

DRUMMING BEHAVIOR AND LIFE HISTORY NOTES OF A  
HIGH-ALTITUDE COLORADO POPULATION OF THE  
STONEFLY *ISOPERLA PETERSONI* NEEDHAM & CHRISTENSON  
(PLECOPTERA: PERLODIDAE)

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ABSTRACT.—Late instar nymphs and adults of a Colorado Hudsonian zone population of *Isoperla petersoni* Needham and Christenson were studied during the summer and early fall months of 1998, when stream temperature ranged from 3.3°C to 8.9°C. Early and middle instar nymphs were absent from July to October, and nymphs attained maximum size in mid-August during the 2nd week of adult field presence, suggesting a univoltine-slow life cycle. Nymphs were carnivorous and fed primarily on chironomid larvae. Adults were present from August to mid-October, with peak numbers of adult males and females occurring in mid-September and late September, respectively. Fecundity of field-collected females averaged  $94.1 \pm 45.15$  eggs per female in September ( $N = 81$ ) and decreased to  $85.2 \pm 57.6$  in October ( $N = 12$ ). Drumming duets were 2-way (male-female), and female answers followed male calls (nonoverlapped) or began before completion of the male call (overlapped). Male calls averaged  $11.1 \pm 2.09$  beats and female answers averaged  $6.2 \pm 2.99$ , with mean intervals of 118 and 58 ms, respectively. The average number of female answer beats increased from 5.3  $\pm$  2.56 when duets were nonoverlapped, to 6.6  $\pm$  3.08 when overlapped.

*Key words:* stonefly, drumming, life history, Perlodidae, behavior.

The stonefly genus *Isoperla* is widely distributed throughout the Holarctic region and contains approximately 131 species worldwide (Illies 1966, Zwick 1973). It represents the largest stonefly genus in North America, with 57 documented species. Szczytko and Stewart (1979a) provided a revision of 20 western North American species (except *I. decolorata* Ricker), including descriptions of the eggs and nymphs of 19 and 12 species, respectively. Three western species have subsequently been discovered (Szczytko and Stewart 1984, Bottorff et al. 1990a).

The large eastern fauna has remained a problematic group taxonomically and biologically because of the cryptic external morphology of adults and poorly known eggs and nymphs; it is currently under revision by S.W. Szczytko (personal correspondence) and contains substantially more than the currently recognized 33 species. Definitive separation of most *Isoperla* species requires aedeagal eversion and its description in males, and description of associated eggs, nymphs, and females.

Despite the diversity and importance of this large group as lotic food web components and

generally biological indicators of good water quality, relatively little is known about their behavior, life history, and ecology. Their drumming behavior, which can be a useful line of evidence for delineating species (Stewart et al. 1988), has been described for only 19 North American *Isoperla* species (Szczytko and Stewart 1979b, Maketon and Stewart 1984, Stewart et al. 1988), and detailed life histories have been published for only 13 of them (Stewart and Stark 1988, Sandberg and Szczytko 1997) largely because nymphs have not been correlated with adults and therefore are unknown for most species.

*Isoperla petersoni* is a widely distributed western species, from Alaska where it is common in most clearwater streams (Stewart et al. 1990) southward to Utah. It was included for Colorado in a later electronic list of Stark et al. (1973), but that record has been deleted since no literature record can be substantiated. Its adult emergence and nymphal growth have been described only from eastern Alaskan North Slope populations (Stewart et al. 1990), and its drumming behavior has not been studied. In its southernmost range in Colorado, it occurs

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at high elevations between 3109 and 3444 m and is one of the last regional *Isoperla* species to emerge (Baumann et al. 1977). This research was conducted on a population in Boulder County, Colorado, which we discovered in 1998.

#### SITE DESCRIPTION

This study was conducted on an *I. petersoni* population from a northern unnamed tributary of the North Fork Middle Boulder Creek, Boulder County, Colorado. The study reach is a 1st-order stream located approximately 40°00'27"N, 105°39'56"W, and is about 2 km east of Arapaho Pass (3629 m) on the Arapaho Glacier Trail near the abandoned Fourth of July Mine (elevation 3414 m). The study site is in the Hudsonian life zone dominated by trees with stunted growth. The alpine zone begins approximately 100 m north and 50 m west of the study site. The stream flows through a wet meadow near scattered clusters of blue spruce (*Picea pungens* Engelman), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.)), and Engelmann spruce (*Picea engelmanni* Parry ex Engelman), most of which have been stunted by high winds and snow. The riparian vegetation consists of short stands of willow (*Salix* sp.) and alder (*Alnus* sp.), which are more prevalent at the lower tributary reaches, and herbaceous annuals and perennials including elephants head (*Pedicularis* sp.), gentian (*Gentiana* sp.), Indian paintbrush (*Castilleja* sp.), fireweed (*Epiobium* sp.), and short grasses and sedges along the stream margins.

