

# 12 Vibrational Communication and Mate Searching Behavior in Stoneflies

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## INTRODUCTION

The order Plecoptera is composed of the northern hemisphere suborder Arctoperlaria and the southern hemisphere suborder Antarctoperlaria (Illies, 1966; Zwick, 1973, 1980). Research over the past four decades on about 150 species from Europe, New Zealand and North America has established that the typical mating system of Arctoperlaria involves the sequence of:

1. Encounter site aggregation of sexes near the time of emergence (Stewart, 1994).
2. Species-specific calling by males with vibrational signals, initially during a ranging, nonoriented search for females.
3. Duet establishment when females within communicable range answer with vibrational signals then become stationary.
4. A localized search by the moving male orienting toward the stationary female until location and mating are accomplished.

The duetting portion of this system generally conforms to the Plecoptera model described by Bailey (2003). Further, research has established that the intersexual vibrational duetting portion of this mating system in stoneflies is one of the most diverse and complex known in insects (Rupprecht, 1967, 1969, 1976; Stewart, 1994, 1997, 2001; Stewart and Maketon, 1991; Zeigler and Stewart, 1977).

In contrast, observations over many years by stonefly specialists in Australia, New Zealand and South America, and experiments with several New Zealand species, including *Stenoperla*, have failed to detect drumming in any species of Antarctoperlaria, suggesting that members of that suborder have never adopted vibrational communication. Stewart (2001) hypothesized that they may have evolved highly specific encounter site aggregation behavior patterns, possibly supplemented by as yet undiscovered intersexual communication modes that bring the sexes sufficiently close enough together to accommodate mate-finding.

Newport (1851) first used the term drumming to describe stonefly communication; his and other early observations by MacNamara (1926), Brinck (1949), Briggs (1897) and others (Stewart 2001) were qualitative descriptions of the abdominal tapping behavior noted in various species. The first quantified studies (Rupprecht, 1967, 1969; Zeigler and Stewart, 1977; Szczytko and Stewart, 1979) established that:

1. Signals were produced by percussion with either the unmodified or specialized distal, ventral portion of the abdomen.
2. Duets were either “two-way” (male call–female answer) or “three-way” (male call–female answer–male reply) sequences.
3. Male calls were more diverse and complex than either female answers or male replies, and signals of sexes and duet pattern were species–specific fixed action behaviors.
4. During duetting, males searched for stationary females.

Further studies from the 1980s to the present, mostly by K.W. Stewart and students, using pairing experiments and playback experiments with computer-modified male calls to live females, and other experimental protocols, have expanded our knowledge mainly in discovery of:

1. Additional methods of signal production by males, other than percussion.
2. Additional complex male signal patterns, seemingly derived from ancestral monophasic signals by changes in number of beats, rhythm, amplitude modulation and phasing or grouping of signal beats.
3. Duetting patterns additional to call–answer sequences, including grouped and “symphonic” male–female exchanges.
4. Conspecific characters and informational content of male calls as recognized by females (Zeigler and Stewart, 1986; Stewart and Maketon, 1990).
5. That communication distances may be up to 8 m on a suitable substrate (dry woody stems), and
6. That vibrational calls on a resonant substrate can be communicated to females sitting also on a resonant substrate over short distances of 10 to 200 cm (Stewart and Zeigler, 1984).

Since the early quantitative studies of Rupprecht (1967) and Zeigler and Stewart (1977) there have been major advances in technology ranging from recording on cassette tapes and analyzing signals with oscilloscopes to the current digital recording on minidisks and analyzing with computer sound software. Sandberg and Stewart (2003) addressed the question of whether this change in technology had substantially affected the accuracy of signal parameter description, and therefore capability to compare favorably historical descriptions of particular species with current ones from the same or different populations. They found that signals of five species recorded and analyzed with old and current technology were favorably comparable, and suggested that precise duplication of signals of a species over time cannot be expected due to extraneous sources of variation, such as temperature and light conditions, at recording, instrument calibration integrity, population (dialect) variation, age of adults recorded (Zeigler and Stewart, 1985) and variation in number of signals of pairs successfully recorded.

