 2006 (23-24°C, 3-11d)	50	4		5.2±1.0	(n=1)		?		?

charted interval pattern mean (dashed line), omitting final intervals with only one observation and individual interval variation was represented by the interval standard deviation (boxes) and interval range (vertical lines or whiskers) for each successive interval.

RESULTS

All the following signal beats and time intervals were expressed as range and mean ± standard deviation so that the mean symbol would not be needed. Abbreviations were defined for "interval" (i) and "day old" (d). The age of field collected *Isoperla* adults was defined as the number of days they were held in captivity until recorded.

Isoperla acula. Bottorff et al. (1990a) provided the first description of drumming behavior for this species from an Amador County stream. In this study, sixty-six call signals were recorded from six, 1–6d males at 20.8–21.2°C. Males called with varied beat-interval patterns (or signals) of 3–13 short but acoustically distinctive rubs (6.1±2.3), with rub durations of 30.3±10.3 ms (Fig. 1, Table 2). The inter-rub intervals were 413.8±55.2 ms and call durations were (722.9–5874.4), 2261.7±1115.9 ms. The inter-rub interval call pattern was erratic with several fluctuations (Fig. 6) with an interval difference of 25.4 ms (i12 omitted, n=1). The inter-rub pattern decreased from 414.4 ms (i1) to the minimum of 405.3 ms (i4), increased erratically to the maximum of 430.8 ms (i8), and finally decreased erratically to 415.2 ms (i11). Because the mean interval difference was greater than 10 milliseconds, the signal type was determined to be varied beat-interval. The rub drumming method has only been observed in one other perlodid, *I. ouachita* Stark & Stewart from Arkansas with a series of 6–27 rubs/call (Stewart et al. 1988).

The call method is updated to include both monophasic tapping and varied beat-interval rubbing (Table 1), because 11 of the 66 calls had 1–3 percussive abdominal taps mixed with rubs. Bottorff et al. (1990a) reported monophasic tapping and less beats/signal than rubs/signal here (Tables 2 and 3). Their analysis may have failed to detect rub signals due to the limitations of using a storage oscilloscope which can not play back the audio. They also reported an overall interbeat call interval of 356.8±32.6 ms (198.6–486.6 ms) (Table 3), which was less than what was reported here for inter-rub interval (Table 2). It is possible that these beat or rub counts and interval differences were due to differences in age or an environmental variable such as temperature. Recording for this study was conducted 3–4°C lower than Bottorff et al. (1990a) and could explain the longer average intervals observed here.

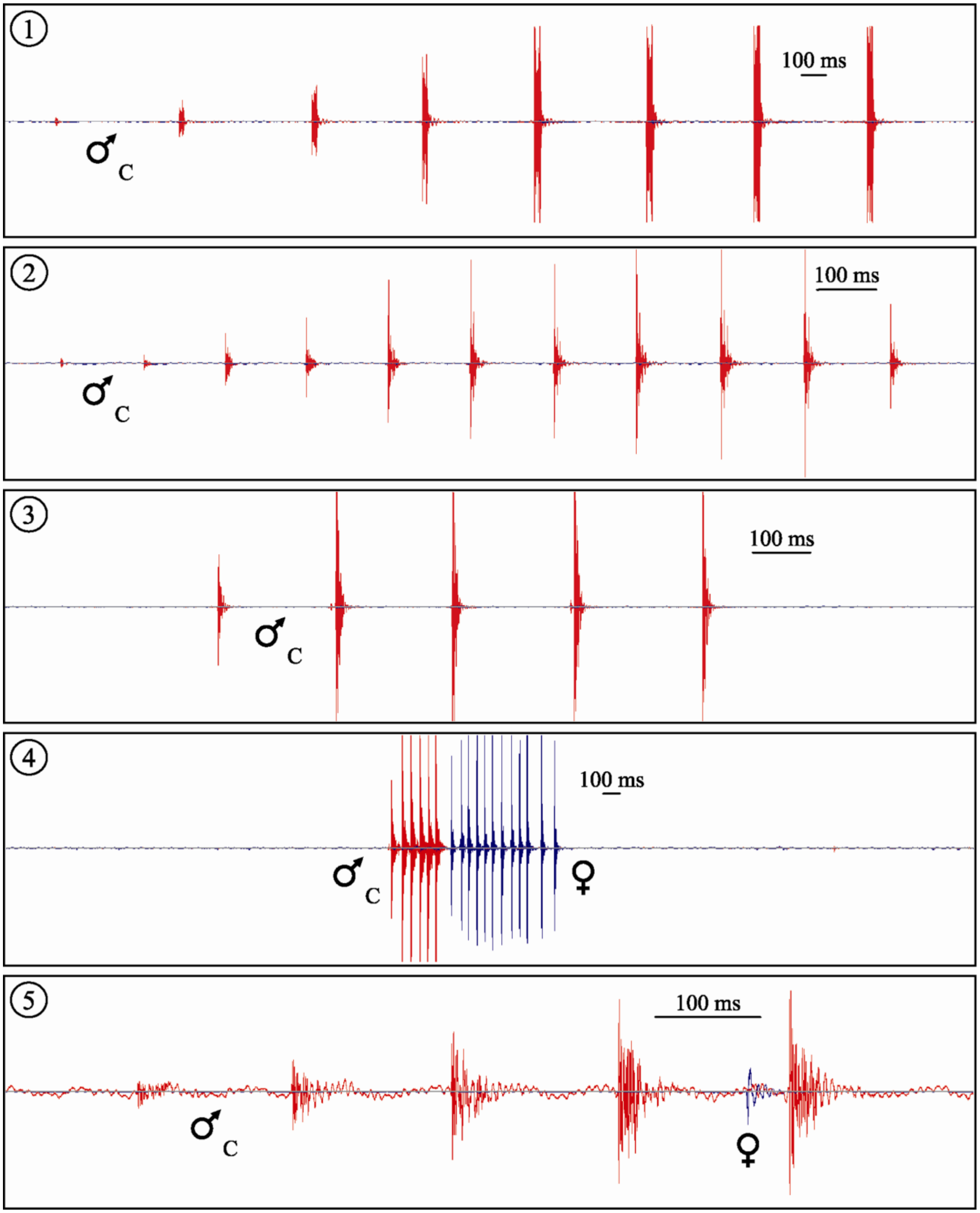
Bottorff et al. (1990a) stated that the *I. acula* call was most similar to *I. morhi* Frison, specifically in relation to beat interval. In this report the *I. acula* call was most similar in average inter-rub interval to the average interbeat interval of *I. similis* (Hagen) (413.8 versus 425.9 ms, respectively) from Virginia but differed in having slightly more average beats (6.1 versus 5.3, respectively) (Stewart et al. 1988).

***Isoperla adunca*.** Bottorff et al (1990a) first described the drumming behavior of this species from an Amador County stream. In this study, one hundred forty-nine call signals were recorded from eight, 1–6d males at 20.0°C. Males called with varied beat-interval patterns of 7–22 beats (11.7±2.8) with intervals of 151.5±8.6 ms (Fig. 2, Table 2). Call durations were (869.0–3349.1), 1617.3±428.5 ms. The mean interval call pattern decreased and increased twice (Fig. 7) with an interval difference of 13.0 ms. The pattern decreased slightly from 152.1 ms (i1) to a minimum of 149.1 ms (i4), then increased slowly to 156.5 ms (i13), and finally increased erratically to a maximum 160.1 ms (i18) followed by a slight decrease to 160.0 ms (i19). The last two intervals each had a single observation and continued to increase to 184.8 ms (i21).

Bottorff et al. (1990a) described the call pattern as monophasic and reported less average beats/signal and lower mean interbeat intervals than this study (Table 3). Their interbeat intervals ranged from 31.5–259.3 ms, which completely overlapped the range reported here (Table 2), suggesting that their adults (no ages reported) may have been recorded over several days to weeks and variation may have been due to increased age.

Bottorff et al. (1990a) also stated that the *I. adunca* call was most similar to *I. coushatta* Szczytko & Stewart (Stewart et al. 1988), in relation to beats/signal and interval. In this report the *I. adunca* call was most similar in average interbeat interval to *I. sobria* (151.1±8.6 versus 151.1+5.8 ms, respectively) from Oregon recorded in 2004, but differed in having more average beats (11.7 versus 5.2, respectively) (Sandberg & Stewart 2006).