The tributary flows 1.5 km before joining with the North Fork Middle Boulder Creek. The water source of the seeps and flowing springs forming the tributary consists of nearby permanent snowfields and the South Arapaho Glacier. Typical stream substrates include gravel, cobble, and boulders that form alternating riffles, small waterfalls, and pools. Areas that include cobble substrate are tightly embedded and limit the effectiveness of kicknet sampling. However, much of the study reach substrate is covered with aquatic moss (*Hygrohypnum* sp.) that provides cover for nymphs and emerging adults. Other stoneflies collected in the tributary include *Sweltsa borealis* (Banks), *Plumiperla diversa* (Frisson), *Zapada haysi* (Ricker), *Megarcys signata* (Hagen), and

*Kogotus modestus* (Banks). Mayflies collected include *Drunella coloradensis* (Dodds), *Cinygmula ramaleyi* (Dodds), and *Cinygmula par* (Eaton).

#### METHODS AND MATERIALS

We collected late instar nymphs qualitatively at approximately weekly intervals from 26 July to 26 September 1998 with a triangular-frame kicknet fitted with a 600- $\mu$ m-mesh bag. Stream temperature during this period ranged from 3.3° to 8.9°C. Access by foot to the study site was delayed until July due to extended presence of deep snow well into June 1998 that limited ability to sample through the nymphal growth period. Senior author Sandberg traveled to Colorado in mid-December 1999 to attempt collection of nymphs for winter growth determination. Avalanches in the area caused trail closure and prevented access to the study tributary. Typically, <33 nymphs were sampled from this sparse population and preserved weekly; they were hand-picked from each kicknet sample that also contained moss and debris. Additional late instar nymphs were transported live to the laboratory for rearing. These we maintained in styrofoam cups containing stream water from the North Fork Middle Boulder Creek, Buckingham Campground (elevation 2896 m). Temperature and photoperiod were adjusted in a refrigerator to simulate stream environmental conditions, and cups were checked twice daily for emergence. Reared adults were preserved in 80% ethanol.

We determined nymphal growth by interocular distance (IOD) measurements made with a calibrated ocular micrometer fitted to a stereo-dissection microscope. The IOD is the shortest distance between the eyes. Sex was determined using the presence (female) or absence (male) of a gap in the posterior setal row of the 8th abdominal sternite (Stewart and Stark 1988). Food habit was determined from midgut and hindgut contents, removed by dissection and identified to the lowest practical taxonomic level.

Adult presence data and sex ratios were determined from weekly beating sheet samples of adults taken from riparian vegetation within 1 m of the stream margins. Collecting effort on each sampling date was duplicated as closely

as possible and consisted of beating riparian vegetation for about 3 hours within 1 m of the stream margin. Emergence timing and sex ratios of laboratory-reared adults were compared with presence and sex ratios of field-collected adults.

On 21 August 1999 we collected late instar nymphs at the study site for rearing. Eight virgin males and 6 virgin females were successfully reared in a Fridgid Units Living Stream™, and drumming signals from pairings of these were recorded at room temperatures of 20–24°C, under fluorescent room light of about 70 foot candles. Digital sound recordings were made with a Sony MiniDisc (model MZ-R37) and Optimus Electret omnidirectional condenser microphones in a sound-dampened, partitioned recording chamber described by Stewart and Zeigler (1984). We made digital, computer-generated graphic facsimiles from recorded signals played into a computer and translated with the sound editing and analyzing software Audiowave (Voyetra-Turtle Beach Inc.) and Acid WAV (Polhedric Software). The latter program displayed each stereo channel (male-left, female-right) with unique colors, assisting in the determination of signal characteristics. Clear, well-defined signals of both males and females were measured to determine number of drum beats, beat intervals to nearest 1 ms, duet duration, and for overlapped duets the interval between the 1st female response beat and the male beat immediately before it. For nonoverlapped duets, the male-female interval (interval between end of male call to start of female answer) was also measured.

