DRUMMING BEHAVIOR OF SELECTED NEARCTIC STONEFLIES (PLECOPTERA)

THESIS

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By

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ABSTRACT

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Drumming was recorded for 11 of 13 Nearctic stonefly species, representing 4 families. Both male and female signals were obtained from 5 species, and were either 2-way or 3-way communications. Signals were species-specific; those of males and females varied from 3-39 and 1-14 beats/signal, respectively. Duration of male signals varied from 105-8,016 ms; those of females, except *Perlinella drymo* (1 beat), varied from 402-1318 ms. Signals among related taxa showed greatest similarities. Duration of male signals of *Perlinella drymo* became progressively shorter at each of 4 temperatures from 7-29°C. Females of *Perlinella drymo* would only repeatedly answer male signals recorded at near their own temperature, and would not repeatedly answer recorded male signals of 8 other species.

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CHAPTER I

INTRODUCTION

The term "drumming" has been used to describe the sound or vibration-producing activities of a variety of animals, including: male ruffed grouse (Bent, 1932), male great spotted woodpeckers (Pynnonen, 1939), Isoptera soldiers (Busnel, 1963), male Death-Watch beetles (Gahan, 1918), some Homoptera (Ossiannilsson, 1949) and female psocids (Pearman, 1928). Of these, only the psocids strike the abdomen against the substrate as in Plecoptera.

Newport (1851) first used the term drumming in reference to stonefly communication. Until the recent excellent works of Rupprecht (1967, 1969, 1972, 1974, 1976), only qualitative descriptions of this interesting phenomenon have appeared (Briggs, 1897; Macnamara, 1926; Brink, 1949, 1955, Jewett, 1959; Gaufin et al., 1966). Rupprecht (1969) described behavior and quantitative aspects of drumming in 15 Palearctic species and has dealt with dialects (*Diura bicaudata*, Rupprecht, 1972), species specificity, nature of the signal, structure and function of the vesicle and hammer and behavior associated with drumming.

Essentially, drumming involves the production of vibrations produced by striking the distal, ventral section of the abdomen on the substrate. Rupprecht (1976) reviewed the parts such as the vesicle and hammer that are used in drumming and classified them according to families. The males of some species and females of most that drum, strike unmodified parts against the substrate to produce signals. In general, males drum throughout their existence, but only virgin females have been reported to drum (Rupprecht, 1967). The vibrations of larger species are audible for considerable distances, across a quiet room. Individual strokes of the abdomen can be observed in species with slow signals, but the succession of strokes appear as a blur in species with rapid signals. Males initiate the communication, females answer (often with signal overlap) and in some species the male answers. Thus, communication, in species that drum, is 2-way or 3-way, and has heretofore been interpreted as a calling behavior between the sexes. In some species, signalling is interspersed with searching by the male until he locates the female; in others, both males and females search, stopping occasionally to drum (Rupprecht, 1967). Mating usually results immediately after location. In cases where male stoneflies encounter a non-virgin female, a "rejection response" or "attitude," consisting of the female raising her abdomen so as to prevent copulation, is exhibited (Rupprecht, 1967).

No description of drumming behavior nor quantitative aspects of drumming in Nearctic stoneflies have been published, although Roger Haike (personal communication) has recorded the signals of some species of Montana stoneflies on tape. The objective of this study was to record and study the drumming signals and behavior of Nearctic species from the Southwest and Southern Rocky Mountains and gather preliminary data on effects of temperature on drumming.

CHAPTER II

MATERIALS AND METHODS

Thirteen species, collected from various localities in Texas and Colorado (Table 1) were studied. Drumming signals were recorded from adults reared from mature nymphs; signals of *Claassenia sabulosa* (Banks) were also recorded from field-collected adults.

Texas species studied were *Hydroperla crosbyi* (Needham and Claasen), *Paragnetina fumosa* (Banks), *Acroneuria arenosa* (Pictet), *Perlesta placida* (Hagen), *Perlinella drymo* (Newman), *Zealeuctra arnoldi* (Ricker and Ross), *Zealeuctra claasseni* (Frison) and *Zealeuctra hitei* Ricker and Ross . Signals of *Pteronarcella badia* (Hagen), *Pteronarcys californica* (Newport), *Isogenoides zionensis* Hanson, *Claassenia sabulosa* (Banks), and *Hesperoperla pacifica* (Banks) were recorded from specimens collected in the upper Dolores and Gunnison Rivers of Colorado.

Mature, field-collected nymphs were held until emergence in styrofoam containers kept in environmental chambers at simulated stream temperatures and 12 h light-12 h dark cycle. Virgin and mated adults were kept in the same chambers, except during drumming experiments when they were removed to room conditions .5-1 h before recording attempts. Some *P.*

drymo, Z. arnoldi and Z. hitei nymphs were reared in a well ventilated shaded portable outdoor laboratory where recordings of their drumming signals were made. Light and temperature conditions were monitored with a Kahl Model 268WA620 light meter and a thermometer. Temperature variations in the outdoor lab varied from 7-29°C; successful recordings of P. drymo and Z. arnoldi were obtained at several temperatures within the range.

The recording setup consisted of (1) a small box or styrofoam cup, hereafter called the drumming chamber, (2) a Sony ® ECM-95S Electret condensor microphone, and (3) a Sony ® Model TC-90A or Model TC-142 cassette tape recorder. High fidelity Sony ® and Ampex ® tapes were used for recording. Early recordings were made using a 10 oz styrofoam cup, with a saran-wrap cover held in place by a cut-out lid. For these recordings, the square microphone was inserted into a cut-out opening at the bottom of the cup. Some recordings of P. drymo, Z. hitei, Z. claasseni, Z. arnoldi, Z. arenosa and P. fumosa were obtained with this chamber, but its use was discontinued early in the study because of the tendency for vibrations of the styrofoam material itself, caused by the drumming of the experimental animals, to produce less desirable oscilloscope tracings. Over 90% of the signals were obtained using a 11 x 9 x 3 cm partitioned box, constructed of manilla file folder paper and masking tape and covered with a clear plastic petri cover to allow visual observation during drumming. Rupprecht (personal communication) has used a similar chamber for his work. The microphone was taped to the table and the manilla drumming chamber rested on a pair of foam rubber pads above the microphone, separated from it by a 3 mm space. This arrangement was found to produce better acoustical quality in the taped signal than when the drumming chamber was allowed to rest directly on the microphone.

