John B. Sandberg 2009. Vibrational communication (drumming) of the western nearctic stonefly genus *Hesperoperla* (Plecoptera: Perlidae).
Illiesia, 5(13):146-155. Available online: http://www2.pms-lj.si/illiesia/papers/Illiesia05-13.pdf

VIBRATIONAL COMMUNICATION (DRUMMING) OF THE WESTERN NEARCTIC STONEFLY GENUS *HESPEROPERLA* (PLECOPTERA: PERLIDAE)

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ABSTRACT
The drumming signals of both species of the North American stonefly genus *Hesperoperla* are reported. New signals are described for *H. hoguei* and a new call signal character from two new populations is provided for *H. pacifica*. Male calls ranged in complexity from ancestral-monophasic in *H. hoguei* to calls containing both monophasic and derived-grouped components in *H. pacifica*. Intersexual communication was less specialized in *H. hoguei* with 2-way (male call-female answer) duets, and more specialized in *H. pacifica*, having both 2-way and 3-way (male-call, female-answer, male-response) exchanges.

Keywords: Intersexual communication (drumming), signal description, species dialect

INTRODUCTION
The stonefly mate finding system of suborder Arctoperlaria often includes intersexual vibrational communication. The sequence of communication by searching males and stationary females includes: (a) the male call signal (♂C), (b) followed by an unmated female answer signal (♀) if in range, and (c) the male response signal (♂R) that sometimes follows the female answer in certain species (Figs. 1–4). Intersexual drumming exchanges composed of these signal types are species specific and fixed action behaviors representing some of the most diverse and complex known in insects, and follow the evolutionary paradigm of Stewart (2001) and Stewart and Sandberg (2006).

Drumming behavior in North American Perlidae has been described for 14 genera representing 22 species (Graham 1982; Kondratieff et al. 1988; Maketon & Stewart 1984, 1988; Sandberg & Stewart 2006; Stewart et al. 1982; Zeigler 1989; Zeigler & Stewart 1977). The male calls described in these studies are produced by either an unspecialized terminal ventral abdominal sternum (*Agnetina, Paragnetina, Perlesta*) or a specialized structure of the ninth sternum (or hammer) in the other 11 genera (Stewart and Maketon 1991). The call signals in Perlidae are diverse and produced by three methods: (a) abdominal-substrate tapping that includes monophasic (10 species), diphasic (5 species) and grouped (2 species); (b) abdominal substrate-rubbing only (3 species); and (c) combinations of abdominal tapping and rubbing (2 species) (Table 1).

The drumming behavior of *Hesperoperla pacifica* (Banks) has been reported for two Colorado populations (Zeigler & Stewart 1977). They described the male call as monophasic, but state in their discussion that "signals sounded raspy or scratchy" and that "sub-peaks and blurs appeared on oscilloscope tracings" making measurements and descriptions difficult. This suggested uncertainty of the male *H. pacifica* call and prompted an investigation of the drumming for this species in

accessible populations of northern California.

The objectives of this study were to record and analyze the drumming signals of reared-virgin and field-collected adult *Hesperoperla hoguei* Baumann & Stark and *H. pacifica*. The analysis included characterization of ♂C, ♀, and ♂R signals, intersexual exchanges and graphic descriptions of average call patterns using bar charts. In previous drumming studies, emphasis was placed on overall drumming characters (mean beats/call, average interbeat interval). Interbeat, intergroup and intragroup average interval patterns were undescribed, or only partially described in the text, or described using text and tables (Table 2. in Sandberg and Stewart 2006). By providing descriptions of individual average interbeat, intergroup, and intragroup interval patterns of male calls, it may be possible to differentiate between or among species with similar or overlapping overall average drumming characters.

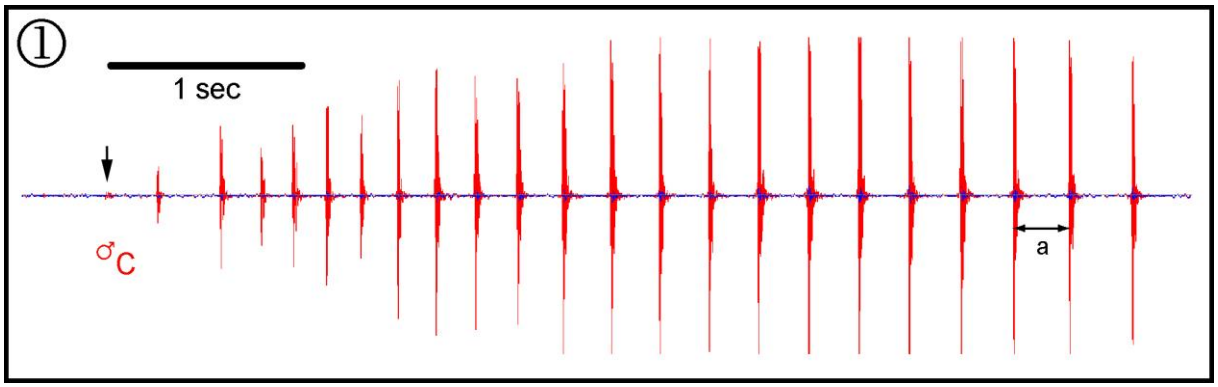

Fig. 1. *Hesperoperla hoguei* 23 beat monophasic male call. Collected from Domingo Spring, Plumas Co., CA, J. Sandberg, October 2006. Arrow = First call beat, a = Interbeat interval 21 (i21) and ♂C = male call.