Drumming amplitude of all recorded signals was low; this complicated identification of specific male call and female answer drumbeats. We attempted audiocassette recordings made with a Marantz (model PMD 340) recorder early in the recording sessions but abandoned them due to noise obliteration of the low-amplitude drum beats, and therefore poor generation of graphic facsimiles. Digital recordings provided increased discrimination between drumbeats and noise interference. In some instances the beat(s) of the overlapped female answer fell at the exact time of male call beat(s). These duets were not included in the analysis because the resolution power of the signal analysis software did not allow definitive measurement of these “masked” events.

## RESULTS AND DISCUSSION

Emergence was not observed in the field; however, we collected several exuviae using the beating sheet or hand-picked them from exposed, moss-covered rocks. Adults reared in the laboratory emerged both during the day ( $N = 33$ ) and evening ( $N = 27$ ) throughout the emergence period and ecdysis required 20–30 minutes. In the field adults were found in low vegetation along the stream margin where they had crawled up to seek cover as has been demonstrated for other *Isoperla* (Hynes 1967, Jop and Szczytko 1984, DeWalt and Stewart 1995).

The presence of adults at North Fork Middle Boulder Creek from early August through the 1st half of October indicated that *I. petersoni* has an extended emergence. *Isoperla petersoni* adults ( $N = 18$ ) from eastern Alaska North Slope streams also emerged over an extended period, from June to mid-August (Stewart et al. 1990). Therefore, in terms of length of adult presence, this southern-latitude Hudsonian zone population is similar to the Alaskan population, but the onset of presence is later by 2 months (June vs. August). The 1st adult male was collected on 8 August 1998 when stream temperature was 7°C (Fig. 1). The field sex ratio (male:female) of 225 adults was 1.1:1. A substantially lower sex ratio of 0.4:1 was observed for the 67 individuals reared in the laboratory. Adult field presence lasted 68 days and was assumed complete when the last adult was observed on 10 October. Although 0.6 m of snow had fallen on 1 October, several adults were collected from willow brush after snow was carefully removed. The last 3 nymphs were collected in the field on 26 September (Fig. 2), 2 weeks before the end of adult field presence.

Mean fecundity of field-collected adult females was  $92.9 \pm 46.44$  eggs ( $N = 94$ ), but decreased slightly over time from  $94.1 \pm 45.15$  in September ( $N = 81$ ) to  $85.2 \pm 57.63$  in October ( $N = 12$ ). This may have been due to the small number of females remaining late in the emergence cycle for analysis, or to the possibility that later-emerging females were smaller. Smaller females late in the emergence cycle have been noted for other stoneflies (Khoo 1968, Schwarz 1970, Sheldon, 1972, Cather and Gaufin 1975, Orberndorfer and Stewart 1977, Snellen and Stewart 1979), even

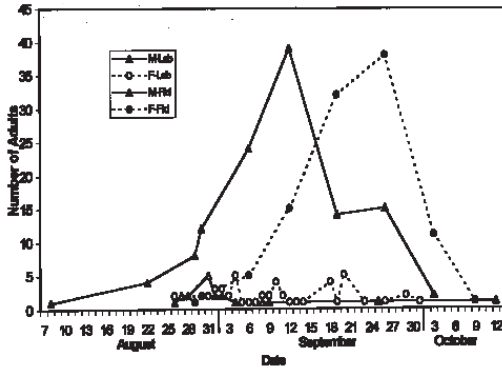


Fig. 1. Field ( $N = 225$ ) and laboratory ( $N = 67$ ) adult presence and emergence of *Isoperla petersoni* from the North Fork Middle Boulder Creek, 1998. Field data indicated by dark symbols, laboratory data by light; males indicated by solid lines, females by dashed lines.