## **SIGNALING METHODS**

Males produce their vibrational calls by four basic methods: percussion, scratching (scraping), rubbing and tremulation. Percussion, as the name implies, involves tapping on substrate with the apical-ventral portion of the abdomen; the body contact surface may be either the unmodified sternum or variously modified abdominal appendages or surfaces such as vesicles, lobes, knobs or

hammers (Stewart and Maketon, 1991). Males without such specialized structures all produce percussion or tremulation calls. Scratching (scraping) involves a short drag of the abdomen as it contacts the substrate, producing a raspy sound on resonant substrates, and rubbing involves a prolonged percussion stroke always with the textured ventral surface of a knob or hammer. The textured surface may be ridged or papillous. We have described this unique vibration-producing behavior as an abdominal-substrate stridulation, and on a resonant substrate it produces a squeaking sound. So far as presently known, females normally produce their answering signals by percussion (or only in Chloroperlidae by tremulation), without specialized structures other than possibly the subgenital plate.

## SIGNAL COMPLEXITY AND PATTERNS

Male call signals and patterns vary greatly among different taxa in diversity and complexity (Stewart, 1997, 2001), probably because they contain the parameters that convey to females specific male identity. The basic types of calls include:

1. Simple, percussive monophasic calls with approximately even interbeat time intervals and little amplitude modulation (Figure 12.1).
2. Calls of slightly changed and intermediate complexity having variable length, number of beats, and rhythm of interbeat time intervals (examples Figure 12.2, Figure 12.3). These are common types of calls, represented by numerous species in all nine arctoperlarian families, with two to 40 drumbeats and 13 to 3350 msec interbeat intervals.
3. Diphasic percussive calls having two phases, each with several beats of different number and different interbeat intervals and rhythms (examples Figure 12.4, Figure 12.5).
4. Grouped calls with percussive bursts, each of few beats and variable intraburst time intervals (examples Figure 12.6, Figure 12.7, Figure 12.8).
5. Scratch or rub calls of one to seven strokes of variable duration, amplitude rhythm and inter-stroke intervals (examples Figure 12.9, Figure 12.10).
6. Tremulation calls of vibrations produced in plants by pushup — or forward–backward rocking motion of the whole body (Alexander and Stewart, 1997), without striking the substrate (example Figure 12.11).