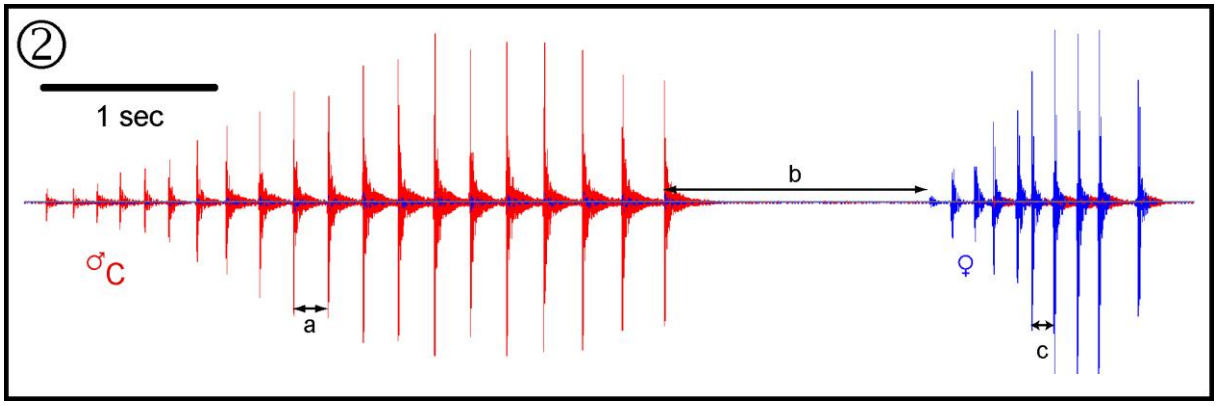

Fig. 2. *Hesperoperla hoguei* 2-way monophasic exchange. Collected from Domingo Spring, Plumas Co., CA, J. Sandberg, September 2007. ♀= female answer, a = ♂ interbeat interval, b = (♂C-♀) exchange interval, c = ♀ interbeat interval.

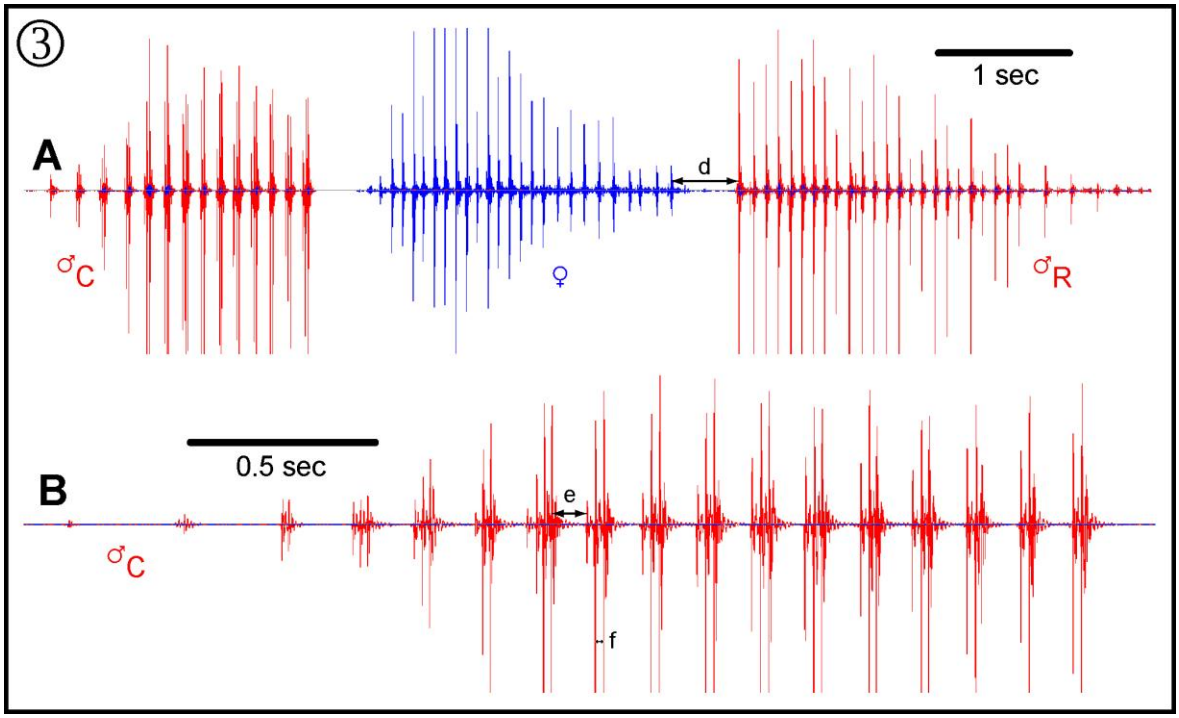

Fig. 3. *Hesperoperla pacifica* drumming. A. 3-way exchange, ♂C monophasic and grouped, ♀ and ♂R monophasic answer and response respectively. B. Male call with 1st monophasic beat followed by 16 grouped signals. Reared from Butte Creek, Butte Co., CA, J. Sandberg, April 2007. d = (♀-♂R) exchange interval, e = inter-group interval, f = intra-group interval.