***Isoperla baumanni*.** Eighty-three calls from nine males and four answers from one female were recorded at 21.1°C (ages ranged 1–5d). Males called with varied beat-interval patterns and the female answer was always one beat with either overlapped (n=1) or 2-way sequenced exchanges (n=3). The males called with signals ranging from 3–8 beats (4.8±1.0) with intervals of 206.3±29.3 ms (Fig. 3, Table 2). Call durations were (336.2–1321.1), 783.0±230.1 ms. The sequenced ♂c-♀ exchange interval (between the last call beat and the single answer beat) was 153.1±4.3 ms (Table 2). The one female overlapped answer followed the third call beat (i4) by 155.9 ms. The three sequenced duets had durations of (835.8–1080.2), 904.5±117.9 ms. The mean interval call



Figures 1–5. Stonefly drumming signals. 1. *Isoperla acula* varied beat-interval multi-rub call. 2. *I. adunca* varied beat-interval call. 3. *I. baumanni* varied beat-interval call. 4. *I. bifurcata* sequenced varied beat-interval duet, STGC. 5. *I. denningi* varied beat-interval call and interspersed answer. ♂C = Call, ♀ = Answer, and ♂R = Response.

pattern was a decreasing sigmoid curve (Fig. 8) with an interval difference of 38.7 ms. Intervals decreased from a maximum of 213.4 ms (i1) to 204.0 ms (i2), increased slightly to 206.6 (i4), then decreased to 199.2 ms (i5), and finally decreased to a minimum of 174.7 ms (i6). Interbeat interval 7 decreased to 161.9 ms (n=1).

This is the first *Isoperla baumanni* drumming description and increases the number of species known to drum within its probable species group (*I. sobria* complex) to four (Table 1). The average number of beats/call for *Isoperla baumanni* was most similar to *I. acula* (Bottorff et al. 1990a) and *I. sobria* from Oregon recorded in 2004 (Sandberg & Stewart 2006) (Table 3). The *I. baumanni* average interbeat interval was most similar to the mid-western species, *I. transmarina* (Newman) (206.3 vs. 200.2 ms, respectively) (Graham 1982).

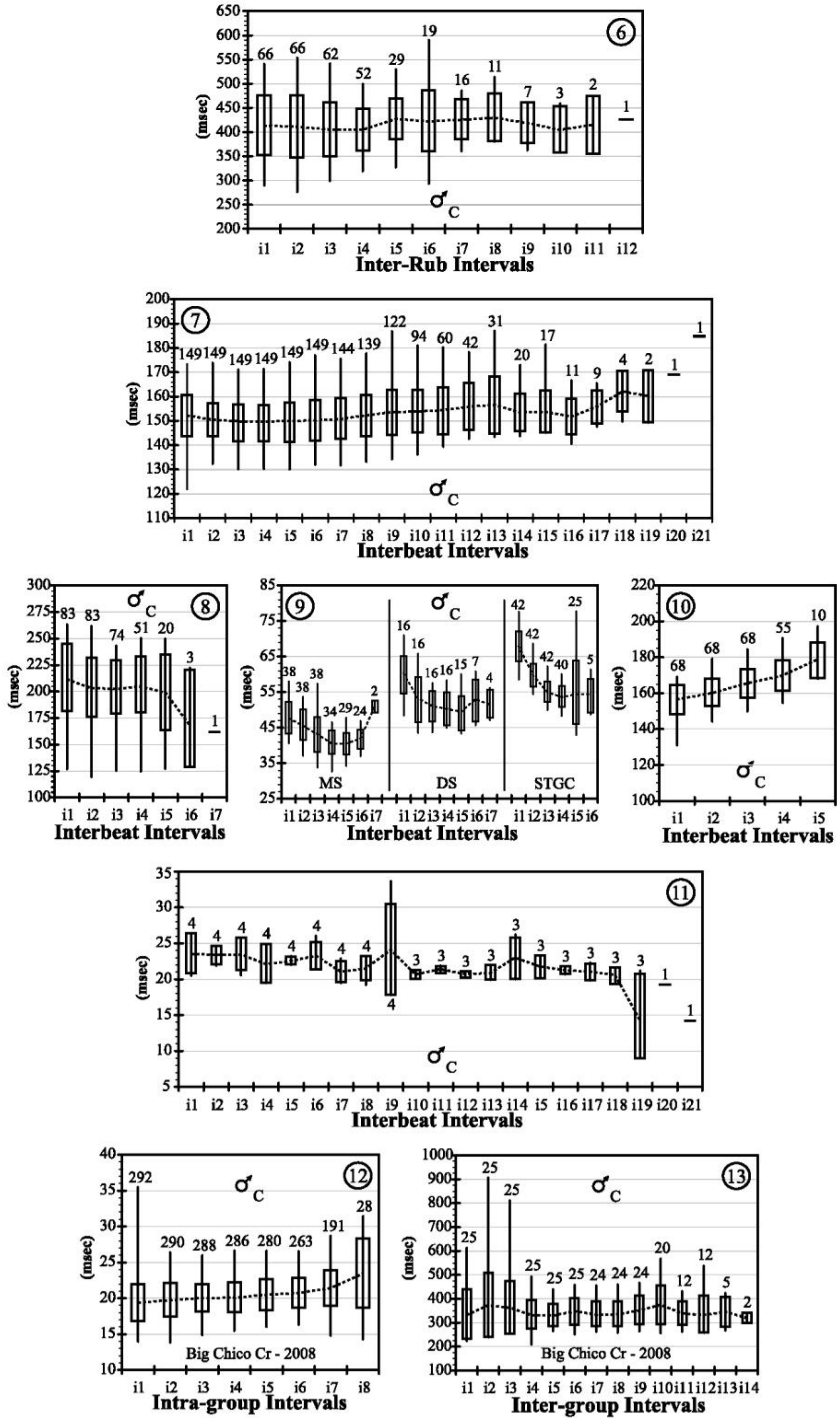
Isoperla bifurcata Bottorff et al. (1990a) and Sandberg & Stewart (2006) previously described this species from El Dorado County, California and Oregon, respectively (Table 1). In this study, the drumming behavior of three California locations from Plumas County (Mosquito Spring creek and Domingo Spring) and Tehama County (Spring Tributary of Gurnsey Creek) are described.

Mosquito Spring creek. Thirty-eight signals were recorded from six, 1–3d males at 20.5–21.1°C. Males called with varied beat interval patterns of 4–8 beats (6.3±1.1) with intervals of 43.6±4.8 ms (Table 2). Call durations were (140.7–316.7), 233.1±43.1 ms. The mean interbeat interval call pattern decreased and increased (Fig. 9 left) with an interval difference of 10.5 ms. Intervals decreased from 47.3 ms (i1) to a low of 40.4 ms (i4), and then increased abruptly to 50.9 ms (i7).

Domingo Spring. Sixteen signals were recorded from three, 1–7d males at 20–22°C. Males called with varied beat-interval patterns of 5–8 beats (6.6±1.0) with intervals of 52.6±6.1 ms (Table 2). Call durations were (229.2–405.8), 296.0±67.62 ms. The mean interval call pattern decreased and increased irregularly (Fig. 9 center) with an interval difference of 10.9 ms. Intervals decreased from 59.9 ms (i1) to a low of 49.0 ms (i5), then increased irregularly to a maximum interval of 52.7 ms (i6), and finally decreased to 51.7 ms (i7).

Spring Tributary of Gurnsey Creek. Forty-two signals from two males and 15 answers from one female were recorded at 21–22°C (ages ranged 5–8d). The males and female signaled with varied beat-interval calls and answers, with 2-way exchanges that were either sequenced (n=12) or overlapped (n=3). The two males called with signals of 4–7 beats (5.7±0.7) with intervals of 58.5±6.9 ms (Fig. 4, Table 2). Call durations were (198.1–339.8), 273.2±40.6 ms. The number of beats per female answer signals was 2–12 (6.7±2.3) with intervals of 67.5±15.5 ms (Fig. 4, Table 2). Answer durations were (51.3–651.6), 382.3±146.22 ms. In sequenced exchanges, the ♂c-♀ exchange interval was 67.5±15.5 ms; for overlapped answers, the female inserted her first answer beat within the 5th or 6th call interval (i5-i6) and the overlapped ♂c-♀ exchange interval was 51.9±6.7 ms. The durations of all sequenced and overlapped ♂c-♀ exchanges were (523.4–1030.1), 767.6±124.2 ms. The mean interval call pattern decreased and then slightly increased (Fig. 9 right) with an interval difference of 14.1 ms. Intervals decreased from the maximum of 67.9 ms (i1) to a minimum of 53.7 ms (i4), and then increased slightly to 54.0 ms (i6). The female answer interval pattern was erratic with an interval difference of 19.2 ms (no figure). Intervals decreased from 64.4 ms (i1) to a low of 56.9 ms (i2), then increased erratically to a high of 76.1 ms (i7), and finally decreased to 71.4 ms (i8). The final three intervals decreased to 44.6 ms (i9), increased to 92.9 ms (i10), and decreased to 83.3 ms (i11) (n=1 for each).