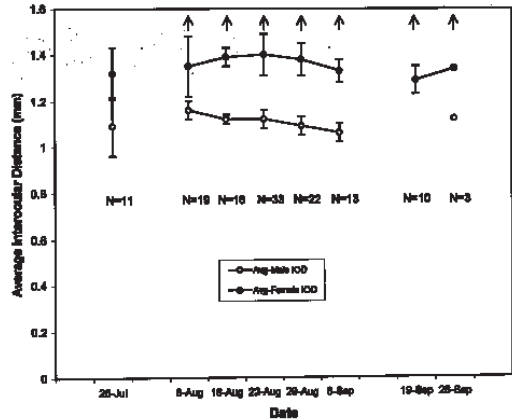


Fig. 2. Late instar growth of 127 *Isoperla petersoni* nymphs in North Fork Middle Boulder Creek, 1998. Black circles = average female IOD, open circles = average male IOD, vertical lines = standard deviation, arrows = adult presence,  $N$  = male and female sample size.

though we did not measure *I. petersoni* females. Laboratory-reared females produced 6 egg masses with average egg counts increasing slightly from  $92.5 \pm 58.69$  in late September ( $N = 2$ ) to  $119.5 \pm 14.25$  in early October ( $N = 4$ ).

Winter growth of nymphs was not documented due to inaccessibility of the study site from November to June. However, the absence of early instars at the end of the snow-free season in mid-October and again in early July when nymphs had attained maximum size (Fig. 2) suggested a univoltine cycle. We assume the eggs hatched over a short period and that the majority of nymphal growth occurred over winter, presumably under an insulative snow cover. Our nymph collections late in the growth cycle did not include a wide size range; however, the Alaskan population (Stewart et al. 1990) did have a wide range in monthly size of nymphs from fall through spring, suggesting a flexible life cycle that ranged from univoltine-slow to semivoltine. The latter was represented by a slow, winter-growing portion of the cohort that was recruited in late summer, or possibly by an egg diapause.

Sexual size dimorphism of 127 nymphs was observed throughout the sampling period, with average IOD for males and females of  $1.11 \pm 0.06$  and  $1.36 \pm 0.09$ , respectively. Maximum average size was attained first by male nymphs ( $1.16 \pm 0.04$  mm) on 8 August ( $N = 7$ ), followed by female nymphs ( $1.40 \pm 0.09$  mm,  $N = 15$ ) on 22 August (Fig. 2). Mean IOD for

both sexes then decreased for the remaining sample dates.

*Isoperla petersoni* was carnivorous from late July to mid-September. Chironomidae (91.4%) and Ostracoda (5.6%) formed the majority of food items ingested (Table 1). The highest frequency of empty midguts and hindguts was observed during the onset of emergence between late August and early September. The predominance of chironomid larvae as the prey of *I. petersoni* is consistent with observations for other *Isoperla* (Frison 1935, Minshall and Minshall 1966, Richardson and Gauvin 1971, Fuller and Stewart 1977, 1979, Sandberg and Szczytko 1997).

Vibrational communication signals were recorded from 8 males and 6 females from 3 to 13 September 1999. Duets consisted of simple monophasic male calls (5–19 beats) and female responses (1–14 beats). Females varied their responses from nonoverlapped (Fig. 3A) to overlapped (Fig. 3B); when overlapped, they began answering after the 7th male call beat (Fig. 3C). We analyzed a total of 228 signals; 134 were overlapped, 55 nonoverlapped, and 39 were lone male calls (Table 2). Male calls had 11 mode beats ( $\bar{x} = 11.1 \pm 2.09$ ) with average beat intervals of  $118 \pm 9$  ms. The mean number of call beats increased slightly for overlapped duets ( $11.6 \pm 1.32$ ) and decreased slightly to  $11.0 \pm 1.48$  for nonoverlapped duets. The average number of answer

TABLE 1. Taxa found in the midgut and hindgut of 124 *Isoperla petersoni* nymphs collected July to September 1998 from a high-altitude stream in Colorado.