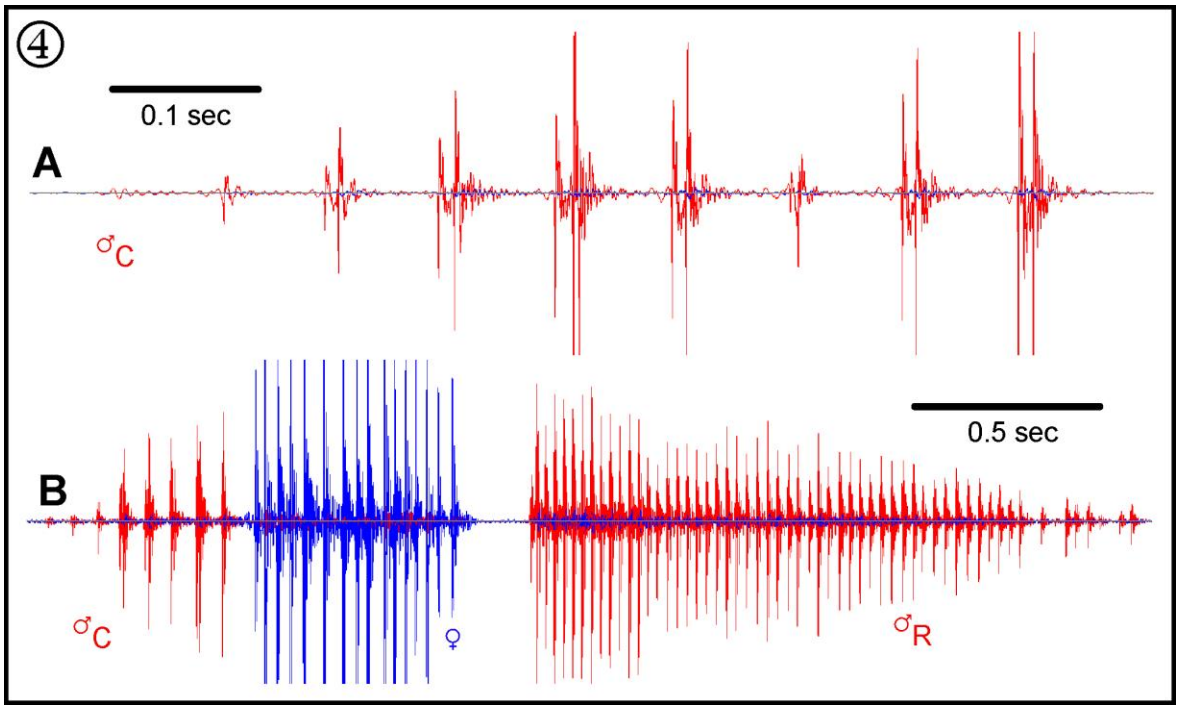

Fig. 4. *Hesperoperla pacifica* drumming. A. Male call with 1st, 2nd and 7th beats monophasic and the others grouped. B. 3-way exchange. Reared from Domingo Spring, Plumas Co., CA, J. Sandberg, June 2007.

MATERIALS AND METHODS

Adults of the two species were obtained in the field by using a beating sheet and aspirator or virgin adults were reared from mature larvae collected as follows (same arrangement in Table 2): (**1**) *Hesperoperla hoguei*, Plumas Co., CA, Domingo Spring, Domingo Springs Campground, 8 mi (12.9 km) NW of Chester on Old Red Bluff Rd., J. Sandberg, 01/X/2006 (Live Adults); (**2**) *H. hoguei*, Plumas Co., CA, Domingo Spring, Domingo Springs Campground, 8 mi (12.9 km) NW of Chester on Old Red Bluff Rd., J. Sandberg, 11/VIII/2007 (Mature Larvae), 28/VIII/2007 (Live Adults), 21/IX/2007 (Live Adults); (**3**) *H. pacifica*, Butte Co., CA, Butte Creek, Butte Creek Ecological Preserve, Honey Run Rd., 2.9 mi (4.7 km) E of Skyway intersection, J. Sandberg, 07/ & 13/IV/2007 (Mature Larvae), 17/V/2007 (Live Female); (**4**) *H. pacifica*, Plumas Co., CA, Domingo Spring, Domingo Springs Campground, 8 mi (12.9 km) NW of Chester on Old Red Bluff Rd., J. Sandberg, 06/V/2007 (Mature Larvae), 19/V/2007 (Live Adults), 09/VI/2007 (Mature Larvae). Additionally, the *H. pacifica* drumming characters of this study are compared to the results of Zeigler and Stewart (1977) for two populations from the Upper Delores and Gunnison Rivers, Colorado, 14–15/VI/1975; their recording temperatures ranged from 24–26°C at 80 foot-candles (*Hesperoperla pacifica*[5] in Table 2).