The descriptions from this study and the two previous studies (Bottorff et al. 1990a; Sandberg & Stewart 2006) were difficult to compare (Tables 2 and 3). All recordings were made between 20–24°C and ages ranged from 1–8d. Of the five locations, the average interbeat interval for the Spring Tributary of Lake Davis individuals was longest (58.5 ms) and the Mosquito Spring creek individuals was shortest (43.6 ms). The cause for these different mean intervals from different locations is unknown but suspected to be the result of natural variation. The range of temperatures and ages at the time of recording for each additional location was varied with some overlap for each study. To have determined if temperature or age had an influence upon mean intervals and interval patterns, all non-test



Figures 6–13. Stonefly signal inter-rub, intra- and inter-group and interbeat interval patterns. 6. *Isoperla acula* varied beat-interval pattern. 7. *I. adunca* varied beat-interval pattern. 8. *I. baumanni* varied beat-interval pattern. 9. *I. bifurcata* varied beat-interval patterns. 10. *I. denningi* varied beat-interval pattern. 11. *I. laucki* monophasic pattern. 12–13. *I. marmorata* monophasic intra-group and varied inter-group patterns. Mean=dashed line; Standard deviation=box; Range=vertical line; Number of intervals above range.

environmental and physiological variables should have been kept constant. In other studies, the effect of increased age was tested for its effect upon drumming and was suspected to decrease the rate of *Pteronarcella badia* signal production (Zeigler & Stewart 1985). The effect of decreased temperature possibly increased the *Isogenoides zionensis* Hanson average beat interval (Sandberg & Stewart 2005). However, neither study entirely correlated the suspected causes with the varied effects observed.

Isoperla denningi. Sixty-eight calls from two males and 14 answers from one female were recorded at 21.1–22.8°C (ages ranged 3–4d). Males called with varied beat-interval patterns, and females answered male calls with monophasic 1-beat answers with 2-way exchanges that were either sequenced (n=3) or overlapped (n=11). The two males called with signals of 4–6 beats (5.0±0.6) with intervals of 163.3±9.9 ms (Fig. 5, Table 2). Call durations were (480.4–909.6), 646.0±98.8 ms. The female answer was always one beat (Fig. 5, Table 2). In sequenced exchanges, the ♂c-♀ exchange interval was 130.1±11.3 ms; for overlapped answers the female inserted the one answer beat within the 3rd or 4th call interval (i3-i4) and the overlapped ♂c-♀ exchange intervals were 131.7±10.9 ms. The durations for sequenced and overlapped exchanges were similar (621.0–909.6, 684.8±80.9 ms versus 619.1–748.6, 680.0±65.1 ms, respectively). The mean interval call pattern increased steadily (Fig. 10) with an interval difference of 21.8 ms. The pattern increased from a minimum of 156.5 ms (i1) to a maximum of 178.3 ms (i5) with approximately 5 ms increases at each interval.

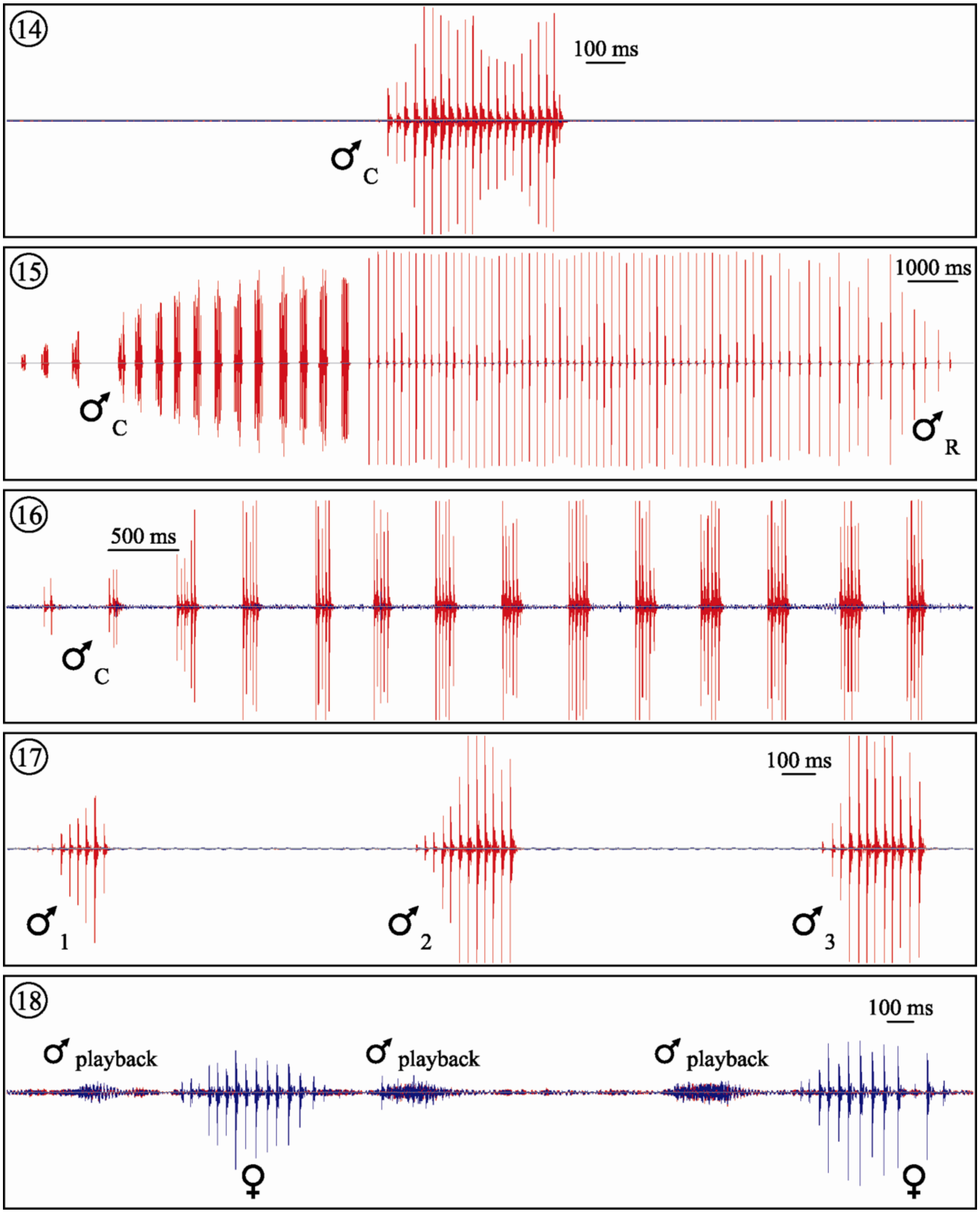
This is the first *Isoperla denningi* drumming description and increases the number of species known to drum within the *I. sordida* species complex to five, not including *I. sordida* (Table 1). The average beats/call for *I. denningi* was similar to several species: *I. fulva*-5.6 beats (Szczytko & Stewart 1979b NM-CO), *I. miwok* 2nd call-5.0 beats (Bottorff et al. 1990a CA), *I. signata* Claassen-5.3 beats (Maketon & Stewart 1984 OK), and *I. sobria*-5.2 beats (Sandberg & Stewart 2006 OR-2004), however these species all differed from *I. denningi* in mean interbeat interval. The average interbeat interval was most similar to *I. montana* (Banks)-168.6 ms (Stewart et al. 1988 WV) and *I. sobria*-159.1 ms (Sandberg & Stewart 2006 OR-2001), but differed in beats/signal. The steady increasing mean interbeat interval pattern of *I. denningi* (Fig. 10) will help to distinguish it from *I. sobria* (Figs. 39–41).

Isoperla laucki. Only four monophasic call signals were recorded from two, 2–3d males at 22.2°C. The males called with signals ranging from 10–22 beats (17.5±5.2) with intervals of 21.6±3.0 ms (Fig. 14, Table 2). The call durations were (222.8–449.5), 367.9±99.6 ms. The mean interval call pattern was approximately even (Fig. 11), decreasing slightly with an interval difference of 9.3 ms. The pattern increased slightly from 23.6 ms (i1) to a maximum of 24.1 ms (i9), and then decreased erratically to a minimum of 14.9 ms (i19). Intervals (i20-i21) were 19.2 and 14.2 ms, respectively (n=1 for each).

This is the first drumming description for this species and because only four observations were made, is considered preliminary. This late and extended emerging spring seep species rarely moved in the drumming chambers and further recordings will be necessary to document the full extent of variation among signals and the female answer. The average beats/signal for this species was most similar to *I. decepta* Frison-16.0 beats (Virginia) and *I. ouachita* Stark & Stewart (Arkansas)-18.5 beats (Stewart et al. 1988). The average interbeat interval was most similar to *I. miwok* ranging from 24.5–26.7 ms (Bottorff et al. 1990a CA).

Isoperla marmorata. The drumming behavior of this species from two California Sierra Nevada locations (Big Chico Creek, 2008, Butte County and North Fork Cosumnes River, 2009, El Dorado County) is reported for the first time.