Males and females were placed in the two visually-isolated compartments of the drumming chamber. In most instances, no inducement was required to stimulate drumming activity of males. In some instances, jostling of the chamber, tapping on the table, or playing tapes of previously recorded males was required to induce drumming.

Video recordings of the audio signals were obtained by playing the cassette tapes into a Tektronix 7623A oscilloscope. Oscilloscope tracings of the signals were stored on the screen until measurements or photographs could be made. Time intervals were measured in millimeters on the oscilloscope screen and later converted to milliseconds. Oscilloscope photographs were made from many of the tracings, using a Polaroid ® CR-9 oscilloscope camera and Polaroid ® Type 107 black and white film.

Signal duration, number of beats and inter-beat intervals were the parameters analyzed for drumming signals of each species. Values relating to the duration of inter-beat intervals were normally expressed as $\bar{x} \pm$ S.D. Behavior during drumming was observed. Species specificity was tested in *P. drymo* females by playing tapes of their own males recorded at different temperatures and of males of other species to them.

CHAPTER III

RESULTS AND DISCUSSION

Pteronarcella badia

Range and $\bar{x}$ no. of beats/male signal were 6-9 beats and 7.04 beats respectively (Fig. 1; Table 1). Only one nine-beat signal was recorded. Inter-beat intervals at 25-26°C started at 56±4 ms and lengthened gradually to 95±7 ms at the end of the signal. Range and $\bar{x}$ duration of male signals at 25±1°C were 356-558 ms and 438 ms, respectively. No hammer or vesicle is present for drumming in males of *P. badia*.

The female signal varied more than that of the male, with a range and $\bar{x}$ no. of beats of 1-10 beats and 5.96 beats, respectively. Inter-beat intervals of female signals gradually lengthened as the signal progressed (Fig. 1). The first interval of a typical 6-beat signal at 26°C was 65±4 ms, with the last interval being 105±12 ms. Range and $\bar{x}$ duration of female signals at 25±1°C were 78-731 ms and 402 ms respectively.

Intervals between male and female signals ranged from 20-165 ms, however 16% of male-female exchanges showed one-beat overlap of the two signals, so that the female began just before the last beat of the male signal. No relationship between such overlap, and number of beats in the male or female signal was evident.

Only two of the 50 recorded male-female signals contained a male "answer" following the female signal. Both "answers" were 4 beats long with a $\bar{x}$ duration of 198 ms. At 26°C, the three inter-beat intervals were 66 ± 1, 62 ± 1, and 70 ± 2 ms respectively. These 2 answers never overlapped the female signal, but were separated from it by intervals of 56 ms and 196 ms respectively.

Male and female signals normally build in amplitude as they progress (Fig. 1), the first beat of the female signal sometimes being very weak. In most recordings, the female response sounds like a soft echo of the male signal.

Males and females of *P. badia* drummed very readily in the lab with no inducement. Females always became still after receiving and responding to the initial male signal. Males searched actively, stopping only to signal. The two observed cases of male "answering" the female response occurred at the beginning of a series of male-female exchanges. This "answering" ceased after the first two complete exchanges and never reoccurred in that series. As exchanges continued without successful location of the female by the male, the female occasionally shortened her signal to fewer beats as time passed.

Pteronarcys californica

Range and $\bar{x}$ no. of beats/male signal were 5-8 beats and 6.7 beats, respectively (Table 1; Fig. 2). Inter-beat intervals at 26±1°C lengthened gradually from 249±24 ms to 277+15 ms as the signal progressed. Range and $\bar{x}$ duration of male signals were 1125-1870 ms and 1518 ms, respectively. No hammer or vesicle is present for drumming in males of *P. californica*.

Range and $\bar{x}$ no. of beats/female signal were 4-8 beats and 6 beats, respectively. Inter-beat intervals at 25-26°C lengthened gradually from 233±19 ms to 285±6 ms as the signal progressed. Range and $\bar{x}$ duration of female signals were 801-1840 ms and 1318 ms, respectively. A one-beat overlap between male and female signals occurred only when the female response had 8 beats (Fig. 2). Most female responses followed the male signal by from 346-728 ms.

Most of the exchanges were 3-way, with the male "answering" the female signal. Range and $\bar{x}$ no. of beats of male answers were 4-13 beats and 7.4 beats respectively. Inter-beat intervals lengthened gradually from 207±21 ms to 279±21 ms as the signal progressed. These answers followed the female signal by 76-939 ms, with no incidence of overlap.

Adults of *P. californica* are large (males over 3 cm in length) with slow and awkward movements compared to the other species studied. Individual up-and-down strokes of the abdomen can be clearly seen on both male and female signals due to the long inter-beat intervals.

Amplitude of male signals normally built to a maximum towards the middle of the signal, declining for the last 2-3 beats (Fig. 2). Taped male signals sounded much like a person knocking on a wooden door. Amplitude of the female signal rose progressively as did the male signal, but amplitude of the female signal was normally less than that of the male. Overall signal amplitude of female signals normally decreased in a long series of male-female exchanges, becoming lower with each successive signal. The female signal, as in Pteronarcella badia, sounded like a soft echo of the male signal.

Unlike females of other species studied, females of P. californica often searched actively after drumming contact with a male was established. Long series of signals between male and female were uncommon. After 10-12 exchanges the male often stopped signaling. Three-way signals were common, and did not usually convert to 2-way signals in a series of exchanges, as was observed in other species.

Pteronarcella badia and Pteronarcys californica are presently restricted to the Nearctic region; this is the first published account of drumming signals for any representatives of the Pteronarcyidae. They have ca. the same no. beats/signal (Table 1) and similar patterns of inter-beat time intervals/signal (Fig. 1, 2). Only the longer inter-beat intervals of *P. californica* appear to give specificity to the signals.

Hydroperla crosbyi

Approximately 30 pairs of *H. crosbyi* were observed in the lab and near streamside under natural conditions. No indication of drumming was observed or recorded for this species. Males lack a hammer or vesicle.

