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The Drumming of *Isoperla pallida* Aubert and *Guadalgenus franzi* (Aubert) (Plecoptera, Perlodidae), and Review and Evolutionary Considerations of Southern Iberian Peninsula Perlodidae

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ABSTRACT—The drumming calls of two perlodid species from Southern Spain (Sierra Morena, Jaén) are analyzed and described. Nineteen calls from one male of *Guadalgenus franzi* were recorded, showing a simple call pattern composed of two beats with an average duration between them of 184.32 msec (range: 165–227). This is the simplest call pattern yet discovered in the Plecoptera. The female of this species also presented a simple call consisting of only one beat. The male of *Isoperla pallida* showed an ancestral call pattern, more simple than the other Iberian *Isoperla* species (*I. grammatica, I. nevada* or *I. curtata*, all of them with multiphasic drumming calls or *I. bipartita* with a notably different model consisting of rubbing). Calls from six different males (the female did not drum) consisted of an average of 65.94 beats (range: 25–83) with a duration average of 1462.69 msec (range: 548–1835), regularly repeated with intervals with a duration average of 22.27 msec (range: 17–30). With this study, the vibrational calls of all the Perlodid species from the Southern Iberian Peninsula, except *Perlodes microcephalus* and *Besdolus bicolor*, are known. Moreover, it presents the first record and description of the call of the monospecific genus *Guadalgenus*. An evolutionary approach to the vibrational communication diversification in the perlodids of the Southern Iberian Peninsula is presented, showing a complexity graduation from the more simple drumming calls (shown by *Hemimelaena flaviventris* and *G. franzi)* to the rubbing call of *I. bipartita* and intermediate drumming calls of other *Isoperla* species, consistent with the drumming evolution paradigm of Stewart (2001) .

Key Words: Vibrational communication, drumming, stonefly, Perlodidae, Plecoptera

INTRODUCTION

Intersexual communication using low-frequency, substrate-borne vibrations is a little explored mode of communication in arthropods (Stewart, 1997, 2001). Intersexual vibrational communication appears to have evolved its most complex form in the Arctoperlarian Plecoptera as a mechanism for mate encounter and pair forming (Stewart *et al*., 1995; Stewart, 1997). Stoneflies produce vibrational signals by percussion (drumming), rubbing (or scraping), tremulation (abdominal or body jerking), or combinations of these methods (Stewart, 1997). Vibrational calls are genetically programmed and can be considered as a fixed-action, species-specific behavioral pattern (Szczytko and Stewart, 1979a, 1979b), useful for inferring phylogenies within the order (Stewart and Zeigler, 1984). Particularly interesting, is the study of the effects of evolutionary pressures in the diversification of vibrational calls among species (inside the same genus and between related genera) from the same family sharing the same geographical distribution area.

Stonefly drumming has been known from the XIX century (Newport, 1851), and was first quantified some decades ago by Rupprecht (1968). Since then, the vibrational calls of about 160 world species have been studied, principally in North America (Stewart, 1994) and, to a lesser extent, in Europe and Japan.

Nine species of Perlodidae exist in the Southern Iberian Peninsula: *Besdolus bicolor* (Navás, 1909), *Guadalgenus franzi* (Aubert, 1963), *Perlodes microcephalus* (Pictet, 1833), *Hemimelaena flaviventris* (Pictet, 1841), *Isoperla bipartita* Aubert, 1962, *I. curtata* Navás, 1924, *I. grammatica* (Poda, 1761), *I. nevada* Aubert, 1952 and *I. pallida* Aubert, 1963 (Sánchez-Ortega and Tierno, 1996).

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G. franzi and *H. flaviventris* represent monospecific stonefly genera, the first one with a Iberic distribution and the second one with a Iberic-North African distribution (Sánchez-Ortega and Alba-Tercedor, 1987). The drumming calls of the *G. franzi* are unknown. *H. flaviventris* drumming calls were described by Tierno de Figueroa et al. (1998). *P. microcephalus* is widely distributed European species, but is a relict one in the South of Iberian Peninsula, where it is only present in scarce number in the Sierra Nevada (Sánchez-Ortega and Alba-Tercedor, 1987), and *B. bicolor* is an Iberian endemic species, scarcely distributed by Central Spain, with a punctual cite in the South (Zwick and Weinzierl, 1995). The drumming calls of these two species have not been previously recorded. *Isoperla* is an Holarctic Plecoptera genus with a high number of species. Four Iberic endemic species are present in the Southern Iberian peninsula: *I. bipartita*, *I. curtata*, *I. nevada* and *I. pallida* (Sánchez-Ortega and Alba-Tercedor, 1987). The drumming calls of the first three of them have been studied (Tierno de Figueroa and Luzón-Ortega, 2002; Tierno de Figueroa et al., 2000; Tierno de Figueroa and Sánchez-Ortega, 1999). Another *Isoperla* species, *I. grammatica*, with a wide European distribution is also present (Sánchez-Ortega and Alba-Tercedor, 1987). The drumming call of this species has been studied in other parts of its distribution area: Central Europe by Rupprecht (1968, 1969, 1983, 1984) and Northern Spain by Membiela and Vidal (1998).