Sample date (1998):	07/26	08/08	08/16	08/22	08/29	09/06	09/19	% of total
Number of organisms								
Number dissected :	11	19	16	33	22	13	10	124
Plecoptera			1		2			0.63
<i>Zapada</i> sp.				1	1			0.42
Baetidae					1			0.21
Chironomidae	5	1	1		1			1.67
Orthocladiinae	10	2		2	1			3.13
<i>Cricotopus/Orthocladius</i> sp.	56	17	49	86	14		1	46.55
<i>Diplocladius</i> sp.	1							0.21
<i>Paraorthocladius</i> sp.	6	1	2	7	8			5.01
<i>Parametriocnemus</i> sp.				1				0.21
<i>Rheocricotopus</i> sp.				1				0.21
Tanytarsini				1	2			0.63
Diamesinae	9	2	2	3	1			3.55
<i>Diamesa</i> sp.	12	53	34	30	10			29.02
<i>Psuedodiamesa</i> sp.	1	1	1	2				1.04
<i>Pagastia</i> sp.			3					0.63
<i>Prosimulium</i> sp.	3	1			1			1.04
Ostracoda	14	7	2	2			2	5.64
Hydrachnidia				1				0.21
TOTAL	117	85	95	137	42	0	3	100%
Number of midguts/hindguts containing								
Chironomidae parts	4/4	1/6	6/6	11/9	4/4		1/0	
Unidentified insect parts	1/0		5/3	1/0	3/4		1/1	
Unidentified insect eggs	3/0	0/1	1/0					
Unidentifiable material	3/10	2/13	1/12	4/16	4/11	3/4	3/2	
Sand	1/1	2/0		1/3	0/3			
Empty		1/2	1/0	6/9	2/4	10/9	6/8	

TABLE 2. Drumming signal statistical characteristics of *Isoperla petersoni* recorded from 8 males and 6 females between 3 and 13 September 1999 at 20–24°C.

	Total calls, answers, duets and intervals		Nonoverlapped duets		Overlapped duets	
	8♂	6♀	Number of individuals		8♂	6♀
			5♂	6♀		
<b>BEATS</b>						
Number	228	189	55	55	134	134
Mean ± s	11.1 ± 2.09	6.2 ± 2.99	11.0 ± 1.48	5.3 ± 2.57	11.6 ± 1.32	6.6 ± 3.08
Mode	11	4	11	4	11	4
Range	5–19	1–14	8–15	1–11	9–16	2–14
<b>DUET DURATION (MS)</b>						
Mean ± s	1458 ± 163 (N = 189)		1483 ± 170		1448 ± 159	
Mode	1490		1490		1610	
Range	1070–1930		1080–1930		1070–1800	
<b>BEAT INTERVALS (MS)</b>						
Mean ± s	118 ± 9	58 ± 22	118 ± 9	59 ± 27	117 ± 8	58 ± 20
	(N = 2307)	(N = 1178)	(N = 551)	(N = 292)	(N = 1417)	(N = 886)
Mode	120	50	110	50	110	50
Range	90–160	10–290	100–160	10–230	9–160	10–290

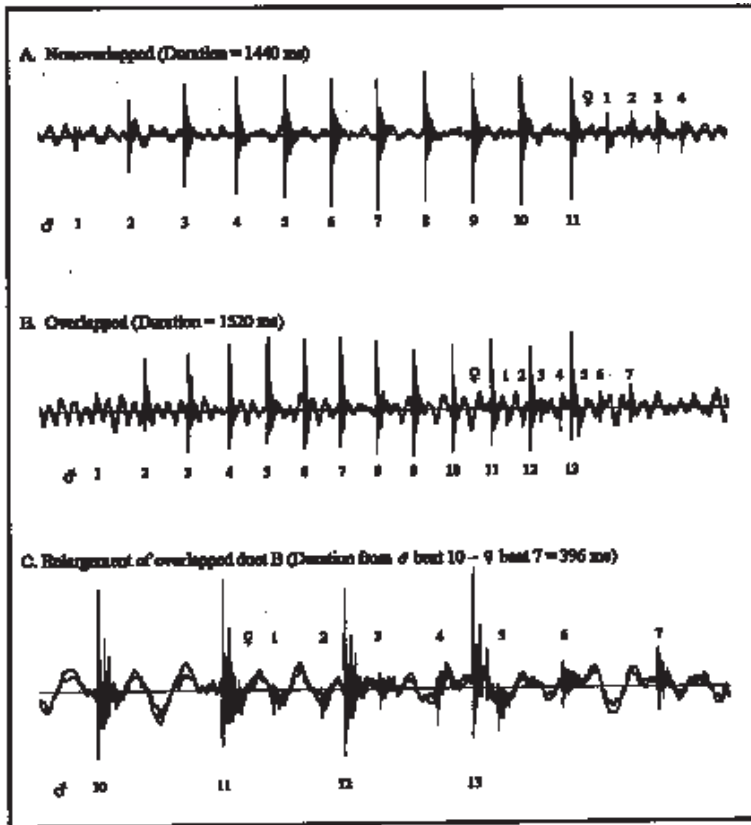


Fig. 3. Duets of *Isoperla petersoni*: A, nonoverlapped male 11-beat, female 4-beat, monophasic exchange, duet duration = 1440 ms; B, overlapped male 13-beat, female 7-beat exchange, duet duration = 1520 ms; C, 4× horizontal, 2× vertical enlargement of duet 3B, segment duration = 396 ms. Numbers above signal indicate female beat number and those below indicate male.