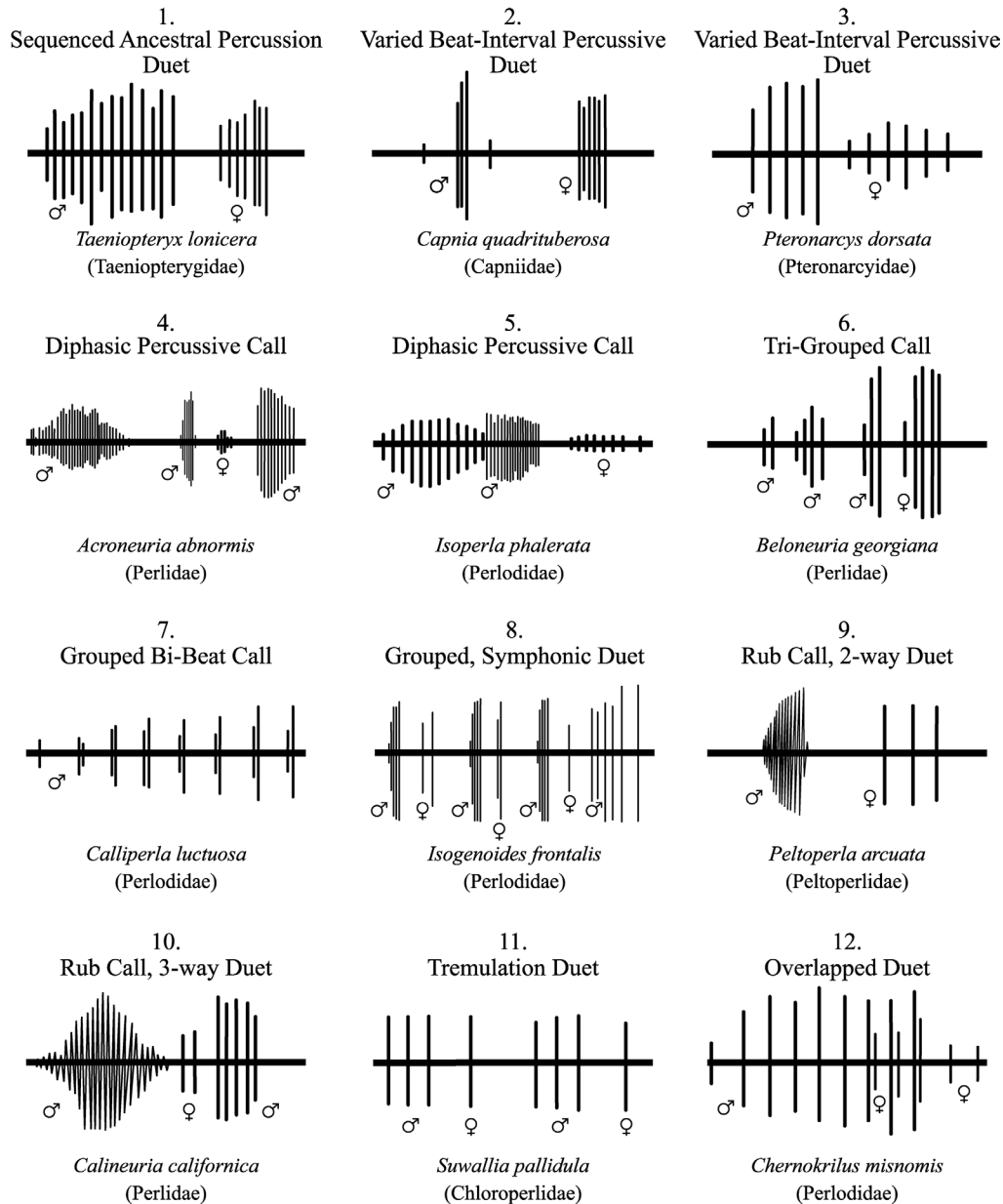
Stewart and Maketon (1990) showed experimentally with five species representing ancestral and derived duet patterns that the critical information content of male calls that females respond to are:

1. A critical minimum threshold of beat or rub number.
2. A discriminate window of beat intervals.
3. Other specific parameters such as the bi-beats of *Calliperla luctuosa*.

Female response signals are always relatively simple, percussive, typically monophasic and usually of few beats (Figure 12.1 through Figure 12.6, Figure 12.8 through Figure 12.10), probably because they need to convey to males only that they have recognized his specificity, and to signal their now stationary location. Notable exceptions in female answers are:

1. The interspersed grouped answers within calls of some species with grouped calls, leading to a symphonic interchange (Figure 12.8).
2. Tremulation answers to males with tremulation calls (Figure 12.11).