Three hundred and forty-four *Hesperoperla* drumming signals obtained from 15 males and 7 females were recorded in this study following the methods of Sandberg and Stewart (2003, 2006) at normal indoor ambient temperatures between 20–22.2°C and incandescent light in Paradise, California. Unless otherwise stated, all numbers of signal beat counts and time intervals in milliseconds (msec) presented in the following descriptions are expressed as mean ± standard deviation.

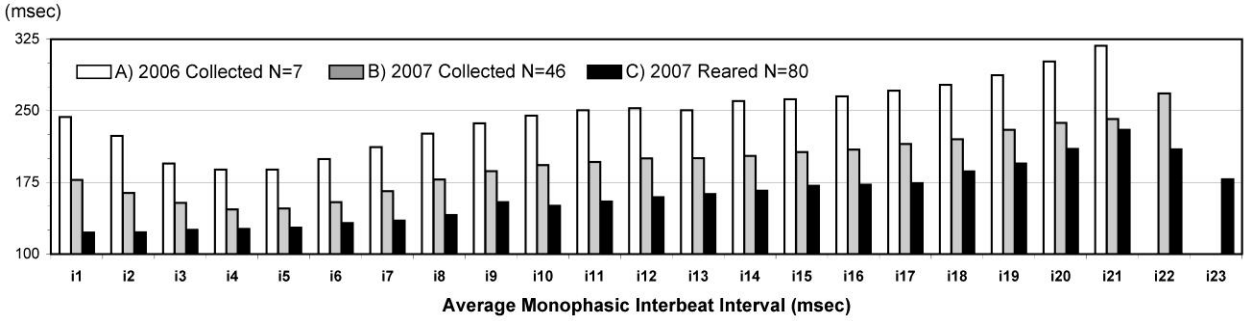

Fig. 5. *Hesperoperla hoguei* simple monophasic 13-24 beat call patterns based upon individual average interbeat intervals i1-i23 (msec) for three Domingo Spring analysis groups. A) White bars = 2006 collected male calls (N=7), B) Gray bars = 2007 collected male calls (N=46) and C) Black bars = 2007 reared male calls (N=80). Y-axis ranges from 100-325 msec.

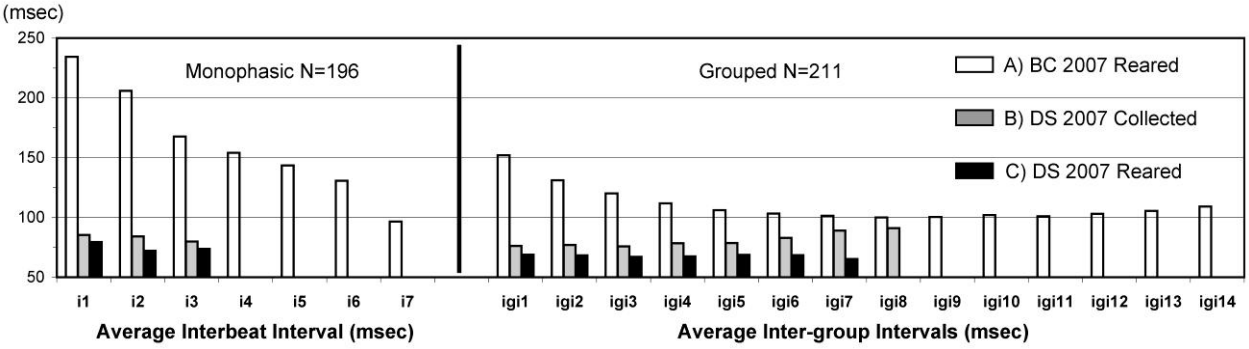

Fig. 6. *Hesperoperla pacifica* complex monophasic-grouped call patterns based upon individual average interbeat intervals i1-i7 and average inter-group intervals igi1-igi14 (msec) for one Butte Creek (BC) and two Domingo Spring (DS) 2007 analysis groups. A) White bars = BC reared male calls (N=120), B) Gray bars = DS collected male calls (N=69) and C) Black bars = DS reared male calls (N=22). Y-axis ranges from 50-250 msec.

RESULTS

Hesperoperla hoguei – New Signal Description

Hesperoperla hoguei was recorded and analyzed in 2006 and 2007. Seven call signals were obtained from one male on 01 October 2006, collected live and recorded the same day (Table 2). The typical 13–22 beat call was monophasic (Fig. 1) with 21 mode beats (19.9 ± 3.1), and 240.6 ± 38.5 msec overall average interbeat intervals (Table 2). The mean duration of male calls was 4537 ± 956 msec. The average interbeat interval call pattern indicated by white bars (Fig. 5A), decreased over the first five beats (i1–i4), increased gradually with occasional stalls through i16, and then increased more rapidly over the remaining 5 beats (i17–i21). This trend of initial call pattern decrease followed by a gradual increase was observed for both *Hesperoperla* species (Figs. 5–6), where individual (not overall) averages for each interbeat (i) or intergroup interval (igi) are graphically expressed in bar charts.