beats increased from  $5.3 \pm 2.56$  when duets were nonoverlapped to  $6.6 \pm 3.08$  when overlapped. The rhythm of male calls was uneven and had gradual interval transitions, which began long ( $131 \pm 9$  ms), then decreased to  $113 \pm 5$  ms for beats 7 and 8, and then returned up to 130 ms for the final intervals.

*Isoperla petersoni* belongs to the *I. sordida* Banks species complex (Szczytko and Stewart 1979b, 1984, Bottorff et al. 1990a) that includes 8 western Nearctic species. Drumming is known for only 3 of them (Bottorff et al. 1990b): *I. adunca* Jewett, *I. bifurcata* Szczytko and Stewart, and *I. miwoc* Bottorff and Szczytko. *Isoperla petersoni* male calls had nearly twice as many mode and average number of beats as other species within the complex. The average male call interval was closest to *I. adunca* (138 ms). *Isoperla petersoni* male and female signals generally fit the ancestral *Isoperla* pattern

(Stewart and Maketon 1991) in being monophasic and involving 2-way vibrational communication with or without overlap of calls-answers. The drumming evolution paradigm of Stewart (2001) indicates that all of these *Isoperla* have achieved specificity from ancestral Plecopteran signals by slight modification of numbers of beats and beat intervals (rhythm). *Isoperla petersoni* average call beat intervals are about median to those of the 24.5 to 356.8 ms range of other known western *Isoperla* species signals. Only a few *Isoperla* species have derived, and more complex, grouped or phased calls (Stewart and Maketon 1991).

#### LITERATURE CITED

- BAUMANN, R.W., A.R. GAUFIN, AND R.F. SURDICK. 1977. The stoneflies (Plecoptera) of the Rocky Mountains. *Memoirs of the American Entomological Society* 31.