The shortness of female answers is not only attributable to the fact that they do not need to convey complex information, as in the male, but also probably to reduce their vulnerability to potential vibration-detecting predators such as spiders. Females remain stationary only for a certain time,

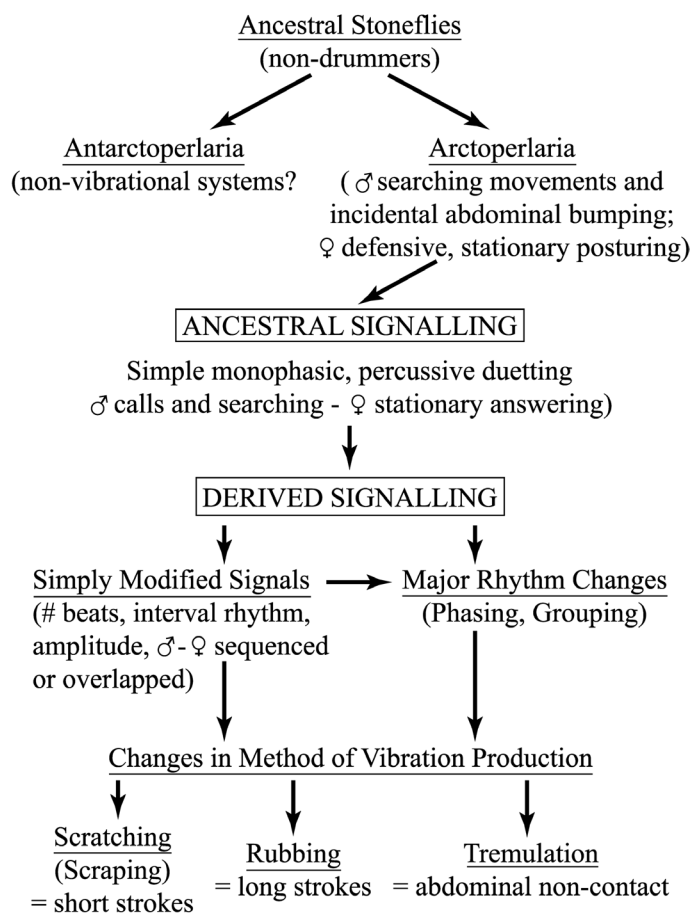


FIGURES 12.1–12.12 Diagrams of stonefly call and duet patterns.

while they presumably are able to measure male search fitness. The only prolonged female answers occur in females of large Perlidae that are larger than the prey threshold of most spiders.

### DUET PATTERNS

Duets are typically either repeated sequences of “two-way” conversations (male call–female answer) (Figure 12.1, Figure 12.6, Figure 12.10), or “three-way” ones (male call–female answer–male reply), or symphonies of grouped calls interspersed by grouped answers (Figure 12.8). In the sequenced duets, the female answer may follow the call after a variable latent time period (Figure 12.4, Figure 12.5, Figure



**FIGURE 12.13** Drumming evolution paradigm (after Stewart 2001).

12.10) or be overlapped with the latter portion of the call (Figure 12.12). A unique pattern, discovered in only one species, *Paraperla wilsoni* Ricker (Stewart et al., 1995), involves a long male call of 101 mode beats, with the female answer of seven mode beats fully embedded within the latter two-thirds of the call.

## EVOLUTION OF STONEFLY DRUMMING

There is obviously no fossil record for vibrational communication, so formulation of an evolutionary scenario of the behavior must rely on the patterns revealed from extant species. Out-group comparisons with the Grylloblattodea, other orthopteroid groups and the stonefly suborder *Antarctoperlaria* (Maketon, 1988) indicate that ancestral stoneflies were nondrummers, and that the *Arctoperlaria* have adopted and refined vibrational communication as an integral part of their mating system. This is further reinforced by the fact that special ventral abdominal structures have not appeared in males of the *Antarctoperlaria*. The first “drumming” in *Arctoperlaria* presumably resulted from the accidental bumping of the unmodified abdomen of males, while searching for females, thus evoking the defensive response of females becoming motionless and stationary. Selection by enhanced finding success of females progressively reinforced the male bumping into a behavioral action, and a similar sequence in females followed, until relatively simple percussive, monophasic duetting became the typical ancestral communication (Figure 12.1, Figure 12.13). This, along with active males searching and stationary female response became the ancestral mating system. Out-group comparisons among *Arctoperlaria* families (Maketon and Stewart, 1988; Maketon et al., 1988) indicate that species-specificity and behavioral isolation were then derived from the ancestral system, and are represented in extant species patterns as:

1. Ancestral (retained).
2. Simple modifications of ancestral number of beats, overlapping of male–female duet, altered beat interval rhythms and amplitude modulation in both male and female signals.
3. Major rhythm changes in male calls by phasing or grouping of beats.
4. Changes in signal production methods, from percussion to scraping or abdominal substrate stridulation (rubbing), or in rare cases tremulation (Figure 12.13).