In 2007, drumming was analyzed separately for adults that were collected live or reared. Forty-six calls and 23 answer signals were recorded from two males and one female, respectively, **field-collected** on 21 September and recorded 23 September. The males had call signals with 20 mode beats (20.6 ± 1.2) and overall average interbeat intervals of 188.5 ± 29.7 msec (Table 2). The average male call duration was 3688 ± 285 msec. The female answer signal had 6 mode beats (7.1 ± 2.7) and overall average interbeat intervals of 147.1 ± 47.7 msec. The typical male-female 2-way exchange was monophasic (Fig. 2) with a mean duration of 6236 ± 255 msec. The average interbeat interval call pattern indicated by gray bars (Fig. 5B), decreased over the first 5 beats (i1–i4), and then increased over the remaining 6–23 beats (i5–i22).

Reared *H. hoguei* adults – Eighty and 64 signals were recorded from three 1–2 day old and one 2–3 day old males and female, respectively, between 29 August and 18 September 2007. The males had call signals with 20 mode beats (17.9 ± 2.6) and overall average interbeat intervals of 149.9 ± 35.9 msec (Table 2). The average male call duration was 2660 ± 476 msec. The female answer signal had 16 mode beats (14.0 ± 2.6) and overall average interbeat intervals of 92.9 ± 27.6 msec. The typical male-female 2-way exchange was monophasic with a mean duration of 5069 ± 512 msec. The average interbeat interval call pattern indicated by black bars (Fig. 5C), increased over the first 22 beats (i1–i21) and then decreased over the last intervals i22–i23. The four individual monophasic calls that made up average intervals i22–i23 had increasing interval patterns.

Hesperoperla pacifica – New Signal Character and Additional Populations

The drumming of *H. pacifica* was examined from two additional populations in northern California (Table 2). Signals are reported separately for collected adults from Domingo Spring and reared adults from Domingo Spring and Butte Creek (Table 2). The male call of this species was first described as simple-monophasic (no grouped beats), by Stewart & Zeigler (1977). The call signals reported here are complex: 196 of 211 analyzed were composed of initial monophasic tapping (1–7 beats), followed by 5–15 grouped signals (from both sites and by collected and reared adults). For this reason the initial monophasic ($♂_1$) and subsequent grouped portions ($♂_2$) of the call were analyzed separately (Table 2). Figure 6A–C reflects the combination call pattern, with initial monophasic average interbeat intervals i1–i7, followed by the grouped portion with average intergroup intervals igi1–igi14. Overall intergroup intervals are reported only in Table 2.

Reared Butte Creek *H. pacifica* – One hundred twenty signals were recorded from three males (1–3 days old) and 25 signals from one female (1–5 days old) (Table 2). Ten signals were recorded and analyzed for the second female, collected live from Butte Creek that answered the audio playback of one previously recorded Butte Creek male call signal (Table 2). Male calls recorded 11–25 April 2007, had initial monophasic tapping with 2 mode beats (2.2 ± 1.1) and overall average interbeat intervals of 213.1 ± 65.3 msec, followed by 6–15 groups with 3 mode beats (2.6 ± 0.7) and overall average intergroup intervals of 18.7 ± 2.8 msec (Table 2). The 1–4 beat grouped signals had decreasing individual average intragroup intervals (19.7 ± 2.8, 17.8 ± 2.2, and 14.7 ± 0.7 msec). Average male call durations were 4633 ± 586 msec. Female answers had 31 mode beats (27.2 ± 8.0) and overall average interbeat intervals of 83.7 ± 17.7 msec. The male-female exchange patterns were 2-way (n=10) and 3-way (n=5) (Fig. 3-A) and their average durations were 2085 ± 305 and 8654 ± 564 msec respectively.

Table 1. Summary of drumming signal characters for 22 species in the stonefly family Perlidae. Abdomen (Abd) with hammer (H), Abdomen with no specialized structure (N), Male call (♂C), Female answer (♀), Male response (♂R), Diphasic call (D), Monophasic signal (M), Grouped call (G), Rub call (R), and Overlapped female answer (O).