Isogenoides zionensis

Only one male of *I. zionensis* was successfully reared and recorded. Range and $\bar{x}$ no. of beats/male signal were 11-19 beats and 15 beats, respectively. Beats were arranged into groupings of from 1-5 beats (Fig. 3). Groupings of 1-3 beats usually appear at the beginning of the signal, followed by grouping of 4-5 beats, usually 4. Most signals (67%) contained 4-5 such groupings, others contained 3 groupings. Inter-beat intervals within groupings were relatively constant at 278±16 ms. Intervals between the groups of beats began at 1208±352 ms and lengthened gradually to 1909±768 ms as the signal progressed. Range and $\bar{x}$ duration of the signal were 5862-11297 ms and 8016 ms, respectively. The beats of recorded male signals had a dull tone, with amplitude of all beats being relatively constant (Fig. 3). Individual abdominal strokes were visibly discernable during the slow and methodical signal. Males exhibit no specialized hammer or vesicle for drumming.

The grouped arrangement of beats in the male signal of *I. zionensis* compares favorably with the similar groupings in the signals of *Diura bicaudata*, *D. nanseni*, *Isoperla grammatica*, *I. görtzii*, *I. oxylepis*, and *I. rivulorum* (Rupprecht, 1969, 1972), which are all members of the family Perlodidae, Holearctic in distribution.

Claassenia sabulosa

Range and $\bar{x}$ no. of beats/male signal were 3-8 beats and 5.4 beats, respectively (Table 1; Fig. 6). Inter-beat intervals at 24°C were relatively constant at 76±5 ms. Range and $\bar{x}$ duration of male signals were 204-445 ms and 327 ms, respectively. Males utilize a well developed hammer for drumming.

Range and $\bar{x}$ no. of beats/female signal were 7-14 beats and 12.3 beats, respectively. Inter-beat intervals at 24°C remained relatively constant at 64±7 ms until the last 2-3 intervals which increased to 92±15 ms. Range and $\bar{x}$ duration of female signals were 502-905 ms and 777 ms, respectively. The male and female signal was separated by 33-298 ms, with no observed cases of signal overlap.

Many of the male-female exchanges were 3-way signals containing a male "answer" after the female signal. Range and $\bar{x}$ no. of beats/male answer were 2-8 beats and 4.5 beats, respectively. Inter-beat intervals normally lengthened from 63±8 ms to 143±29 ms as the answer progressed. Overlap of the female signal and the male answer was observed in all 3-way exchanges, with from 1-4 beats involved in the overlap. No obvious shift from 3-way to 2-way signals occurred as drumming communication continued.

Amplitude of male signals normally increased as the signal progressed (Fig. 6). Amplitude of female signals was usually greater than that of male signals, and was relatively constant throughout the signal. Female signals sounded duller in tone but louder than male signals.

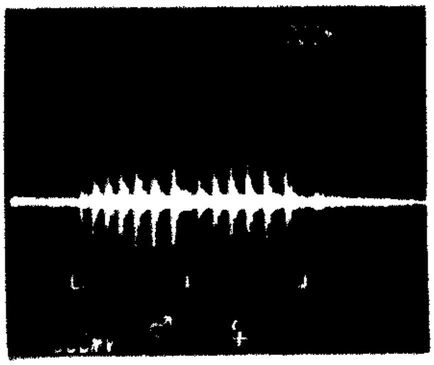
Many signals were recorded in a cabin in Colorado near streamside, under unknown temperature and dim light conditions. These signals were used in estimating no. of beats/signal, but not signal duration or inter-beat intervals. There was no difference in no. beats between signals recorded in the lab and those recorded in the cabin. Signals of adults in drumming chambers, quart jars, and some loose in the room could be heard throughout the night in the cabin.

Males searched after receiving a female response; females became still after receiving the initial male signal. Males on the Gunnison River, Colorado, in August, 1975, exhibited an intensive searching behavior from dusk to after midnight. None were observed drumming during this searching along the rocky banks. Over 50 transforming females observed were mated by both callow (freshly-emerged) and darker (previous days emergence) males before completely freeing themselves from the nymphal exuvium. Males ran over the water's surface between rocks, as well as on the bank, searching for females. This suggests the possibility that combinations of behavior such as drumming and active searching are important in mate location in species such as *C. sabulosa*, and where drumming is perhaps supplementary in vegetation or on suitable substrate, in helping males locate females.

Paragentina fumosa

Only two males of *P. fumosa* were obtained for recording. Range and $\bar{x}$ no. of beats for male signals were 19-30 beats and 24 beats respectively. Inter-beat intervals at 25°C were relatively constant at ca. 37 ms, increasing in length only slightly as the signal progressed (Fig. 4). Some of the signals began differently, with 3 or 4 beats spaced from 100 to 250 ms apart, converting then to the standard signal. Range and $\bar{x}$ duration of male signals were 628-1845 ms and 1065 ms, respectively. Males possess no hammer or vesicle for drumming. The few recordings obtained were made in the previously described styrofoam cup chamber.

Rupprecht (personal communication) recorded the signals of male *Paragnetina immarginata* from the Thornton River near Sperryville, Virginia, in 1974. I am indebted to him for



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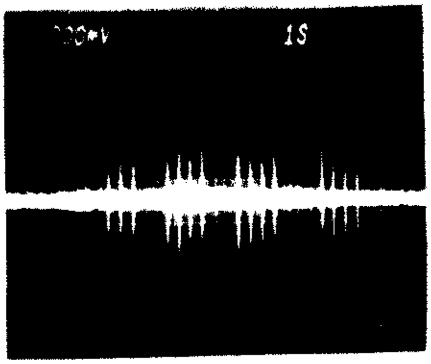

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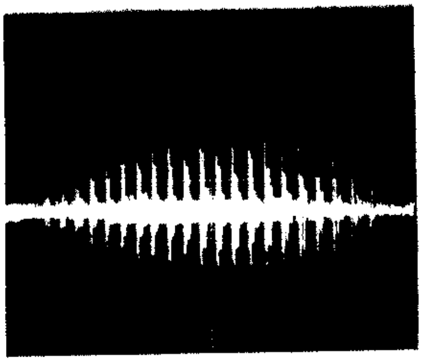

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Fig. 1--Two-way drumming signals of ♂ and ♀ *Pteronarcella* *badia* at 26°C/80 fc.

Fig. 2--Three-way drumming signals of *Pteronarcys* *californica* at 25°C/25 fc.

Fig. 3--Male drumming signal of *Isogenoides* *zionensis* at 26°C/80 fc.