It is assumed here that changes of male signals leading to specificity required concurrent changes in the females capacity to recognize them. The result, from study of a large sample of extant stonefly species, is the exciting, highly derived and complex system of vibrational communication in Arctoperlaria, representing one of the most advanced such systems known in insects.

## FAMILY PATTERNS

Table 12.1 shows a generalized summary of known drumming pattern diversity by arctoperlarian groups and families, relative to absence or presence of specialized drumming structures, signaling methods and pattern polarity. Families appear to fit the paradigm of Figure 12.13. in five basic ways:

1. The euholognathan families, Capniidae and Taeniopterygidae, and the systellognathan family, Pteronarcyidae, have largely retained the ancestral pattern of percussive, monophasic signals, with only enough change in beat number and interval rhythm and partial transition toward specialized vesicles, to derive species specificity (behavioral isolation). The several species of Taenionema, Doddsia, and Oemopteryx that we have tested suggest the possibility that some Taeniopterygidae do not drum.
2. The euholognathan families Leuctridae, and Nemouridae have retained percussion and derived specialized vesicles along with major modifications in percussion rhythm such as phased male calls or call burst groups.
3. The Perlodidae have largely retained percussion, and in some species the more ancestral model of monophasy, but numerous species have derived specialized grouped calls with interspersed grouped answers leading to symphonic duetting.
4. The most specialized calls that involve abdominal contact are made by males rubbing the substrate with a ventral knob (Peltoperlidae) or hammer (Perlidae); calls of the various species we have studied produce one to seven rubs, always answered by females with percussion. *Acroneuria evoluta* Klapálek may represent an evolutionary link in this percussion-to-rubbing method, since some males produce both phases of their calls by percussion, but other males produce phase one by rubbing and phase two by percussion (Maketon and Stewart, 1984).
5. It appears that only some species of the family Chloroperlidae have derived tremulation. *Siphonoperla montana* Pictet and *Siphonoperla torrentium* Pictet produce signals on plants by rapid, noncontact vertical movements of the abdomen (Rupprecht, 1981), and *Suwallia pallidula* (Banks) males produce a three-stroke tremulation signal by forward–backward rocking motions of the whole body (Alexander and Stewart, 1997). Over the years, we have tested several species of *Sweltsa* and other chloroperlid genera, and never detected drumming through recording, possibly missing the possibility of tremulation.

## MATE-SEARCHING

We began approaching the question of searching behavior in relation to drumming in the later 1990s. We had learned quite a lot about the encounter site aggregation, calling and duetting components of the arctoperlarian mating system, but very little about the important steps of ranging and localized search, whereby a male utilizes the vibrational information from a female to find her. Experiments, observations