The flight period of all the perlodid species from Southern Iberian Peninsula is spring-summer, with maximum peaks from May to July, with slight variations in relation to the altitude and latitude (Sánchez-Ortega and Alba-Tercedor, 1987). Only, in the case of *I. nevada* and *I. grammatica* in Sierra Nevada (S Spain) a temporal segregation (and also a spatial one) has been detected with a slight seasonal difference between their capture maximums, later in *I. nevada* (Tierno *et al.*, 1994).

In the present paper, we describe for the first time the drumming calls of *G. franzi* and *I. pallida* and review the vibrational communication of the seven Perlodidae species from the Southern Iberian Peninsula (all of them with hammer or ventral lobe, see Rupprecht, 1976, and with a size oscillating 7–12 mm for *Isoperla* genus, 10–14 mm for *H. flaviventris* and 12–18 mm for *G. franzi*, according with the species descriptions), whose calls are known in light of the drumming evolution paradigm proposed by Stewart (2001), in which Arctoperlarian stoneflies represent the epitome of evolution of vibrational communication. Their ancestral signals were monophasic volleys of evenly spaced drumbeats. Derived signals to achieve species-specificity and possibly enable sexual selection or some measure of reproductive fitness as involved modification of the ancestral form toward complex signals through: changes in the rhythmic patterning of calls, patterns of male-female duetting, and/or changes in the method of signal production such as rubbing or tremulation.

MATERIALS AND METHODS

The specimens of *Guadalgenus franzi* and *Isoperla pallida* were collected in the Martín Pérez seasonal stream from the Sierra Morena (Jaén, Spain), on May, first, 2001. The specimens were transported individually to the laboratory in bottles kept in an ice chest. The drumming signals were recorded over the following four days between 15:30 to 18:00 local time at a temperature between 23 and 26°C, and under natural light entering the room through a window.

Male calls of the two species were recorded by placing individuals in a 2.5×2.5×2.5 cm. bottomless plastic box resting directly on a 7.5 cm diameter, 8 ohm, 0.8 W speaker connected to a Sony CFS-W350L model cassette-recorder. We placed the female close to the male in a separate bottomless plastic box similar to the one containing the male, permitting the pair to communicate with each other with vibrations. Previously to the record, females of both species never were observed drumming when they were in the bottles, such it occurs with the males. Recorded calls were displayed and measured using the IBM-compatible computer program Creative Wave Studio for Windows 1993.

RESULTS

Only a male and a female of *Guadalgenus franzi* were studied. A total of 19 drumming calls from the male (Fig. 1) was obtained, showing a simple call pattern (Stewart, 1997, 2001). The vibrational call was composed of only two beats with an average duration between them of 184.32 msec (range: 165–227; SD=17.11; N=19). This call is simpler than the one described for *Hemimelaena flaviventris* (Tierno de Figueroa *et al.*, 1998), and the simplest yet discovered in Plecoptera.

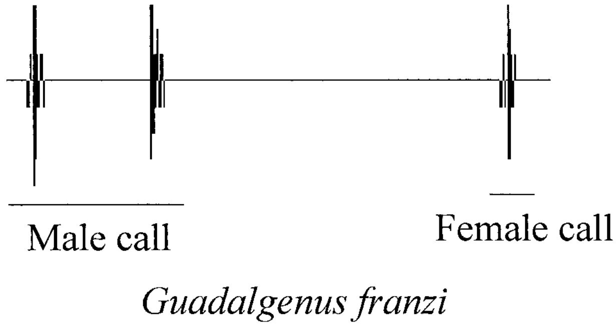

Fig. 1. *Guadalgenus franzi* male and female drumming call.

The female of this species also presented a simple call consisting of only one beat (N=8). Thus, the female call is also simpler than the one presented by *H. flaviventris,* composed of 1 to 3 beats (Tierno de Figueroa *et al.*, 1998), and similar to the one-beat answers of the North American species *Perlinella drymo* (Newman, 1839) (Zeigler and Stewart, 1977).