Fig. 4--Male drumming signal of *Paragnetina* *fumosa* at 25°C/80 fc.

permission to publish the following summary of 42 signals from 2 males. The signal is uniform with a duration of 1±.1 sec., with a constant rate of 26±1 beats/sec. The signals of *P. fumosa* and *P. immarginata* compare favorably, in that both are multi-beat signals of well over 20 beats, and both have relatively constant inter-beat intervals throughout.

There is no evident similarity in no. of beats/male signal between the following members of the sub-family Perlinae: *Claassenia sabulosa*, *Paragnetina fumosa*, and *Paragnetina immarginata* (recorded by Rupprecht), reported herein, and *Perla maxima*, *Perla burmeisteriana*, *Perla marginata*, and *Dinocras cephalotes* reported by Rupprecht (1967, 1969). However, all 5 species do exhibit similar inter-beat interval patterns in that the intervals are realtively constant throughout the signal. Most of the other stonefly signals heretofore reported do not fit this pattern. *Claassenia sabulosa* has recently been moved to the subfamily Perlinae (Stark and Gaufin, 1976).

Acroneuria arenosa

Ten good signals were recorded from one male of *A. arenosa*. These signals were recorded in the styrofoam cup chamber. Vibrations set up in the cup by the rapid beats of the signals resulted in low quality oscilloscope tracings. Only durations of the signals could be measured. Durations ranged from 115-490 ms, with a $\bar{x}$ of 264 ms. The number of beats could not be directly measured, but a conservative estimate would be over 100 beats/sec., which is more rapid than that of any other signal measured. Signals were normally performed in a series, each signal following the next by less than one second. Amplitude of signals in a series usually increased as the series progressed. Males utilize a hammer for drumming. Signals sounded more like stridulations than drumming, but the blurring action of the abdomen was observed during the signals. Stridulation is unknown in stoneflies. Newport (1951) first reported drumming in the genus *Acroneuria*, but this is the first attempt at quantification of a signal of *Acroneuria*.

Hesperoperla pacifica

The range and mean no. of beats/male signal were 8-15 beats and 12.2 beats respectively (Fig. 7; Table 1). Inter-beat intervals at $25\pm1^{\circ}$C were ca. 120 ms and were relatively constant throughout the signal (Fig. 7). Range and $\bar{x}$ duration of the male signal were 749-1463 ms and 1127 ms, respectively. In some signals, the first interval was longer than the rest; in a few others, the intervals lengthened slightly towards the end of the signal. Males of *H. pacifica* utilize a well developed hammer for drumming.

Female signals varied greatly, ranging from 7-26 beats, with a $\bar{x}$ of 14 beats. Inter-beat intervals at 25°C normally became slightly longer as the signal progressed and averaged ca. 63 ms. Range and $\bar{x}$ duration of female signals at 25°C were 444-1462 ms and 826, respectively. Only 7% of the male-female exchanges showed overlap of the two signals. Signals were usually separated by 45-570 ms.

Eight 3-way signals were recorded between males and females (Fig. 7). Range and $\bar{x}$ no. of beats/male answer were 19-35 beats and 25 beats respectively. Inter-beat intervals lengthened gradually as the answer progressed, with a $\bar{x}$ of 68 ms. Range and $\bar{x}$ duration of the male signal were 1265-2467 ms and 1625 ms, respectively. Male "answers" never overlapped the female signal, but rather followed it after an interval of 65-382 ms.

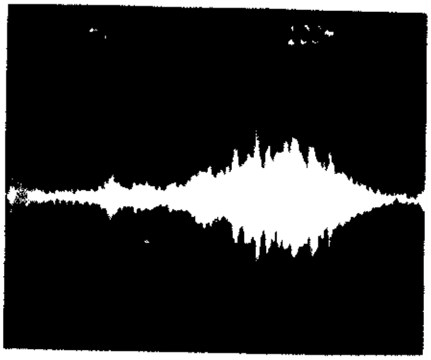
Amplitude of male and female signals was normally greatest in the middle portion. The amplitude of the female signal was usually less than that of the male signal (Fig. 7). Recorded male signals sounded raspy or scratchy due to their method of striking the substrate. The hammer bounces or scrapes a short distance with each blow, as the abdomen is pulled forward slightly. Sub-peaks and blurs show up on oscilloscope tracings of male signals due to this phenomenon, at times making accurate measurements difficult. Recorded female signals sound softer or duller than those of the male, at times producing a fluttery type sound. The male answer sounded different than his initial signal in that the beats were more rapid, and lacked the scraping quality characteristic of the initial signal. Males and females drummed readily in lab with no outside inducement. Females always became still after receiving and responding to the initial male signal. Males searched constantly, stopping only to signal. Three-way signals normally occurred only on the first 3-5 exchanges, after which the male dropped his answer, continuing only to send his primary signal.

Perlesta placida

Approximately 50 pairs of *P. placida* were observed in the lab and near streamside under natural conditions. No indication of drumming was observed or recorded for this species. Males lack a hammer or vesicle.

Perlinella drymo

Males produce a simple, 3-beat signal, answered with a single beat by the female (Figure 8). Of 250 signals by 15 males, the only variations observed were one 4-beat and one 5-beat signal by one male. No variation was found in the single beat response of 32 recorded female signals. Males were never observed to "answer" the female response (i.e. signal was always 2-way). The first inter-beat time interval at 24±1°C (67±4 ms) was always longer than the second (38±3 ms); with the ratio between these intervals being relatively constant at 1:.57. The range and $\bar{x}$ duration of male signals at 24±1°C were 89-114 ms and 105 ms



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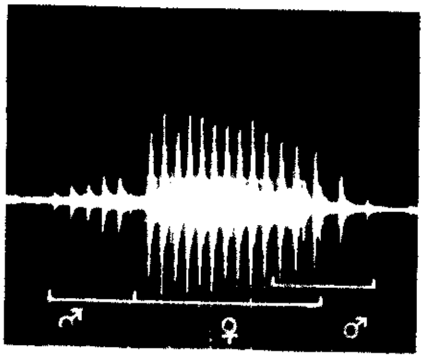