**TABLE 12.1**  
**Summary of Drumming Pattern Diversity of the 9 Arctoperlarian Families**

Group/Family	Number Species	Specialized ♂ Abdominal Drumming Structures	Signaling Method	Evolutionary Scale Range of ♂ Calls
<b>Euholognatha</b>				
1. Capniidae	4	none or vesicles	percussion	ancestral to slightly derived change of beat number and intervals
2. Leuctridae	6	vesicles	percussion	ancestral to derived diphasic bursts or groups
3. Nemouridae	4	vesicles	percussion	all derived; bi-grouped, diphasic or diphasic bursts
4. Taeniopterygidae	7	none or vesicles	percussion	ancestral to slightly derived change of beat number and intervals
<b>Systemlognatha</b>				
5. Chloroperlidae	6	none or lobes	percussion and tremulation	ancestral to diphasic
6. Peltoperlidae	13	knobs	percussion and rubbing	ancestral to diphasic
7. Perlidae	21	none or hammers	percussion or rubbing	ancestral, diphasic or grouped (transitional percussion & rubbing in <i>Acroneuria evoluta</i> )
8. Perlodidae	54	none or lobes	percussion and scratching	ancestral to derived bi-grouped, grouped or bi-beat grouped
9. Pteronarcyidae	8	none	percussion	ancestral to slightly derived change of beat number and intervals

and videotaping were conducted with four species, selected as examples of different encounter site conventions: “ground scramblers on flat or contoured substrates, and bushtoppers and treetoppers on linear or branched live or dead plant parts. The assumption was that the currently arrived-at system of any species should combine effective intersexual signaling with an efficient search modality. First experiments with *Pteronarcella badia* (Hagen) (Abbott and Stewart, 1993) on a flat, gridded surface showed that the average find time for pairs engaging in strong, continuous duetting was significantly shorter than those for nonduetting or anomalously duetting pairs, and that the male localized search pattern was a triangulation, aided by the vibrational cues of answering females. Alexander and Stewart (1996a) videotaped a ground scrambling population of *Claassenia sabulosa* (Banks) with red light at night, and found that males drummed and searched near the shoreline of the Gunnison River, Colorado, on stones that protruded above the shallow marginal water surface. They circled the stones, and then scrambled across the highest and ridged surface of the individual rock encounter sites that were female

emergence sites. Alexander and Stewart (1996b) videotaped pairs of the treetopper *Perlinella drymo* (Newman) on a dead, branched tree limb, and found that duetting increased male searching activity, influenced their directional movements, and decreased the required find time for females, in contrast to nonduetting pairs. Males moving progressively up the limb toward a female, placed high on one of its branches, never called at branch bifurcations, but instead called at a position up the main stem or on the branch just above each fork. Therefore he was able to determine whether an answer came from out on that branch or from behind him, meaning she was further up on the limb. This process was repeated at each fork until he arrived at the branch leading directly to the answering female. The male in most trials found females within 10 min. Finally, Alexander and Stewart (1997) videotaped the tremulating chloroperlid *Suwallia pallidula* Banks in the field, and found that males flew during the afternoon on sunny days and landed on riparian alder where they began calling on stems and leaves with their typical three-stroke signal. Females answered with a typical one-stroke signal, moved to the petiole-leaf junction and became stationary. This position ensured that the male did not have to search entire leaf surfaces, so he searched only the petioles and leaf bases as they were encountered, while intermittently duetting with the female, until she was found. Ensuing copulation occurred on the upper surface of leaves. Therefore, all four species conformed to the proposal that search patterns relate to the type of substrate at encounter sites (Stewart, 1994). The patterns were described as “fly-tremulate-search” for *Suwallia*, “rock to rock” for *Claassenia*, and “fly-run-search” for *Perlinella*.

Vibrational signaling has become a viable evolutionary strategy for Arctoperlaria, offering effective information for a searching caller (male) to locate a responding answerer (female). Male calls contain specific information that allows a female to use an apparently selectively arrived-at neuronal capacity to respond only to a conspecific mate, and possibly to a more fit conspecific mate. Females of *Pteronarcella badia* can discern the search-time fitness of particular males by remaining stationary only for a selectively allocated predator-safe time. If this time is not met, she moves to another position potentially to respond to calls of other males (Abbott and Stewart, 1993). Although there is little research to support it, directional location of a vibrational signal producer is probably determined by the differential time delays in reception of vibrational waves by the sensors of a receiver planted tarsi. In scorpions, direction can be determined by integrating time delays as small as 0.2 msec, received by the subgenual organs of the different legs (Brownell and Farley, 1979).