- BOTTORFF, R.L., S.W. SZCZYTKO, AND A.W. KNIGHT. 1990a. Descriptions of a new species and three incompletely known species of western Nearctic *Isoperla* (Plecoptera: Perlodidae). Proceedings of the Entomological Society of Washington 92:286–303.
- BOTTORFF, R.L., S.W. SZCZYTKO, A.W. KNIGHT, AND J.J. DIMICK. 1990b. Drumming behavior of four western Nearctic *Isoperla* species (Plecoptera: Perlodidae). Annals of the Entomological Society of America 83: 991–997.
- CATHER, M.R., AND A.R. GAUFIN. 1975. Life history and ecology of *Megarcys signata* (Plecoptera: Perlodidae), Mill Creek, Wasatch Mountains, Utah. Great Basin Naturalist 35:39–48.
- DEWALT, R.E., AND K.W. STEWART. 1995. Life histories of stoneflies (Plecoptera) in the Rio Conejos of southern Colorado. Great Basin Naturalist 55:1–18.
- FRISON, T.H. 1935. The stoneflies, or Plecoptera, of Illinois. Bulletin of the Illinois Natural History Survey 20:281–471.
- FULLER, R.L., AND K.W. STEWART. 1977. The food habits of stoneflies (Plecoptera) in the Upper Gunnison River, Colorado. Environmental Entomology 6: 293–302.
- \_\_\_\_\_. 1979. Stonefly (Plecoptera) food habits and prey preferences in the Delores River, Colorado. American Midland Naturalist 101:170–181.
- HYNES, H.B.N. 1976. Biology of Plecoptera. Annual Reviews in Entomology 21:135–153.
- ILLIES, J. 1966. Katalog der rezenten Plecoptera. Das Tierreich, 82. Walter de Gruyter, Berlin.
- JOP, K., AND S.W. SZCZYTKO. 1984. Life cycle and production of *Isoperla signata* (Banks) in a central Wisconsin stream. Aquatic Insects 6:81–100.
- KHO, S.G. 1968. Experimental studies on diapause in stoneflies. I. Nymphs of *Capnia bifrons* (Newman). Proceedings of the Royal Entomological Society of London (A) 43:40–48.
- MAKETON, M., AND K.W. STEWART. 1984. Drumming behavior in four North American Perlodidae (Plecoptera) species. Annals of the Entomological Society of America 77:621–626.
- MINSHALL, G.W., AND J.N. MINSHALL. 1966. Notes on the life history and ecology of *Isoperla clio* (Newman) and *Isoagenus decisus* Walker (Plecoptera: Perlodidae). American Midland Naturalist 76: 340–350.
- ORBERNDORFER, R.Y., AND K.W. STEWART. 1977. The life cycle of *Hydroperla crosbyi* (Plecoptera: Perlodidae). Great Basin Naturalist 37:260–273.
- RICHARDSON, J.W., AND A.R. GAUFIN. 1971. Food habits of some western stonefly nymphs. Transactions of the American Entomological Society 97:91–121.
- SANDBERG, J.B., AND S.W. SZCZYTKO. 1997. Life cycle of *Isoperla lata* (Plecoptera: Perlodidae) in a central Wisconsin trout stream. Great Lakes Entomologist 30(4):143–159.
- SCHWARZ, P. 1970. Autokologische Untersuchungen zum Lubenszyklus von Setipalpia-Arten (Plecoptera). Archiv für Hydrobiologie 67:103–140.
- SHELDON, A.L. 1972. Comparative ecology of *Arcynopteryx* and *Diura* (Plecoptera) in a California stream. Archiv für Hydrobiologie 69:521–546.
- SNELLEN, R.K., AND K.W. STEWART. 1979. The life cycle of *Perlesta placida* (Plecoptera: Perlidae) in an intermittent stream in northern Texas. Annals of the Entomological Society of America 72:659–666.
- STARK, B.P., B.R. OBLAD, AND A.R. GAUFIN. 1973. An annotated list of the stoneflies (Plecoptera) of Colorado Part I. Entomological News 84:269–277.
- STEWART, K.W. 2001. Vibrational communication (drumming) and mate-searching behavior of stoneflies (Plecoptera); evolutionary implications. Proceedings of the XIII International Symposium on Plecoptera. In press.
- STEWART, K.W., AND M. MAKETON. 1991. Structures used by Nearctic stoneflies (Plecoptera) for drumming and their relationship to behavioral pattern diversity. Aquatic Insects 13:33–53.
- STEWART, K.W., AND B.P. STARK. 1988. Nymphs of North American stonefly genera (Plecoptera). Entomological Society of America, Thomas Say Foundation 12:1–460.
- STEWART, K.W., AND D.D. ZEIGLER. 1984. Drumming behavior of twelve North American stonefly (Plecoptera) species: first descriptions in Peltoperlidae, Taeniopterygidae and Chloroperlidae. Aquatic Insects 6:49–61.
- STEWART, K.W., R.L. HASSAGE, S.J. HOLDER, AND M.W. OSWOOD. 1990. Life cycles of six stonefly species (Plecoptera) in subarctic and arctic Alaska streams. Annals Entomological Society of America 83:207–214.
- STEWART, K.W., S.W. SZCZYTKO, AND M. MAKETON. 1988. Drumming as a behavioral line of evidence for delineating species in the genera *Isoperla*, *Pteronarcys*, and *Taeniopteryx* (Plecoptera). Annals of the Entomological Society of America 81:689–699.
- SZCZYTKO, S.W., AND K.W. STEWART. 1984. Descriptions of *Calliperla* Banks, *Rickera* Jewett, and two new western Nearctic *Isoperla* species (Plecoptera: Perlodidae). Annals of the Entomological Society of America 77:251–263.
- \_\_\_\_\_. 1979a. The genus *Isoperla* (Plecoptera) of western North America; holomorphology and systematics, and a new stonefly genus *Cascadoperla*. Memoirs of the American Entomological Society 32. 120 pp.
- \_\_\_\_\_. 1979b. Drumming behavior of four western Nearctic *Isoperla* (Plecoptera) species. Annals of the Entomological Society of America 72:781–786.
- ZWICK, P. 1973. Insecta: Plecoptera. Phylogenetisches System und Katalog. Das Tierreich 94. Walter de Gruyter, Berlin.

Received 31 January 2000

Accepted 31 May 2000