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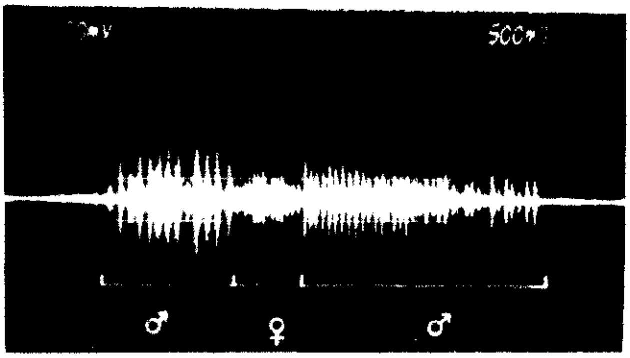

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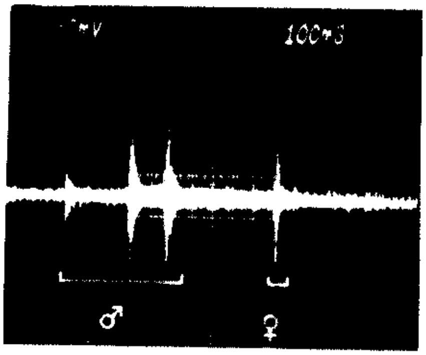

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Fig. 5--Male drumming signal of *Acroneuria arenosa* at 24°C/80 fc.

Fig. 6--Three-way drumming signals of *Claassenia sabulosa* at 25°C/80 fc.

Fig. 7--Three-way drumming signals of *Hesperoperla pacifica* at 26°C/80 fc.

Fig. 8--Two-way drumming signals of *Perlinella drymo* at 10°C/18 fc.

respectively. The interval between the last male beat and the female response was ca. of the same length as that of the male signal. Males of *P. drymo* utilize a well developed hammer for drumming.

Amplitude of the 3 male beats was relatively constant. Amplitude of the female response was normally greater than that of the male, but the audible tone of the female beat was always softer or duller than that of the male. Both sexes usually drummed readily when placed in the drumming chamber at various temperatures and photoperiods (Table 1). On one occasion, it was necessary to play a previously recorded male signal to a pair to initiate drumming.

Females became motionless immediately after receiving the first male signal and remained still except during the response stroke. Males search between signals, after receiving the first female response. A well developed hammer is utilized by males in drumming. Since one virgin pair mated without prior drumming exchanges, it is assumed that drumming is not necessarily a prerequisite or releaser for mating.

Signals recorded at various temperatures in the outdoor laboratory under dim or dark light conditions (Table 1) showed that this species will drum readily at temperatures ranging from 6°-29°C. Since no recordings were attempted outside this range, temperature threshholds of drumming were not specifically established. Analysis of variance showed highly significant differences between the durations of male signals at the four temperatures of 7°, 10°, 13°, and 29°C. Colder temperatures greatly extended duration of the signals (Table 1 and Figures 12-15). A similar effect of temperature has been observed in drumming of the death watch beetle _Xestobium tessallatum_ (Gahan, 1918).

In the limited experiment to test temperature specificity of female response, six females at 23°C always responded to taped male signals recorded at 24°C. Only three of the six responded to male signals recorded at 29°C, and then only for 3-4 signals. Only 1 of the 6 females responded once to a series of male signals recorded at 13°C. No response was observed to male signals at 7° or 10°C. At the end of this series, male tapes recorded at 24°C again elicited response from all six females for more than 10 signals. This suggests that inter-beat time intervals, which were influenced by temperature in males, are the major aspects of the signal to which females respond, and not the number of beats, which remained constant throughout the tested temperature range.

In the limited experiment to test species specificity of female response, the same six females mentioned above, all responded to male signals of _P. drymo_ recorded at 24°C. No response was observed to series of male signals of

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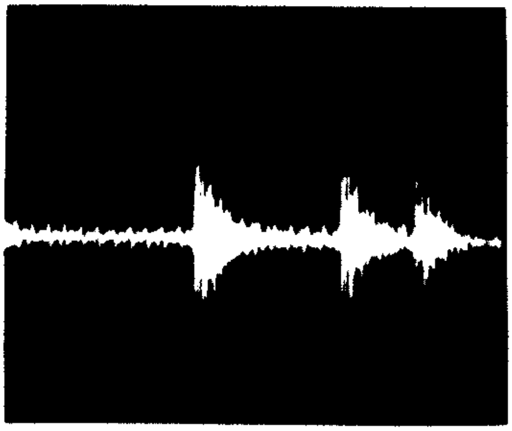

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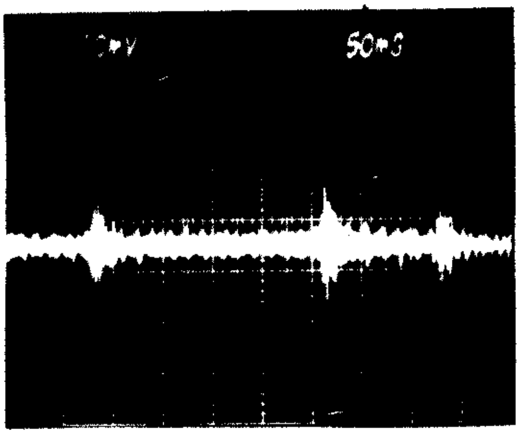

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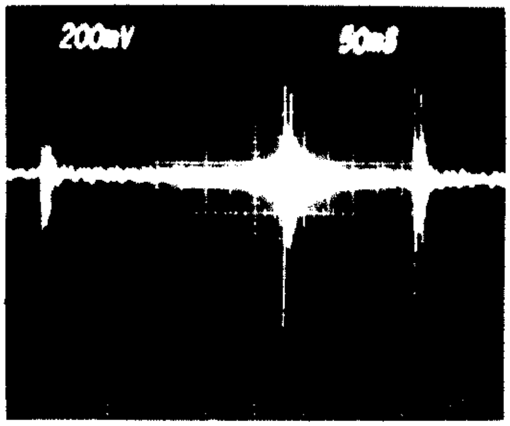

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Fig. 12--Male drumming signal of *Perlinella drymo* at 29°C/60 fc.

Fig. 13--Male drumming signal of *Perlinella drymo* at 13°C/dark.

Fig. 14--Male drumming signal of *Perlinella drymo* at 9°C/dark.

Fig. 15--Male drumming signal of *Perlinella drymo* at 7°C/dark.