Big Chico Creek. Twenty-two male calls and one male response signal were recorded from two, 3d males at 21.7°C. Females from NF Cosumnes River were present in recording chambers when males were recorded but did not answer calls. The males called with grouped signals containing 1–9 monophasic beats/group (7.5±1.2), 7–15 groups/signal (11.8±1.8), and a total of 61–102 beats/signal (Fig. 15, Table 2). Intra-group and inter-group intervals were 20.3±2.4 ms and 347.9±77.9 ms, respectively. The one varied beat-interval response



Figures 14–18. Stonefly drumming signals. 14. *Isoperla laucki* monophasic call. 15. *I. marmorata* grouped call and varied beat-interval response, BCC. 16. *I. marmorata* grouped call, NFCR. 17. *I. miwok* trigrouped call, CC. 18. *I. miwok* varied beat-interval female answers to recorded call playback, TNFCR. ♂C = Call, ♀ = Answer, and ♂R = Response.

signal was long and had 70 beats with intervals of 172.6±29.7 ms (Fig. 15). The group and call durations were (16.0–200.7), 133.1±27.8 ms and (3714.7–7628.2), 5297.5±1028.6 ms, respectively. Males generally do not produce response signals without the female answer signal. This observation may be an aberrant signal and will require further recordings of both males and females to confirm the suspected 3-way exchange type.

The intra-group interval pattern was approximately even (Fig. 12) with an interval difference of 4.1 ms and the inter-group interval pattern was erratic (Fig. 13). The intra-group intervals increased from a minimum of 19.4 ms (i1) to a maximum of 23.5 ms (i8). The inter-group intervals increased and decreased four times throughout the grouped signal ranging from a maximum of 375.5 ms (i2) to a minimum of 321.4 ms (i14).

North Fork Cosumnes River. Ten signals were recorded from three, 4–10d males at 21.1–21.7°C. The males called with grouped signals containing 1–8 monophasic beats/group (5.7±1.7), 4–13 groups/signal (8.8±2.5), and a total of 21–70 beats/signal (Fig.16, Table 2). Intra-group and inter-group intervals were 21.9±3.5 ms and 383.06±116.3 ms, respectively. The males did not produce response signals and females who were present in recoding chambers did not answer male calls. The group and call durations were (15.8–152.7), 104.9±32.6 ms and (1971.4–5929.5), 3904.7±1280.73 ms, respectively.

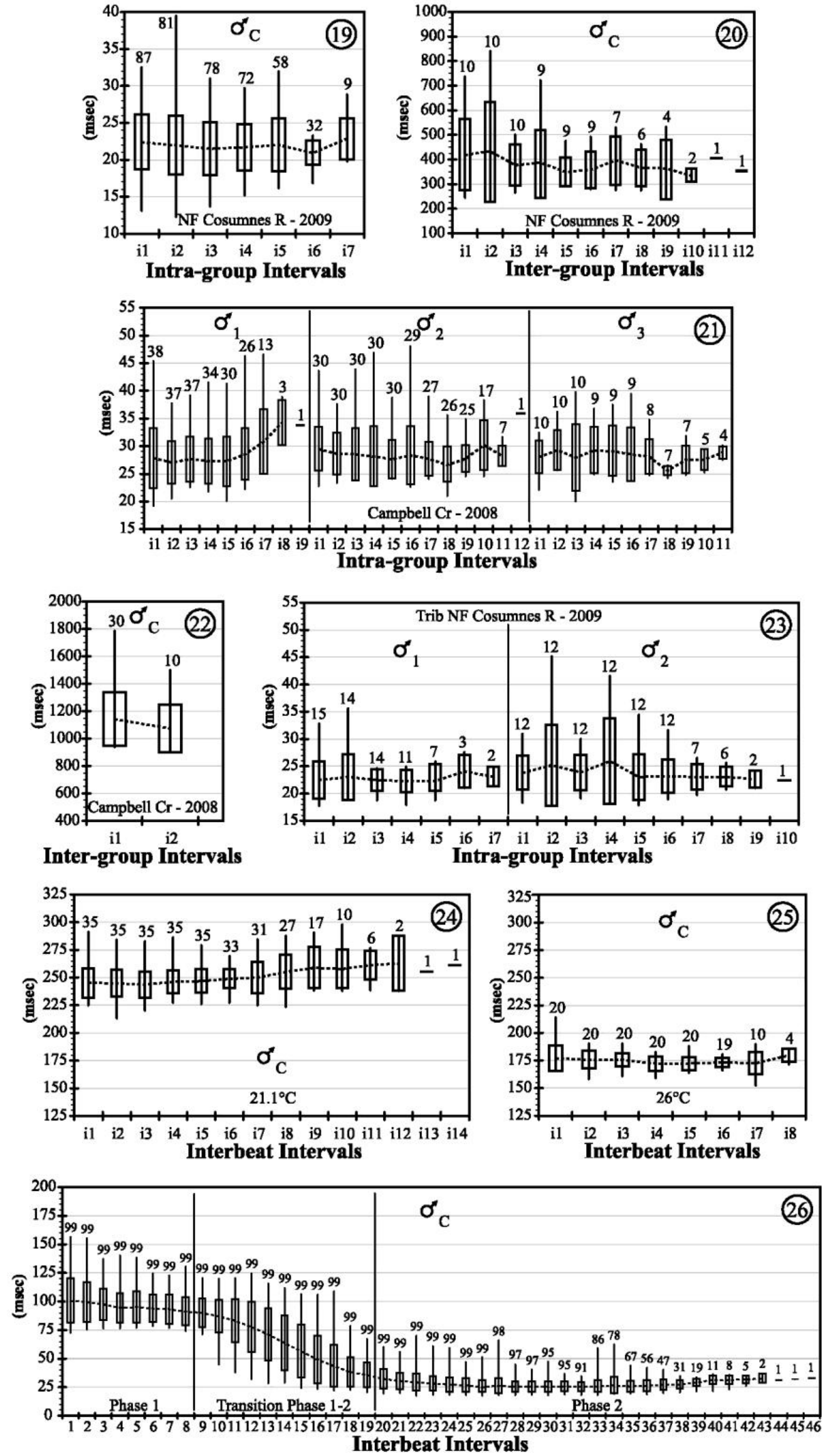
The intra-group interval pattern was approximately even (Fig. 19) with an interval difference of 1.9 ms and the inter-group interval pattern was erratic (Fig. 20). The intra-group intervals decreased from 22.4 ms (i1) to 21.5 ms (i3), increased to 22.0 ms (i5), then decreased to the low of 21.0 ms (i6), and finally increased to a maximum of 22.8 ms (i7). The inter-group intervals fluctuated several times ranging from a maximum of 429.7 ms (i2) to a minimum of 336.7 ms (i10). The overall change in intra-group and inter-group patterns were small and other than the lack of an increasing intra-group interval trend, compared well with the Big Chico Creek patterns. The increased range in age of the North Fork Cosumnes River individuals may account for their slightly less groups/signal, beats/group, and slightly longer intra-group and inter-group intervals.

This is the first drumming descriptions for this species and increases the number of species known to drum within the *I. marmorata* complex to three (Table 1). Other *Isoperla* species with similar average number of beats/signal include *I. fulva* from Oregon-(Table 3), *I. holochlora* (Klapálek)-7.0 (Stewart et al. 1988 VA), *I. miwok*-(Table 2), *I. montana*-6.8 (Stewart et al. 1988 WV), and *I. roguensis* from Butte Creek-(Table 2). The average interbeat interval was most similar to *I. laucki* and *I. miwok* (Table 2), however *I. laucki* had more beats/signal and *I. miwok* calls were limited to a maximum of three groups.

Isoperla miwok. Bottorff et al (1990a) provided the first drumming description of *I. miwok* from an El Dorado County stream. In this study, the drumming behavior of two California Sierra Nevada foothill locations (Campbell Creek, Butte County and an unnamed Tributary of North Fork Cosumnes River, El Dorado County) are described (Table 1).

Campbell Creek. Thirty-eight signals were recorded from four, 1–7d males at 21.1–21.7°C. The males called with 1–3 grouped signals (2.0±0.7), eight calls contained one group, 20 contained two groups, and 10 with three groups (Fig. 17, Table 2). The number of second call groups reported in Table 2 accounts for all calls with two and three groups (30 calls total). The first call group (♂1) had 2–10 monophasic beats/group (6.8±1.6) with intra-group intervals of 27.9±4.7 ms, and for 30 signals that included at least a second call group (♂2), an inter-call-group (♂1-♂2) exchange interval of 1143.4±197.4 ms. The second call group had 6–13 monophasic beats/group (10.4±1.6) with intra-group intervals of 28.3±4.1 ms, and for 10 signals with a third call group (♂3), a ♂2-♂3 exchange interval of 1073.1±174.1 ms. The third call group had 4–12 monophasic beats/group (9.8±2.7) with intra-group intervals of 28.2±3.8 ms. Call durations and total beats/signal were (112.8–3190.3), 1621.2±935.5 ms and (5–32), 17.5±7.5 beats, respectively, and varied by the number of groups produced.