Species	Abd	♂C	♀	♂R	Citation - State
Acroneuria arenosa	H	Rub			Zeigler & Stewart 1977-TX
Acroneuria abnormis	H	Diphasic	(M)	(M)	Stewart et al. 1982-TN, GA
					Maketon & Stewart 1988-KS
Acroneuria carolinensis	H	Diphasic	(M)	(M)	Stewart et al. 1982-WV
Acroneuria evoluta	H	Diphasic tapping	(M)	(M)	Maketon & Stewart 1984-OK
		(D) Rub-Tap, Tap	(M)	(M)	
		(D) Rub-Tap, Tap	(M)		
Acroneuria lycorias	H	Diphasic			Stewart et al. 1982-WI
					Graham 1982-WI
		Tape playback	(M)		Maketon & Stewart 1984-MI
Acroneuria mela	H	(D) Rub-Tap, Tap		(M)	Maketon & Stewart 1988-KS
Agnetina capitata	N	Diphasic			Ziegler 1989-PA
Agnetina flavescens	N	Monophasic			Graham 1982-WI
			(M) (O)		Maketon & Stewart 1984-OK
Attaneuria ruralis	H	Diphasic			Maketon & Stewart 1988-KS
Beloneuria georgiana	H	(G) Tri-grouped	(M)		Stewart et al. 1988-NC
Calineuria californica	H	Rub	(M)	(M)	Stewart et al. 1982-CA
Claassenia sabulosa	H	Monophasic	(M)		Zeigler & Stewart 1977-CO
Doroneuria baumanni	H	(R) Bi-rub	(M)		Maketon & Stewart 1984-CA
Eccoptura xanthenes	H	Grouped	(M) (O)		Maketon & Stewart 1988-GA
Hansonoperla appalachia	H	(M) 3-beat	(M) 1-beat		Maketon & Stewart 1988-WV
Hesperoperla pacifica	H	Monophasic	(M)	(M)	Zeigler & Stewart 1977-CO
Paragnetina fumosa	N	Monophasic			Zeigler & Stewart 1977-TX
Paragnetina kansensis	N	Monophasic	(M)		Stewart et al. 1982-MS
Paragnetina media	N	Monophasic	(M)		Stewart et al. 1982-WI
			(M) (O)		Maketon & Stewart 1988-AR
Perlesta sp.	N	Monophasic			Maketon & Stewart 1988-KS
Perlinella drymo	H	(M) 3-beat			Zeigler & Stewart 1977-TX
			(M)		Sandberg & Stewart 2006-IA
Perlinella ephyre	H	(M) 3-beat			Kondratieff et al. 1988-AR

The average interbeat interval call pattern of reared Butte Creek males indicated by white bars decreased throughout the 1–8 beat (i1–i7) initial monophasic portion (Fig. 6A). In the following grouped portion, the average intergroup interval pattern changed at about midpoint (igi9). Average intergroup intervals decreased over the first nine groups (igi1–igi8), then increased only slightly in the remaining six groups (igi9–igi14) (with the exception of igi11 that decreased).

Field-collected Domingo Spring *H. pacifica* – Sixty-nine and 28 signals were recorded from five males and two females, respectively, on 19 May and 09 June 2007 (Table 2). Male calls recorded 19–20 May and 10–12 June, had initial monophasic tapping with 1 mode beat (1.6 ± 0.7) and overall average

interbeat intervals of 84.6 ± 12.6 msec, followed by 5–9 groups with 2 mode beats (2.0 ± 0.3) and overall average intergroup intervals of 13.4 ± 2.4 msec (Table 2). The 1–4 beat grouped signals had decreasing individual average intragroup intervals (13.5 ± 2.5, 13.0 ± 1.2, 11.8 (n=1) msec). Average male call durations were 661 ± 155 msec. Female answers had 30 mode beats (26.7 ± 9.7) and overall average interbeat intervals of 70.6 ± 16.1 msec. The male-female exchange patterns were 2-way (n=28) and 3-way (n=1) and their average durations were 2906 ± 827 and 5271 (n=1) msec respectively.

The average interbeat interval call pattern of field-collected Domingo Spring *H. pacifica* indicated by gray bars decreased throughout the 1–4 beat (i1–i3) initial monophasic portion (Fig. 6B). For the following grouped portion (igi1–igi8), the average intergroup interval pattern was relatively constant, increasing throughout the 9 groups (except igi3, which decreased).

Reared Domingo Spring *H. pacifica* – Twenty-two signals were recorded from two males (3 days old) and 6 signals from two females (1–3 days old) (Table 2). Male calls recorded 16–18 June 2007, had initial monophasic tapping with 1 mode beat (1.7 ± 0.7) and overall average interbeat intervals of 76.6 ± 8.1 msec, followed by 5–8 grouped signals with 2 mode beats (1.9 ± 0.3) and overall average intergroup intervals of 12.2 ± 1.7 msec (Table 2 and Fig 4-A). Average male call durations were 612 ± 53 msec. Female answers had 12 mode beats (11.3 ± 3.3) and overall average interbeat intervals of 46.6 ± 14.7 msec. The male-female exchange patterns were 2-way (n=6) and 3-way (n=2) (Fig. 4-B) and their average durations were 1205 ± 113 and 3724 ± 220 msec respectively.

The average interbeat interval call pattern of reared Domingo Spring *H. pacifica* indicated by black bars changed during the 1–4 beat (i1–i3) initial monophasic portion (Fig. 6C), first decreasing (i2) and then increasing slightly (i3). The following average intergroup interval pattern changed very slightly twice, first decreasing (igi1–igi3), then increasing (igi4–igi5), and finally decreasing again (igi6–igi7).

DISCUSSION

The drumming signals of *Hesperoperla* are species specific. The description of *H. hoguei* simple-monophasic calls and answers bring the total of this signal type in Perlidae to 11 species. Three species, *Agnetina flavescens* (Walsh) (Maketon and Stewart 1984), *Paragnetina kansensis* (Banks) (Stewart et al. 1982), and *P. media* (Walker) (Maketon and Stewart 1988, Stewart et al. 1982) were similar to *H. hoguei* with 10–20 average beats/call but differed in interbeat intervals. The *H. pacifica* complex call is the first report of a combination monophasic-grouped signal type and brings the male call total with at least grouped components in Perlidae to three species. *Beloneuria georgiana* (Banks) males call with tri-grouped signals and *Eccoptura xanthenes* (Newman) males use a variable number of groups/call containing 2–4 beats/group (Maketon and Stewart 1988).