Pteronarcys californica, *Isogenoides zionensis*, *Claassenia sabulosa*, *Hesperoperla pacifica*, or *Zealeuctra claasseni* recorded at 24±1°C. Four of the six females answered the first two taped signals of male *Pteronarcella badia*, recorded at 24°C. After five signals, only two females continued to respond, and after 10 signals, only one female continued to answer. Female responses were initiated before the 6-8 beat signal of male *P. badia* (Figure 1) had finished, indicating that females were keying on the first few (3?) beats of the signal which were somewhat similar to those of *P. drymo*. However, such communication between sexes of these two species does not occur in nature, since their ranges do not overlap. Taped male signals of *Zealeuctra arnoldi* and *Zealeuctra hitei* each elicited response from one of the six females of *P. drymo*. After two signals, the female "recognized" that the male signal was "incorrect," and response stopped. Again the female *P. drymo* response to the males of these two species began long before the multi-beat signals of the males (Figure 9 and 11) were completed. Thus it appears that females will occasionally respond experimentally to the male signals of other species; however, seasonal succession of emergence in sympatric species and geographic separation in allopatric species would normally prevent even limited communication in nature. At the end of the above series of tests, male *P. drymo* signals at 24°C were again played to the females, and all six females responded for more than 10 signals.

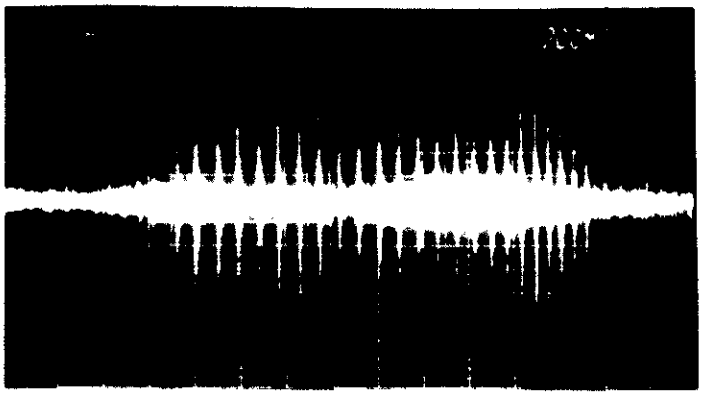
Responses from five different females of P. drymo were also obtained by imitating the male signal by tapping a pencil on the table near them.

The results for Acroneuria arenosa, Hesperoperla pacifica, Perlista placida and Perlinella drymo are the first quantified accounts of the drumming signals for members of the Acroneuriinae. No evident similarities were detected in their signals (Perlesta placida did not drum).

Zealeuctra arnoldi, claasseni, and hitei

Only male signals of Zealeuctra were successfully recorded, all in the styrofoam cup chamber. Two females of Z. arnoldi were observed drumming, but no recordings were obtained. Amplitude of beats was greatest in the middle to late middle portions of the signals (Fig. 9, 10, 11). Many of the recorded signals were too weak to produce good oscilloscope tracings so most of the no. of beats/signal data comes from counts made while listening to the signals at only 25% their original speed.

Range and $\bar{x}$ no. of beats/male signal of Z. arnoldi were 21-33 beats and 28.8 beats, respectively (Table 1). Interbeat intervals at $24 \pm 1^{\circ}C$ decreased gradually from ca. 80 ± 11 ms to ca. 51 ± 5 ms with the last 4-5 intervals being fairly constant (Fig. 9). Range and $\bar{x}$ duration of male signals



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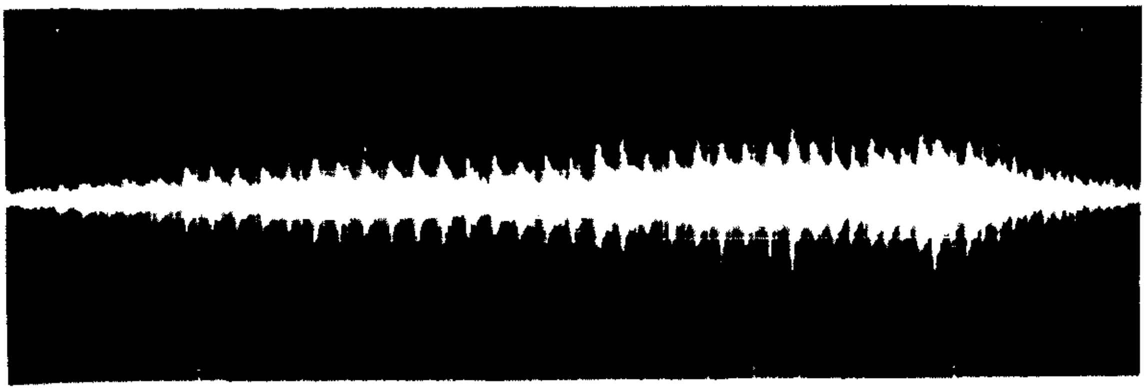

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Fig. 9--Male drumming signal of *Zealeuctra arnoldi* at 24°C/80 fc.

Fig. 10--Male drumming signal of *Zealeuctra claasseni* at 24°C/80 fc.

Fig. 11--Male drumming signal of *Zealeuctra hitei* at 10°C/34 fc.

TABLE 1

DRUMMING CHARACTERISTICS OF 11 STONEFLY SPECIES FROM COLORADO AND TEXAS DECEMBER, 1973--DECEMBER, 1975

Species Collection Date Locality $\frac{\text{temp. }^{\circ}\text{C}}{\text{foot candles}}$	$\frac{\text{No. Recordings}}{\text{No. Individuals}}$			No. Beats/Signal $\frac{\text{Mode}}{\bar{x} \pm \text{S.D.}}$			Signal Duration in ms $\bar{x} \pm$ S.D.		
	♂	♀	♂	♂	♀	♂	♂	♀	♂
Pteronarcella badia 6/14-15/75 Gunnison R. Gunnison Co., Colo. and 6/17/75 Dolores R. Montezuma Co., Colo. $\frac{25 \pm 1^{\circ}\text{C}}{80\text{ fc}}$	$\frac{104}{3}$	$\frac{48}{1}$	$\frac{2}{1}$	$\frac{7}{7.04 \pm .54}$	$\frac{6}{5.96 \pm 2}$	$\frac{4}{4 \pm 0}$	437.9±41	402.4±152	198.5±5
Pteronarcys californica 6/17/75 Dolores R. Montezume Co., Colo. $\frac{25 \pm 1^{\circ}\text{C}}{30\text{ fc}}$	$\frac{33}{2}$	$\frac{8}{2}$	$\frac{7}{2}$	$\frac{6}{6.72 \pm .9}$	$\frac{..}{6 \pm 1.9}$	$\frac{..}{7.4 \pm 3.6}$	1518±215	1318±479	1460±807