The intra-group interval patterns of this trigrouped call differed slightly (Fig. 21). The first call group (♂1) intra-group interval pattern increased slightly (Fig. 21 left) with an interval difference of 7.2 ms. Intra-group (♂2) intervals decreased and



Figures 19–26. Stonefly signal interbeat, intra- and inter-group interval patterns. 19–20. *Isoperla marmorata* monophasic intra-group and varied inter-group patterns. 21–22. *I. miwok* monophasic intra-group and varied inter-group patterns, CC. 23. *I. miwok* monophasic intra-group interval patterns, TNFCR. 24–25. *I. mormona* varied beat-interval pattern, 21.2°C and monophasic pattern, 26°C. 26. *I. pinta* diphasic pattern with transition intervals (vertical lines). Mean=dashed line; Standard deviation=box; Range=vertical line; Number of intervals above range.

increased slightly (Fig. 21 center) with an interval difference of 3.4 ms. Intra-group (♂3) intervals fluctuated slightly (Fig. 21 right) with an interval difference of 3.7 ms. It would be difficult to determine if the three call group patterns differed from each other, however, neither had interval differences greater than 10 ms and were considered monophasic. The inter-group interval pattern decreased from 1143.4 ms to 1073.1 ms (Fig. 22).

Tributary of North Fork Cosumnes River. Fifteen calls from one male and six answers from two females were recorded at 20.5–21.5°C (ages ranged 2–5d). The males called with grouped signals and females with varied beat-interval answers. The females, although in the recording chamber with calling males, only answered the playback of previously recorded calls and answered either once (n=4) or twice (n=1) (Fig. 18). The male called with 1–2 grouped signals (1.8±0.4), three calls contained only one group, and 12 contained two groups. The number of first call groups reported in Table 2 accounts for all calls with at least one group (15 total). The first call group (♂1) had 2–8 monophasic beats/group (5.4±1.6) with intra-group intervals of 22.7±2.9 ms, and the ♂1-♂2 inter-call-group exchange interval was 1049.7±263.0 ms. The second call group (♂2) had 7–11 monophasic beats/group (8.3±1.4) with intra-group intervals of 23.9±4.7 ms. Call durations and total beats/signal were (70.2–1836.3), 1079.9±539.1 ms and (4–17), 12.1±3.6 beats, respectively. Female answer signals had 13–16 beats (14.3±1.5) with intervals of 54.0±12.6 ms and durations of (599.1–817.4), 719.4±87.0 ms.

The intra-group interval patterns of bigrouped calls were approximately even (Fig. 23). The first call group (♂1) intra-group interval pattern fluctuated slightly (Fig. 23 left) with an interval difference of 1.8 ms. Intra-group (♂2) intervals also fluctuated slightly (Fig. 23 right) with an interval difference of 3.3 ms. The answer interval pattern decreased, and then increased irregularly with an interval difference of 30.8 ms (not charted). The answer intervals decreased from 48.1 ms (i1) to a minimum of 44.7 ms (i2), then increased irregularly to 75.5 ms (i15). The grouped call interval patterns for the TNFCR male (Fig. 23) were slightly lower than those from Campbell Creek (Fig. 21) and suspected to be the result of natural variation caused by differences in age or temperature.

Bottorff et al. (1990a) described the male call as a rapid succession of two or three identical monophasic calls with 2-way to 6-way ♂c-♀ exchanges. This is the definition of a grouped signal type and the call and answer descriptions are updated here (Table 1). Normally for grouped signal analysis, the individual groups of a call are analyzed as a combined, single group and the intra-group and inter-group measurements are stacked one above each other in spreadsheet cells for the calculation of descriptive statistics. In this and the previous study, individual call groups were analyzed separately in order to make individual call group comparisons. The ranges in data reported here for two additional locations compared well to those of Bottorff et al. (1990a) (Tables 2 and 3).

Isoperla mormona. Szczytko & Stewart (1979b) and Sandberg & Stewart (2006) previously described the drumming behavior of this species from Utah and Colorado, respectively. In this study, individuals from the California Sierra Nevada foothills (El Dorado County) were recorded at two different ambient temperatures, and had overlapping but slightly different ranges in age at the time of recording.

Greenwood Creek, 21.2°C. Thirty-five signals were recorded from two, 3–8d males at 21.2°C. The males called with varied beat-interval patterns of 6–15 beats (9.6±1.9) with intervals of 248.7±13.5 ms (Fig. 27, Table 2). Call durations were (1233.1–3416.6), 2153.4±476.0 ms. The mean interval call pattern irregularly increased (Fig. 24) with an interval difference of 19.0 ms. The pattern decreased from 245.1 ms (i1) to a minimum of 243.6 ms (i3), then increased irregularly to 262.7 ms (i12). The final two intervals (i13–i14) first decreased to 255.5 ms, and then increased to 260.9 ms (n=1 for each).

Greenwood Creek, 26.0°C. Twenty signals were recorded from one, 4d male at 26.0°C. The male called with monophasic patterns (or signals) of 6–9 beats (7.6±0.9) with intervals of 174.4±7.7 ms (Table 2). Call durations were (888.2–1463.1), 1160.1±157.3 ms. The mean interval call pattern at this temperature also irregularly increased (Fig. 25) with an interval difference of 7.8 ms. The pattern decreased from 177.1 ms (i1) to a minima of 172.2 (i4 and i5), then increased irregularly to 179.9 ms (i8). The shorter interbeat intervals and decreased beats of this individual were slightly different from the Greenwood Creek individuals at a slightly higher temperature.

It is unknown whether age, temperature, or other physiological or environmental variables caused the observed change in mean interval and beats. The observations here were coincidental and were not conducted using an experimental design to test for the effects of suspected variables. The different average intervals reported here could not be attributed to the effect of temperature alone because age was not kept constant between individuals. The effects of increased age and decreased temperature were suspected, but not confirmed in previous studies to decrease drumming tendency (signals/hour) and to increase beat interval, respectively (Zeigler & Stewart 1985, Sandberg & Stewart 2005).

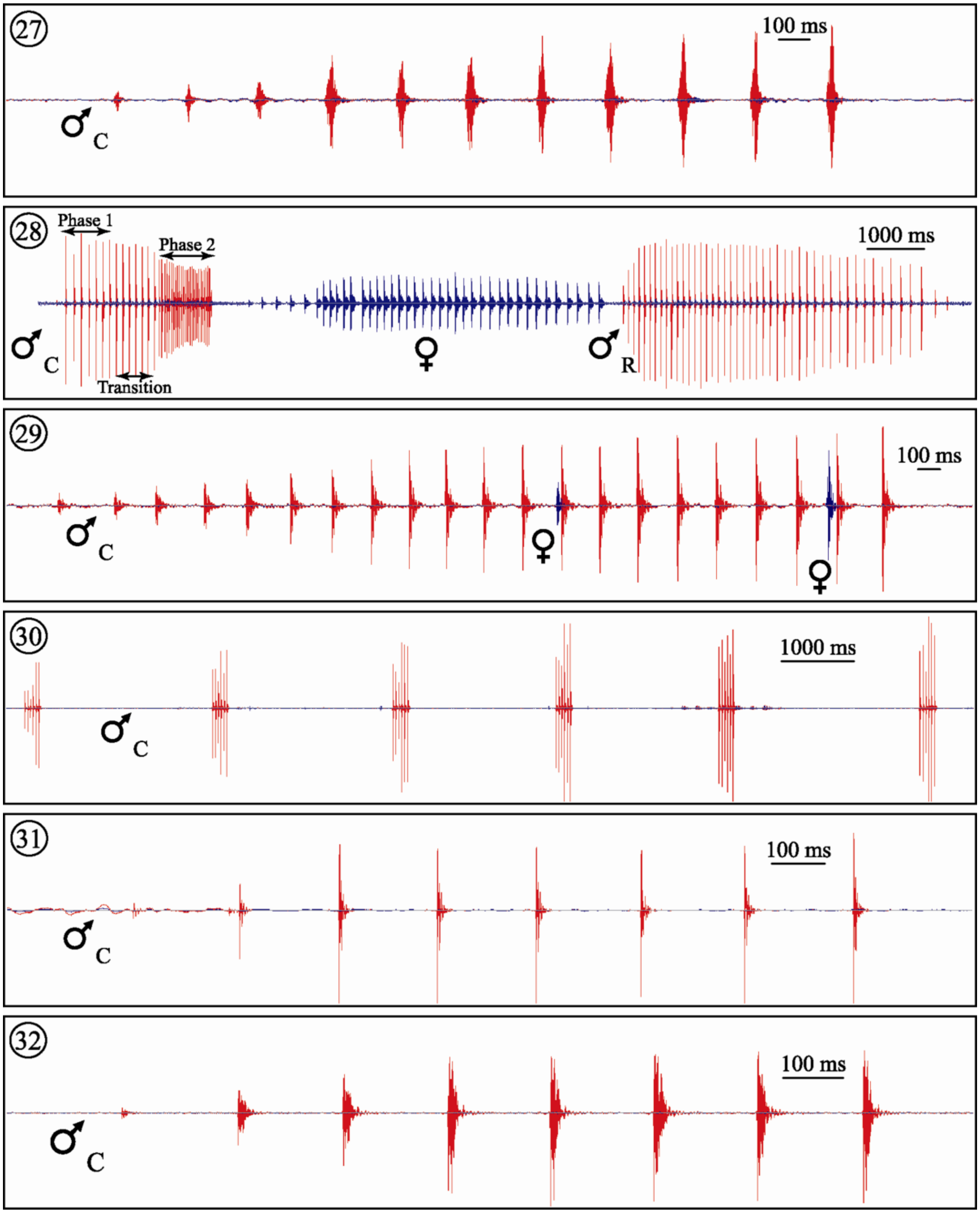
Sandberg and Stewart (2003) described *I. mormona* monophasic drumming signals from a Colorado location (Tables 1 and 3). Their signal description for males of similar range in age (8–12d) and similar temperature (21.0°C) compared favorably with this study's 3–8d Greenwood Creek males at 21.2°C.