The new description of drumming in *H. hoguei* and the revised description of additional California populations for the *H. pacifica* male call character conform to the drumming evolution paradigm of Stewart (2001) and Stewart and Sandberg (2006). *Hesperoperla hoguei* simple monophasic calls and 2-way exchanges are considered ancestral, and *H. pacifica* complex monophasic-grouped calls, 2-way, and 3-way exchanges are derived (Stewart and Zeigler 1984). The combination monophasic-grouped call type is tentatively ranked higher in complexity than grouped signals alone.

Hesperoperla hoguei drumming characters of suspected age classes (older field-collected vs. younger reared) differed somewhat and further our understanding of variability in this fixed action mate finding behavior. Mode and mean male number of beats/call were similar over two years and between age groups (Table 2). The differences included: (a) reared females had more mode and average number of beats/answer than collected females, (b) overall average intervals (Table 2) and individual average interbeat intervals (Fig. 5C) were shorter for reared males, and (c) average call duration for reared male calls (2660 msec) was shorter than collected (3688–4537 msec). Reared *H. hoguei* male average individual interbeat interval call pattern was relatively constant and increased throughout (Fig. 5C). The suspected older collected males produced call patterns that changed from decreasing to increasing intervals. They probably required an initial "warming-up" period to reach a minimum interval after the first 2–4

Species – Location [1-5] Call Type [1-2]	No. Individuals / No. Signals: Call ♂C	Answer ♀	Response ♂R	Range (Mode) No. Beats/Signal / Overall $\bar{x}$ ± SD No. Beats/Signal: Call ♂C	Answer ♀	Response ♂R	Range (Mode) No. Groups/Call / Overall $\bar{x}$ ± SD No. Groups/Call ♂	Overall ♂C Call, ♀ Answer, ♂R Response Interbeat or Inter-group Interval (msec) ($\bar{x}$ ± SD): Call ♂C	Answer ♀	Response ♂R	Overall ♂-♂ Inter-group, ♂C-♀ Call-Answer & ♀-♂R Answer-Response Exchange Intervals (msec) ($\bar{x}$ ± SD): ♂-♂	♂C-♀	♀-♂R
Hesperoperla hoguei [1]	1			13-22 (21)				240.6 ± 38.5					
Collected DS-2006	7			19.9 ± 3.1									
Hesperoperla hoguei [2]	2	1		17-23 (20)	3-12 (6)			188.5 ± 29.7	147.1 ± 47.7			1674.7 ± 205.5	
Collected DS-2007	46	23		20.6 ± 1.2	7.1 ± 2.7								
	3	1		13-24 (20)	7-19 (16)			149.9 ± 35.9	92.9 ± 27.6			1283.8 ± 264.3	
Reared DS-2007	80	64		17.9 ± 2.6	14.0 ± 2.6								
Hesperoperla pacifica [3]													
Monophasic ♂1 ♀ & ♂R	3	2	1	1-7 (2)	14-40 (31)	27-35 (35)		213.1 ± 65.3	83.7 ± 17.7	98.0 ± 22.7		399.3 ± 188.2	697.4 ± 267.3
Reared BC-2007	112	25	5	2.2 ± 1.1	27.2 ± 8.0	32.6 ± 3.4							
Grouped ♂2 Calls	3			1-4 (3)			6-15 (13)	18.7 ± 2.8			111.0 ± 22.1		
Reared BC-2007	120			2.6 ± 0.7			12.5 ± 1.6						
Hesperoperla pacifica [4]													
Monophasic ♂1 ♀ & ♂R	5	2	1	1-3 (1)	9-46 (30)	58*		84.6 ± 12.6	70.6 ± 16.1	46.1 ± 11.2		349.7 ± 136.1	880.6*
Collected DS-2007	63	28	1	1.6 ± 0.7	26.7 ± 9.7	N/A							
Grouped ♂2 Calls	5			1-4 (2)			5-9 (6)	13.4 ± 2.4			78.4 ± 8.9		
Collected DS-2007	69			2.0 ± 0.3			6.7 ±1.2						
Monophasic ♂1 ♀ & ♂R	2	2	1	1-3 (1)	7-16 (12)	48-58 (N/A)		76.6 ± 8.1	46.6 ± 14.7	38.9 ± 14.1		126.1 ± 81.3	466.5 ± 290.6
Reared DS-2007	21	6	2	1.7 ± 0.7	11.3 ± 3.3	53.0 ± 7.1							
Grouped ♂2 Calls	2			1-2 (2)			5-8 (7)	12.2 ± 1.7			68.0 ± 5.4		
Reared DS-2007	22			1.9 ± 0.3			7.0 ± 0.8						
Hesperoperla pacifica [5]	4	3	1	8-15 (12)	7-26 (16)	19-35 (22)	N/A	~120	~63	~68	N/A	45-570	65-382
Monophasic ♂1 ♀ & ♂R	60	44	8	12.2 ± 1.8	14.1 ± 3.7	25.0 ± 5.6							