Table 1--Continued

Species Collection Date Locality $\frac{\text{temp. }^{\circ}\text{C}}{\text{foot candles}}$	$\frac{\text{No. Recordings}}{\text{No. Individuals}}$			No. Beats/Signal $\frac{\text{Mode}}{\bar{x}\pm\text{S.D.}}$			Signal Duration in ms $\bar{x}\pm\text{S.D.}$		
	♂	♀	♂	♂	♀	♂	♂	♀	♂
Isogenoides zionensis 6/17/75 Dolores R. Montezuma Co., Colo. $\frac{25\pm1^{\circ}\text{C}}{80\text{ fc}}$	$\frac{48}{1}$	..	..	$\frac{16}{15\pm2.5}$	..	..	8016±2239	..	..
Paragnetina fumosa 5/21/74 Little Cow Cr., Newton Co., Tex. $\frac{25^{\circ}\text{C}}{80\text{ fc}}$	$\frac{6}{2}$	..	..	$\frac{}{24.2\pm3.8}$	..	..	1065±475	..	..

Table 1--Continued

Species Collection Date Locality $\frac{\text{temp. }^{\circ}\text{C}}{\text{foot candles}}$	$\frac{\text{No. Recordings}}{\text{No. Individuals}}$			No. Beats/Signal $\frac{\text{Mode}}{\bar{x}\pm\text{S.D.}}$			Signal Duration in ms $\bar{x}\pm$S.D.		
	♂	♀	♂	♂	♀	♂	♂	♀	♂
Acroneuria arenosa 3/29/74 Little Cow Cr., Newton Co., Tex. $\frac{24^{\circ}\text{C}}{80\text{ fc}}$	$\frac{10}{1}$	..	..	..	..	..	264±128	..	..
Claassenia sabulosa 5/16/75 Gunnison R. Gunnison Co., Colo. $\frac{24^{\circ}\text{C}}{80\text{ fc}}$	$\frac{77}{4}$	$\frac{53}{3}$	$\frac{34}{3}$	$\frac{6}{5.7\pm1}$	$\frac{13}{9.9\pm2.5}$	$\frac{4}{4.5\pm2}$	327±69	777±89	419±125

Table 1--Continued

Species Collection Date Locality $\frac{\text{temp. }^{\circ}\text{C}}{\text{foot candles}}$	$\frac{\text{No. Recordings}}{\text{No. Individuals}}$			No. Beats/Signal $\frac{\text{Mode}}{\bar{x}\pm\text{S.D.}}$			Signal Duration in ms $\bar{x}\pm$S.D.		
	♂	♀	♂	♂	♀	♂	♂	♀	♂
Hesperoperla pacifica 6/14-15/75 Gunnison R. Gunnison Co., Colo.									
$\frac{25\pm1^{\circ}\text{C}}{80\text{ fc}}$	$\frac{60}{4}$	$\frac{44}{3}$	$\frac{8}{1}$	$\frac{12}{12.2\,\_\,1.8}$	$\frac{16}{14.1\pm3.7}$	$\frac{22}{25\pm5.6}$	1127 ± 194	826 ± 204	1625 ± 416
Perlinella drymo 1/2/74 & 12/30/75 Cedron Dr. Bosque Co., Tex.									
$\frac{29^{\circ}\text{C}}{60\text{ fc}}$	$\frac{52}{1}$	..	..	$\frac{3}{3.07\pm.33}$	..	..	63 ± 10.4	..	..
$\frac{24+1^{\circ}\text{C}}{80\text{ fc}}$	$\frac{74}{9}$	..	..	$\frac{3}{3\pm0}$	..	..	105 ± 6.6	..	..

Table 1--Continued

Species Collection Date Locality $\frac{\text{temp. }^{\circ}\text{C}}{\text{foot candles}}$	$\frac{\text{No. Recordings}}{\text{No. Individuals}}$			No. Beats/Signal $\frac{\text{Mode}}{\bar{x} \pm \text{S.D.}}$			Signal Duration in ms $\bar{x} \pm$ S.D.		
	♂	♀	♂	♂	♀	♂	♂	♀	♂
$\frac{13^{\circ}\text{C}}{0\text{ fc}}$	$\frac{28}{1}$	..	..	$\frac{3}{3 \pm 0}$	..	..	216 ± 7	..	..
$\frac{11^{\circ}\text{C}}{0\text{ fc}}$	$\frac{3}{1}$	..	..	$\frac{3}{3 \pm 0}$	..	..	249 ± 43	..	..
$\frac{10^{\circ}\text{C}}{0\text{ fc}}$	$\frac{32}{1}$	$\frac{32}{1}$	..	$\frac{3}{3 \pm 0}$	$\frac{1}{1 \pm 0}$	..	244 ± 9	0	..
$\frac{9^{\circ}\text{C}}{0\text{ fc}}$	$\frac{9}{1}$	..	..	$\frac{3}{3 \pm 0}$	..	..	358 ± 18	..	..
$\frac{7^{\circ}\text{C}}{0\text{ fc}}$	$\frac{51}{1}$	..	..	$\frac{3}{3 \pm 0}$	..	..	428 ± 28	..	..
$\frac{6^{\circ}\text{C}}{0\text{ fc}}$	$\frac{1}{1}$	..	..	$\frac{3}{3}$	..	..	508	..	..

Table 1--Continued

Species Collection Date Locality $\frac{\text{temp. }^{\circ}\text{C}}{\text{foot candles}}$	$\frac{\text{No. Recordings}}{\text{No. Individuals}}$			No. Beats/Signal $\frac{\text{Mode}}{\bar{x}\pm\text{S.D.}}$			Signal Duration in ms $\bar{x}\pm$S.D.		
	♂	♀	♂	♂	♀	♂	♂	♀	♂
Zealeuctra arnoldi 1/7/75 Unnamed Cr. Hays Co., Tex. $\frac{24\pm1^{\circ}\text{C}}{80\ \text{fc}}$	$\frac{5}{2}$	..	..	$\frac{..}{28.8\pm3}$	..	..	1818±248	..	..
Zealeuctra claasseni 1/20/74 & 1/29/75 Unnamed Cr. Cooke Co., Tex. $\frac{24\pm1^{\circ}\text{C}}{80\ \text{fc}}$	$\frac{11}{3}$	..	..	$\frac{..}{22.9\pm2}$	..	..	1986±116	..	..