Isoperla pinta. Ninety-nine calls from seven males, 45 answers from three females, and five response signals from one male were recorded at 16.6–22.2°C (ages ranged 1–10d). Males called with diphasic signals and female answers and the male responses were varied beat-interval signals. Only one 3-way exchange was recorded with both drummers inside the recording chamber (Fig. 28). The remaining answers (2-way exchanges) and response signals, followed respective calls or answers originating from outside the recording chamber. During the recording sessions, males and females held in Styrofoam cups were placed near the recording chamber to stimulate signaling.

Diphasic calls were a continuous series of beats (only slightly different from the closely related varied beat-interval pattern) composed of monophasic, varied beat-interval, and monophasic interval patterns (Fig. 28). Males called with 27–47 beats/diphasic signal (37.0±3.3) with overall 53.5±32.2 ms diphasic signal intervals (Fig. 28, Table 2). After grouping the raw data into their respective pattern types determined by the mean interval pattern chart (Fig. 26), the mean phase-1 intervals were (72.6–156.4), 95.8±14.8 ms, transition phase intervals were (23.5–124.6), 63.3±26.7 ms, and phase-2 intervals were (17.5–70.2), 27.2±6.1 ms. Diphasic signal durations were (1442.9–2880.6), 1924.5±333.5 ms. The ♂C-♀ exchange interval was 902.5±430.7 ms (n=34). The female answer had 29–62 beats (38.8±8.4) with intervals of 92.4±23.2 ms. Answer durations were (2568.4–6158.7), 3489.5±686.7 ms. The ♀-♂R exchange interval for one 3-way exchange was 436.5 ms. Male responses had 32–50 beats (44.0±7.2) with intervals of 124.0±31.4 ms. The response durations were (3018.4–6512.6), 5334.0±1349.3 ms.

The initial phase-1 beats had longer intervals followed by shorter phase-2 intervals and the decreasing transition intervals between phases were detectable only by examining the interval pattern chart (Fig. 26). Phase-1 intervals (i1-i8) were approximately even and had an interval difference of 9.4 ms. The intervals decreased from 100.8 ms (i1) to 91.4 ms (i8). The transition intervals (i9-19) decreased in a sigmoid-like curve with an interval difference of 54.5 ms. These intervals decreased from 90.0 ms (i9) to 35.6 ms (i19). The phase-2 intervals (i20-i46) were approximately even again and had an interval difference of 7.3 ms. The phase-2 intervals decreased from 32.2 ms (i20) to 26.0 ms (i26), then decreased irregularly to a minimum of 25.4 ms (i32), and finally increased irregularly to a maximum of 32.8 ms (i43). The long answer and response mean interval patterns (not charted) irregularly increased with interval differences of 104.5 and 55.0 ms, respectively. The answer pattern decreased irregularly from 84.3 ms (i1) to 74.0 ms (i6), then increased irregularly to 128.9 ms (i55), and finally holding approximately even for the last intervals (i56-i57). The response pattern decreased from 97.8 ms (i1) to 90.1 ms (i3), and the increased irregularly to 194.6 ms (i48).

This is the first drumming description for this species and increases the number of species known to drum in the *I. phalerata* complex to three (Table 1). *Isoperla slossonae* (Banks), an eastern Nearctic species included in this complex, also produces diphasic male calls (Graham 1982). The diphasic drumming of *I. pinta* was very similar to *I. phalerata* (Smith) from Colorado (Sandberg & Stewart 2006) (Tables 1–3).



Figures 27–32. Stonefly drumming signals. 27. *Isoperla mormona* varied beat-interval call, 21.2°C. 28. *I. pinta* diphasic call and varied beat-interval answer and response. 29. *I. quinquepunctata* varied beat-interval call and interspersed answer. 30. *I. roguensis* grouped call, BC. 31. *I. sobria* varied beat-interval call, BCCH. 32. *I. sordida* varied beat-interval call, FR. ♂C = Call, ♀ = Answer, and ♂R = Response.

The two species overlap in call beats/signal, answer beats/signal and mean intervals but only *I. pinta* had one 3-way exchange. Sandberg & Stewart (2006) reported separate beats/signal and mean intervals for phases 1 and 2 by dividing and aligning the raw call interval data into two groups: phase-1 intervals greater than 60 ms and phase-2 intervals less than 60 ms.

In this study of *I. pinta*, the interval data were not divided and sorted into groups, leaving individual intervals in their original consecutive arrangement (Fig. 26). The total beats/signal and mean interval were determined from the entire diphasic signal intervals 1–46 (Table 2). The phase-1, transition and phase-2 mean interval pattern intervals were determined by the interval pattern chart of intervals 1–46 (Fig. 26) and then selecting only monophasic intervals 1–8 (phase-1), varied beat-intervals 9–19 (transition) and monophasic intervals 20–46 (phase-2) to calculate those summary statistics in Table 2.

For comparison, the *I. pinta* raw interval data were divided and aligned using the Sandberg & Stewart (2006) method except phase-1 intervals were greater than 70 ms, phase-2 intervals were less than 70 ms and no decreasing interval transition was described. The phase-1 and phase-2 interval patterns were graphed (Fig. 33) and the two phases would be similarly described as varied beat-interval signals with mean interval differences greater than 10 ms. This analysis supports an alternate definition for diphasic signal types which are signals having two phases, each with several beats and different interbeat intervals and rhythms (Sandberg & Stewart 2006). The phases in Figure 33 have varying numbers of beats and intervals but have similar decreasing varied-beat interval patterns. By leaving raw interval data undivided and examining the entire signal mean interval pattern, three consecutive patterns are revealed and composed of monophasic, varied beat-interval and monophasic intervals (Fig.26).

Each method for analyzing diphasic signals has problems. The raw data sorting and re-aligning method of Sandberg and Stewart (2006) selectively reduces observed variation of the individual interbeat intervals. If each of the 99 *I. pinta* signals from this study were examined individually, the phase-1 (i1-i8) individual interval differences range from 4.7–54.2 ms and those calls with phase-1 differences greater than 10 ms would not be considered monophasic. Alternatively, by using the mean intervals to determine the interval pattern, individual signal variation is reduced, resulting in a range of mean interval differences that fit the proposed monophasic definition with an interval difference of 10 ms or less. More observations from additional species with diphasic call patterns will be required before the best method and diphasic definition characters can be determined.

Isoperla quinquepunctata. Szczytko & Stewart (1979) and Sandberg & Stewart (2006) previously described the drumming behavior of this species from a three state combination of Colorado - New Mexico - Utah and Colorado, respectively. In this study, twenty-five calls from six males and one answer from one female were recorded at 21.1–22.8°C (ages ranged 2–7d). The males called with varied beat-interval signals, and the female interspersed answer beats within the male call (Fig. 29). Female answers were interspersed within the 12th (i12) and 19th (i19) call intervals. The males called with signals of 11–37 beats (23.0±7.0) and intervals of 191.2±21.9 ms (Table 2). Call durations were (1921.9–7421.1), 4205.6±1523.4 ms. The female 2-beat interspersed answer (n=1) had a 1300.2 ms interbeat interval and followed the male's 12th call beat by 164.9 ms and the 19th beat by 149.6 ms (Table 2). The mean interval call pattern fluctuated irregularly and increased (Fig. 34) with an interval difference of 55.9 ms. The pattern decreased irregularly from 195.1 ms (i1) to a low of 182.9 (i5), then increased irregularly to a maximum of 238.8 ms (i34), and finally decreased to 220.7 ms (i35).

The drumming characters reported in this study appear slightly different from a 1d Colorado male (Sandberg & Stewart 2006) (Tables 2 and 3) and the differences are suspected to be the result of natural variation. The maximum number of call beats/signal and average interbeat interval were higher for the California males, however ranges and standard deviation overlapped between both studies. In general, the Colorado male call pattern first decreased and then increased, but with less irregularity and of slightly shorter average intervals (not charted). The 1d Colorado male was younger than the six males reported in this study which could explain the shorter Colorado male average intervals, but possibly not the decreased beats/signal. Based upon only the number of call beats/signal, it is possible the California individuals represents a drumming dialect for this species, but more recordings of additional males (keeping environmental and physiological variables constant) between the two locations would be needed to test for significant differences.