Table 2. *Hesperoperla* drumming descriptions and overall signal characters. Locations: *H. hoguei*[1] Domingo Spring (DS) 2006, *H. hoguei*[2] Domingo Spring (DS) 2007, *H. pacifica*[3] Butte Creek (BC) 2007, *H. pacifica*[4] Domingo Spring (DS) 2007, and *H. pacifica*[5] Colorado (Zeigler & Stewart 1977). * indicates N=1. *Hesperoperla pacifica* calls were analyzed separately for monophasic beats (♂1) and grouped beats (♂2).

beats of the call before converting to an increasing interval pattern (Fig. 5A–B).

The effects of increased age and decreased temperature upon overall average interbeat intervals for two *Isogenoides* (Plecoptera: Perlodidae) species have been documented (Sandberg and Stewart 2005). In their study, two populations of *Isogenoides elongatus* Hagen were compared (field-collected vs. reared). The field-collected population, assumed so because no nymphs were present, had slightly more beats/call and longer overall average interbeat intervals. Another species from their study, *I. zionensis* Hagen, from a single population, was compared at two temperatures (21-22°C and 18.9°C). The two groups had similar call beats, but overall average interbeat intervals were longer for calls, answers and responses of colder males and females.

The *H. pacifica* overall collected and reared signal characters exhibited little difference between suspected age groups (Table 2). These results concur with Zeigler and Stewart (1985) who also found little difference in number of average beats/call between two *Pteronarcella badia* (Hagen) (Plecoptera: Pteronarcyidae) age groups consisting of 1–2 and 4–5 days of age. In their study the younger males produced calls with slightly more average beats/call than older males, but they did not provide interbeat interval data.

The overall average drumming characters of *H. pacifica* from Butte Creek differed somewhat from Domingo Spring in having slightly more initial monophasic average beats/call, more mode and average beats/group (Table 2), and longer mean total call durations. Butte Creek males were most different from Domingo Spring males with more mode and average number of groups/call and longer interbeat and intergroup intervals (Table 2 and Fig. 6A–C). The above differences indicate that these two California populations may have different dialects. Although a large number of signals were recorded for this analysis (Table 2), tests for differences between populations (Butte Creek vs. Domingo Spring and Collected vs. Reared) could not be performed because observations were only based on only a few individuals from each population. Future studies of dialect differences should emphasize the collection of signal data from more individuals, increasing the power to confirm the statistical significance of population differences.

In addition to overall (Table 2) and individual (Fig. 6) mean drumming character differences between the two populations, *H. pacifica* is allopatric in Butte Creek and sympatric with *H. hoguei* in Domingo Spring. It is possible the isolated Butte Creek population has not been under selective pressure to cause divergence in the number of call beats, groups, interbeat intervals, and intragroup interval characters of its signal. One physical factor with possible affects upon adult behavior between Domingo Spring and Butte Creek is temperature. Water temperature data collected by the author (Hobo model U22-001) indicate that the year long range for Domingo Spring is approximately 45–51°F (7.2–10.6°C) and 37–76°F (2.8–24.4°C) for Butte Creek. Other possible factors affecting adult behaviors include undiscovered environmental influences upon life history such as the difference in elevation that these two populations occur (Butte Creek – 92 m, Domingo Spring – 1547 m).

The drumming results presented in this paper for *H. pacifica* from two new populations help clarify the previous monophasic call description of Zeigler and Stewart (1977). It is probable that the monophasic single beats they described as "raspy or scratchy" and with "sub-peaks and blurs" were actually the call groups described in this paper masked by sound interference or equipment caused distortion. At that time, the authors used an analog cassette tape recorder and one microphone to capture and analyze stonefly drumming signals (Zeigler and Stewart 1977). Additionally, their drumming chamber (11x9x3 cm manila file folder paper box with clear plastic Petri dish lid) was not placed into a second sound resistant chamber (wood box with glass lid), allowing ambient sound interference.

The summary of overall *H. pacifica* signal characters from Zeigler and Stewart (1977) for two Colorado populations concurs with the Butte Creek population data (Table 2). In the previous study, the call was described as monophasic and the number of beats/call character should be compared to the number of call groups/signal in this study (Table 2). Likewise, their overall average male call interbeat interval should be compared to the overall average intergroup interval (♂-♂) of this study (Table 2). The similarities between these three allopatric

populations (CA-Butte Cr., CO-Upper Delores and CO-Gunnison Rivers) support the proposal that the sympatric population of Domingo Spring *H. pacifica* may express a drumming dialect.

ACKNOWLEDGEMENTS

Sincere thanks go to the following for assistance with collections, rearing, recording, data analysis, and reading early drafts: Allison Brigham, Pete Ode, Dan Pickard, Andy Rhen, Brady Richards, Joe Slusark, Jennifer York and three anonymous reviewers.

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Received 24 July 2009, Accepted 19 August 2009, Published 15 September 2009