Table 1--Continued

Species Collection Date Locality $\frac{\text{temp. }^{\circ}\text{C}}{\text{foot candles}}$	$\frac{\text{No. Recordings}}{\text{No. Individuals}}$			No. Beats/Signal $\frac{\text{Mode}}{\bar{x}\pm\text{S.D.}}$			Signal Duration in ms $\bar{x}\pm$S.D.		
	♂	♀	♂	♂	♀	♂	♂	♀	♂
Zealeuctra hitei 12/29/73 & 1/2/74 Cedron Dr., Bosque Co., Tex. $\frac{24\pm1^{\circ}\text{C}}{80\text{ fc}}$	$\frac{7}{3}$	..	..	$\frac{..}{39\pm3}$	..	..	2400±100 (ca.)	..	..

were ca. 1600-2200 ms and ca. 1818 ms respectively. Inter-beat intervals of two signals recorded at 12°C had lengthened to ca. 170 ms.

Range and $\bar{x}$ no. of beats/male signal of *Z. claasseni* were ca. 19-25 beats and ca. 22.9 beats, respectively (Table 1). Inter-beat intervals at 24±1°C remained relatively constant at 112±3 ms for the first half of the signal, with the intervals gradually decreasing to 67±ms in the second half. Range and $\bar{x}$ duration of signals were ca. 1900-2200 ms and 1986 ms, respectively.

Range and $\bar{x}$ no. of beats/male signal of *Z. hitei* were ca. 35-45 beats and ca. 39 beats, respectively (Table 1). Inter-beat intervals at 24±1°C started at ca. 60 ms, dropped to ca. 50 ms for most of the signal, and finally dropped to ca. 33 ms for the last 4-8 beats. Range and $\bar{x}$ duration of male signals were ca. 2300-2500 ms and ca. 2400 ms, respectively. Inter-beat intervals of one signal recorded at 10°C had lengthened to ca. 117 ms.

Males of *Zealeuctra* utilize a vesicle for drumming. Male *Zealeuctra* signals generally sounded like a coin running down (increasing in frequency) after being spun on a hard surface. One case of the rejection response or attitude of mated females to males was observed in the field by a *Z. hitei* female approached by a male.

All 3 species of *Zealeuctra* had multi-beat signals (over 20 beats/signal) and inter-beat intervals which shortened as the signal progressed, unlike most of the other male signals studied. These are the first signals to be described from the family Leuctridae.

CHAPTER IV

CONCLUSIONS

Eleven of 13 Nearctic species of stoneflies studied drummed, including 2, 1, 5, and 3 representatives, respectively, of the families Pteronarcyidae, Perlodidae, Perlidae, and Leuctridae. One Perlodid, *Hydroperla crosbyi*, and one Perlid, *Perlesta placida* did not drum. In addition, Rupprecht recorded the male signals of *Paragnetina immarginata* from Virginia in 1974. Success in obtaining the female answering signals was achieved in 5 of the 11 drumming species studied. In addition, drumming of 2 females of *Zealeuctra arnoldi* was observed, but no recordings were obtained. In all species where males and females drummed, the male always initiated the communication. In most species, the female became still after receiving the initial male signal, while the male searched actively. In *Pteronarcys californica*, both the males and females searched during drumming communication.

Signals were either 2-way or 3-way communication between male and female. In *Pteronarcella badia* and *Hesperoperla pacifica*, communication converted from 3-way to 2-way after the first 2-5 exchanges in a signal series. In *Claassenia sabulosa* and *Pteronarcys californica*, communication was usually 3-way, with no noticeable pattern change occurring in a series.

Mean no. of beats and $\bar{x}$ duration of male signals varied highly among the 11 species, 3-39 beats and 105-8016 ms, respectively. The pattern of inter-beat time intervals varied greatly among species lending specificity to signals with similar no. of beats. The pattern of inter-beat time intervals was relatively constant throughout the signal in male signals of *Paragnetina fumosa*, *Claassenia sabulosa*, and *Hesperoperla pacifica*. In male signals of *Pteronarcella badia* and *Pteronarcys californica*, the intervals become progressively longer throughout the signal, and in *Perlinella drymo* and 3 species of *Zealeuctra*, the inter-beat intervals become shorter as the signal progresses. In *Isogenoides zionensis*, distinct groupings of beats comprise the signal.

The answering signal of female *Perlinella drymo* consisted of a single beat. Mean no. of beats and $\bar{x}$ duration of the other females ranged from 1-14.1 beats and 402.4-1318 ms, respectively. The basic pattern of inter-beat time intervals in female *Pteronarcella badia*, *Pteronarcys californica*, *Claassenia sabulosa* and *Hesperoperla pacificia* were the same as those of their respective males described above. Their signals generally sounded like soft echos of the male signal.

A significant effect of temperature on signal duration, and therefore inter-beat time intervals, was shown in male

Perlinella drymo signals. Signals became progressively shorter at each of 4 temperatures ranging from 7-20°C. This effect of temperature on signal duration suggests that all future drumming studies should include temperature data with each signal description. Females of *P. drymo* would only repeatedly answer male signals recorded within 2°C of lab temperature at the time of the experiment. This suggests that the duration of inter-beat intervals within the male signal is the prime character recognized by females, and that, experimentally, the female answer is temperature specific. Females of *P. drymo* repeatedly answered taped male signals of only 1 of 9 other species played to them. The first 3 beats of *Pteronarcella badia* male signals were apparently similar enough in inter-beat time intervals to elicit a response. In nature these 2 species do not coexist.

All signals recorded were species-specific, with greatest similarity generally exhibited among realted species (*Zealeuctra*) and genera. Too many gaps in knowledge of drumming remain to enable a characterization of patterns within families or genera that might prove to be valuable input in establishing phylogenetic realtionships. Zwick (1973) suggested that the value of such data will probably be very great.

A virtual wealth of knowledge concerning drumming in stoneflies remains to be elucidated. The degree of occurrence among species, whether communication functions exclusively for mate-finding, whether active substrate selection occurs, the effects of external physical conditions, and possible variations within a species (dialects) are just a few of the areas needing investigation.

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