Isoperla roguensis. Sandberg & Stewart (2006) first reported the drumming behavior of this species from Oregon. In this study, individuals from two additional locations were recorded from Butte Creek, Butte County, CA and from the type location, Rogue River, Curry County, OR (Table 1).

Butte Creek. Thirty-six signals were recorded from six, 3–8d males at 19.4–20.0°C. The males called with grouped signals of 1–6 groups/signal (1.9±1.2), 3–9 monophasic beats/group (6.0±1.2), and a total of 3–36 beats/call (Fig. 30, Table 2). Intra-group and inter-group intervals were 38.1±3.2 ms and 2284.0±405.7 ms, respectively. Group and call durations were (76.6–298.5), 188.9±46.4 ms and (76.6–12409.4), 2455.8±2991.5 ms, respectively. The intra-group interval call pattern was an increasing-decreasing curve (Fig. 35) with an interval difference of 4.6 ms. The pattern increased irregularly from 37.4 ms (i1) to 39.3 ms (i4) and then decreased to the last interval 34.7 ms (i8). The inter-group interval pattern increased and decreased (Fig. 36) with an interval difference of 607.4 ms. Intervals increased from 2274.8 ms (i1) to a maximum of 2487.9 ms (i2), and then decreased to a minimum of 1880.5 ms (i4).

Rogue River. Five signals were recorded from one male at 20.5–21.1°C. The male called with grouped signals of 1–4 groups/signal (2.4±1.1), 3–6 monophasic beats/group (4.8±0.7), and a total of 5–19 beats/call (11.6±5.1) (Table 2). Intra-group and inter-group intervals were 34.7±3.9 ms and 2512.4±959.6 ms, respectively. Group and call durations were (66.1–165.1), 133.2±25.7 ms and (120.4–9075.4), 3837.1±3276.5 ms, respectively. The intra-group interval call pattern was an increasing-decreasing curve (Fig. 37) with an interval difference of 2.7 ms. The pattern increased from 34.2 ms (i1) to 36.9 ms (i3), and then decreased to 33.6 ms (i4). Interval 5 was 32.6 ms (n=1). The inter-group interval pattern decreased (Fig. 38) from 2564.6 ms (i1) to 1805.9 ms (i2) with an interval difference of 758.8 ms.

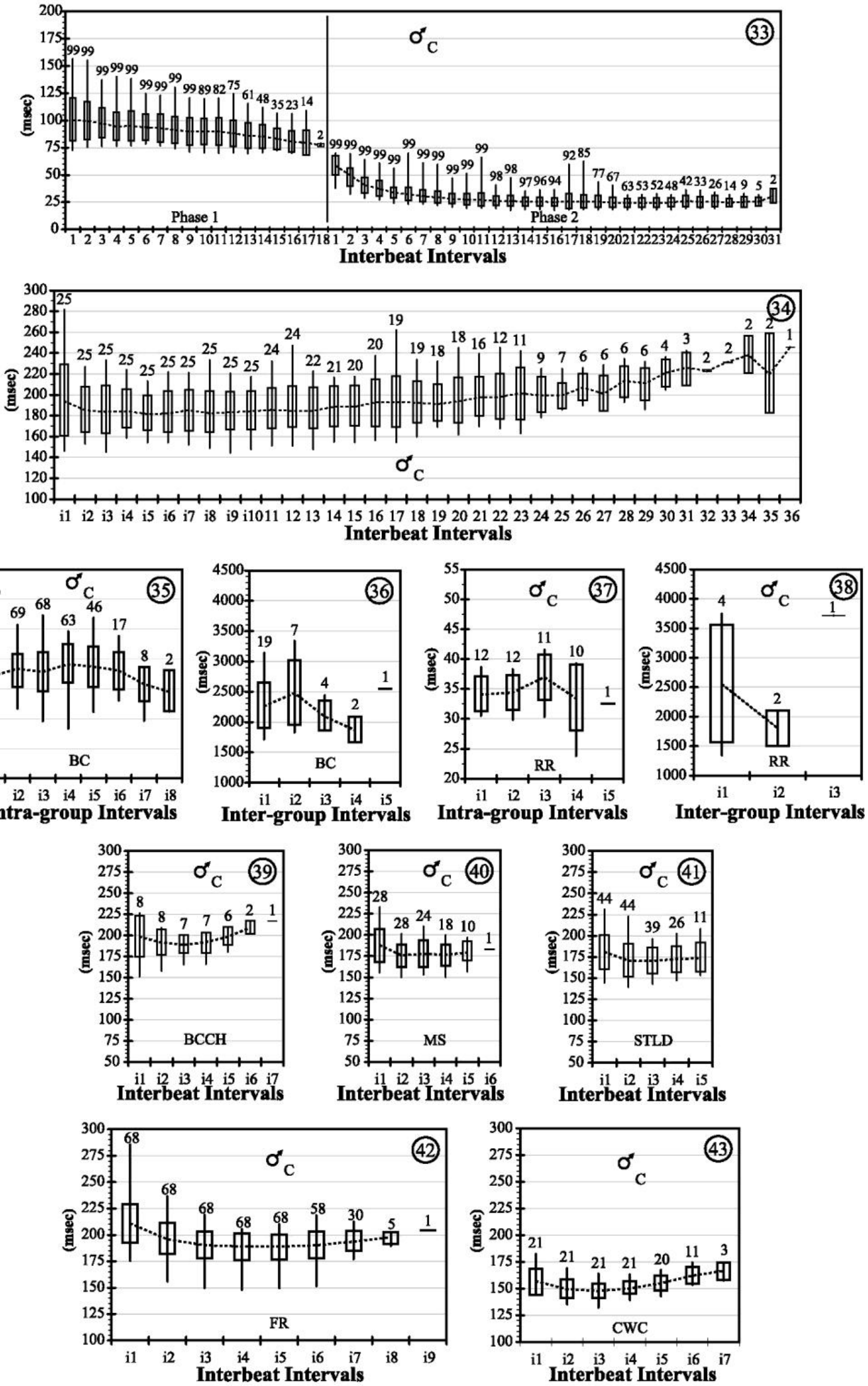
The first description for this species from Fall River, OR (Sandberg & Stewart 2006) was based upon a 1d male and female at an un-recorded room temperature (Table 3). The range of beats/call and average interbeat intervals overlapped with slight differences (Tables 2 and 3), however, the male calls were grouped for the two locations reported in this study (Table 1). Upon re-examination of the Sandberg & Stewart (2006) description data, 16 of 128 recordings should have been described as grouped with 2–3 groups/signal and inter-group intervals within the range of the two locations reported here.

The factors that led the previous authors to describe their Fall River exchanges as monophasic signals were: 1) the very long intervals between grouped signals (inter-group intervals), 2) the female had overlapped answers (27 out of 105, 2-way exchanges), and 3) the short 27.9 ms ♂c-♀ sequenced exchange intervals were typical of monophasic 2-way and 3-way exchanges. A similar description update from monophasic to grouped calls is suggested for *I. miwok* in this study, with long inter-group intervals and from 2-way to 6-way exchanges (Fig. 17, Tables 2 and 3).

The drumming signals of three species in the *Isoperla marmorata* complex have now been described, however *I. fulva* Claassen was not collected in California for this project (Tables 1 and 3). The calls of *I. marmorata* and *I. roguensis* are grouped signals and *I. fulva* from Colorado had monophasic calls (Sandberg & Stewart 2003). *Isoperla fulva* from Oregon should be re-examined to verify that it may sometimes produce grouped calls with an answering female.

Isoperla sobria. Sandberg & Stewart (2003, 2006) previously described the drumming behavior of this species from New Mexico and Oregon, respectively. In this study, individuals from three California Sierra Nevada locations were recorded including, Butte Creek at Cherry Hill Campground, Butte Co., Mosquito Spring creek and a Spring Tributary of Lake Davis, Plumas County.

Butte Creek at Cherry Hill Camp Ground. Eight signals were recorded from one, 5–8d male at 21.1–21.7°C. The male called with varied beat-interval patterns of 3–8 beats (5.9±1.5) with intervals of 195.6±15.8 ms (Fig. 31, Table 2). Call durations were



Figures 33–42. Stonefly signal interbeat, intra- and inter-group interval patterns. 33. *Isoperla pinta* diphasic pattern, phase-1>70 msec, phase-2<70 msec. 34. *I. quinquepunctata* varied beat-interval pattern. 35–38. *I. roguensis* monophasic intra-group and varied inter-group interval patterns. 39–41. *I. sobria* varied beat-interval (39–40) and monophasic (41) patterns. 42–43. *I. sordida* varied beat-interval patterns. Mean = dashed line; Standard deviation = box; Range = vertical line; Number of intervals = number above range.

(360.4–1419.3), 953.5±311.3 ms. The mean interval call pattern was a slight decreasing-increasing curve (Fig. 39) with an interval difference of 19.8 ms. Intervals decreased from 199.3 ms (i1) to 189.7 ms (i3), and then increased to 209.46 ms (i6). The last interval (i7) increased to 216.7 ms (n=1).

Mosquito Spring creek. Twenty-eight signals were recorded from four, 1–5d males at 20.0–23.8°C. The males called with varied beat-interval signals of 3–7 beats (4.9±1.1) with intervals of 179.7±15.8 ms (Table 2). Call durations were (352.2–1120.5), 699.4±202.7 ms. The mean interval call pattern decreased, and then increased slightly (Fig. 40) with an interval difference of 12.1 ms. The pattern decreased from a maximum of 187.5 ms (i1) to a minimum of 175.4 ms (i2), and then irregularly increased to 180.9 ms (i5).

Spring Tributary of Lake Davis. Forty-four signals were recorded from one, 4–6d male at 21.1–26.7°C. The male called with monophasic signals of 6–8 beats (7.4±0.9) with intervals of 194.4±15.6 ms (Table 2). Call durations were (283.3–1021.4), 662.1±218.6 ms. The mean interval pattern decreased and increased slightly (Fig. 41) with an interval difference of 9.8 ms. Intervals decreased from a maximum of 180.5 ms (i1) to a minimum of 170.7 ms (i3), and then increased slightly to 174.9 ms (i5).

These additional observations overlap in beat counts with those of two previous studies (Sandberg & Stewart 2003, 2006). However, the California individuals of this study had longer average interbeat intervals (Tables 2 and 3) despite being somewhat younger with smaller ranges in age. The interbeat interval patterns from this study (Figs. 39–41) varied in description and detail, however, with only slight differences and the signal description is updated to both monophasic and varied beat-interval (Table 1).

Isoperla sordida. This is the first drumming description for this species and increases the number of species known to drum in the *I. sordida* complex to six, including *I. denningi* (Table 1). In this study, signals from two locations are described from Fall River, OR and Cold Water Creek, CA. The Oregon location was approximately 1 km downstream from a high-volume spring and 1300 m above sea level. The California location was a small snowmelt fed stream at over 2700 m above sea level.

Fall River. Sixty-eight signals were recorded from one, 4–6d male at 21.1–26.7°C. Males called with varied beat-interval patterns of 6–8 beats (7.4±0.9) with 194.4±15.6 ms intervals (Fig. 32, Table 2). Call durations were (936.9–1871.2), 1240.6±192.5 ms. The mean interval pattern decreased and increased in a gentle arc (Fig. 42) with an interval difference of 22.3 ms. The pattern decreased from 210.8 ms (i1) to 188.5 ms (i5), and then increased to 197.1 ms (i8). The last interval (i9) increased to 204.5 ms (n=1).

Cold Water Creek. Twenty-one signals were recorded from one, 2–3 d male at 22.2–24.4°C. Males called with varied beat-interval signals of 5–8 beats (6.6±0.8) with 153.3±9.4 ms intervals (Table 2). Call durations were (609.0–1114.3), 851.6±148.4 ms. The mean interbeat interval pattern decreased and increased in a broad arc first (Fig. 43) with an interval difference of 18.1 ms. Intervals decreased from 156.3 ms (i1) to a minimum of 148.0 (i3), then increased to a maximum of 166.1 ms (i7) (Fig. 42). The individuals from these two locations had similar beats/signal and interval pattern curves, but the mean interbeat interval was faster for the Cold Water Creek individuals and is possibly due to their younger age.

The *I. sordida* average beats/signal is most similar to four previously reported species: CO-*I. fulva* with 7.8±0.9 beats (Sandberg & Stewart 2003), VA-*I. holochlora* with 7.0 mean beats (Stewart et al. 1988), CA-*I. miwok* 3rd group with 7.0 mean beats (Bottorff et al. 1990a), and Arkansas-*I. morhi* with 7.3±4.4 beats (Stewart et al. 1988), but differed from these in average interbeat intervals. The interbeat interval was most similar to these previously reported species: TX-*I. sagittata* Szczytko & Stewart with 181.4±10.1 ms (Stewart et al. 1988), and WI-*I. transmarina* with 200.2±59.3 ms (Graham 1982), but differed in average beats/signal. In this study, *I. sordida* average beats/signal was most similar to Greenwood Creek-*I. mormona* and average interbeat interval was most similar to Butte Creek-*I. sobria*.

DISCUSSION

The use of interval pattern charts has improved the accuracy of stonefly drumming descriptions. Previous drumming descriptions either omitted these details or only partially described the interval pattern in written descriptions or tables (Sandberg & Stewart 2006). Tierno De Figueroa et al. (2000) described the drumming behavior of *Isoperla curtata* Navás from Italy, and first used a box and whisker chart to describe its varied beat-interval pattern over intervals i1–i27. The interval pattern is a "vibrational fingerprint" revealing individual intervals that change over successive beats and describes the variation within each individual interval and the entire signal. Future research will be more accurate using the additional interval details provided for the various drumming signal types in this study. The monophasic signal type was defined as signals with approximately even intervals (Stewart & Sandberg 2006). This definition is too broad and provided no limit for the term "approximately" to consistently differentiate monophasic from the slightly more complex varied beat-interval signal. In this study, monophasic patterns were determined by subtracting the minimum from the maximum mean interval, providing a mean interval difference. Monophasic signals are proposed in this study to have a mean interval difference of 10 ms or less, and varied beat-interval signals with interval differences greater than 10 ms. The diphasic call signal described in this study contained three consecutive signal types composed of monophasic, decreasing varied-beat interval, and monophasic intervals. The diphasic pattern definition will require additional interval details to make it distinctive from highly variable varied beat-interval patterns in future studies.

In this study, a male and female of each species and from the same location was usually present in the recording chamber except for *I. marmorata* from Big Chico Creek, *I. sobria* from Butte Creek, and *I. sordida* from Cold Water Creek. For these exceptions, signals were recorded with adults from different locations or without a female. In total, eight *Isoperla* species from this study lack female answers and these should be considered provisional data. Analyses of drumming duets are essential because the female presumably chooses which male calls to answer as her means of determining fitness, selecting only those calls that fall within a range of variation which is distinctive to her species (Zeigler & Stewart 1985).

The general drumming characters in Table 1 are listed using species complexes based upon adult male and ovum morphological characters (Szczytko & Stewart 1979a). The complexes are arranged from least specialized (*I. quinquepunctata* complex) to most specialized (*I. sordida* complex) (Table 1). Drumming signal types also range in complexity from least specialized to most and include, monophasic, varied beat-interval, diphasic and grouped signal patterns (Stewart 2000, Stewart & Sandberg 2006). The majority of *Isoperla* drumming signals have been described as monophasic and the majority of male calls for western Nearctic species are also monophasic (Table 1). Three of the five *I. quinquepunctata* complex species known to drum, produce simple and slightly more complex, monophasic and varied beat-interval signals, respectively. The one exception, *I. acula*, produced signals by tapping and rubbing the abdomen. These somewhat more specialized perlodid rub signals have short durations as compared to the rub signals of the families Perlidae and Peltoperlidae, who usually produce a single, prolonged rub call. Those species with increased drumming complexity (diphasic and grouped signals) are distributed throughout the remaining complexes with no apparent progression (Table 1). Drumming however, may act as an important isolating mechanism along with the proposed aggregation and movement behaviors described by Stewart (1994) and different peak emergence periods. There are three *Isoperla* species from Butte Creek at the Butte Creek Ecological Preserve. In this study, *I. pinta* began emergence in February with diphasic calls, followed by *I. roguensis* with grouped calls, and finally by *I. quinquepunctata* with monophasic and varied beat-interval calls. All three have been collected on the same day in early April and each has a distinct drumming pattern used for mate location.

This report increases the number of described drumming signals for Nearctic *Isoperla* to 41 species, of which 20 have western distributions and 14 are from California (seven endemics). This study provides preliminary detailed drumming characters and signal descriptions in preparation for the next stage in Nearctic stonefly drumming research. Previous studies have focused primarily upon providing baseline descriptive knowledge, however, the next California drumming study should examine the variability of the previous descriptions through carefully controlled experimental research. A common assumption made throughout this and other studies is that increased adult stonefly age influences the number of beats/signal and intervals. The effect of temperature is also thought to influence beat and interval drumming characters. Therefore future drumming studies should be designed to limit or control all environmental and physiological variables (age, temperature, time of day, humidity, etc.) and compare the individual interval results for test groups at different environmental or physiological conditions. Furthermore, once baseline signal variability is described for the effects of environmental and physiological variables upon drumming characters, then additional experiments can be designed to test for differences between populations at different locations. These experiments could be used as evidence for species identification, or delineating new species from within cryptic or sibling species groups (Stewart et al. 1988).

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