It was not observed overlapping between male and female calls. Intervals between male call and female answer were very variable and oscillated between 215 msec. and more than 4000 msec. Moreover, in one case the female repeated the answer twice (with intervals of 376 and 775

Fig. 2. *Isoperla pallida* male drumming call.

msec.).

Isoperla pallida (Fig. 2) also showed an ancestral call pattern (Stewart, 1997) with simple modifications of percussion increasing the beat number (Stewart, 2001), extremely long (only surpassed by the *I. nevada* call) and simpler than other studied Iberic *Isoperla* species. Thus, *I. grammatica*, *I. nevada* and *I. curtata*, present multiphasic drumming calls (Membiela and Vidal, 1998; Tierno de Figueroa and Sánchez-Ortega, 1999; Tierno de Figueroa *et al.*, 2000) and *I. bipartita,* exhibit a notably different vibrational communication pattern consisting in rubbing (Tierno de Figueroa and Luzón-Ortega, 2002). The male drumming call of *I. pallida* consisted of 65.94 beats (range: 25-83; SD=15.5; N=16) with a duration of 1462.69 msec (range: 548-1835; SD=352.56; N=16) regularly repeated with intervals with a mean value of 22.27 msec (range: 17-30; SD=1.74; N=974), obtained from six different males (from more than 10 studied specimens).

Although five females of *I. pallida* were also located close to the males in separate plastic box, they never drummed.

DISCUSSION

It has been pointed out that intersexual vibrational calls are species-specific (Szczytko and Stewart, 1979a, 1979b) and could play an important role as an isolating reproductive mechanism (Tierno de Figueroa and Sánchez-Ortega, 1999). This idea could be supported by the fact that from the nine perlodid species present in the Southern Iberian Peninsula, almost all of them can share habitat. Thus, *I. curtata* has been collected by us from the same locality and with the same flight period as *H. flavinentris, I. pallida* and *G. franzi.* The same thing occurs with *I. curtata* and *I. bipartita* in other streams and potentially all of them can share habitat with *I. grammatica* (Sánchez-Ortega and Alba-Tercedor, 1987). *I. grammatica* and *I. nevada* seem to have a spatial and temporal segregation between them (Tierno *et al.*, 1994). *P. microcephalus* and *B. bicolor* present a punctual distribution in Southern Iberian Peninsula (Sánchez-Ortega and Alba-Tercedor, 1987; Zwick and Weinzierl, 1995).

Rupprecht (1969, 1983) noted that sympatric species of *Isoperla* showed more different call models than the allopatric ones. This idea could be supported by the call analysis of studied species in Southern Iberian Peninsula (Table 1). In fact, we have detected a gradual complexity in the vibrational calls of all these perlodids. *H. flaviventris* and *G. franzi* are monospecific genera and show call patterns deviating only by number of beats and intervals from ancestral patterns (Stewart, 2001) (Fig. 3). In other genera, such as *Isoperla*, where some species coexist, the call must be subject to selective pressures related with its role as an isolating reproductive mechanism.

Fig. 3 shows a theoretical evolution of Southern Iberian male perlodid species: increasing or decreasing beat number, changes of intervals or rhythm inside a sequence, division of calls into phases, and derived signal production by rubbing. This model is consistent with the evolution paradigm of Stewart (2001). These data (Table 1; Figs. 1–3) corroborate the previously proposed hypothesis that in male Arctoperlarian stoneflies, sexual selection acts to favor derivation from the ancestral monophasy to calls with altered (more or fewer) beats, distinct interbeat intervals (often phased and/or grouped) and/or changed method of vibration production such as with *I. bipartita* rubs (Table 1; Fig. 3). In many cases, these changes lead to calls that are more complex than ancestral ones.

Stewart *et al.* (1995) indicated that seven species of stoneflies in different families and genera have derived what might be considered “evolutionarily converged” calls into 3-beat signals. They hypothesized that this trend toward deriving such 3-beat calls (particularly in the families Peltoperlidae, Perlodidae and Perlidae) might represent a minimal amount of information (two interbeat time intervals) necessary for female recognition of potential calling conspecific mates. If correct, 3-beat calls would represent an evolutionary end-point of derived reduction of beats, with their corresponding interval alterations, of ancestral signals that could achieve communicative isolation. They pointed out that the intervals of the seven species known to have 3-beat calls were species-specific, without overlap, and that none of them was known to co-occur in time and place. Our discovery here of the 2-beat call of *G. franzi* now demonstrates that only a single time interval is required, at least for females of some species, for female recognition. And, if time intervals are important recognition parameters in percussion-produced signals, as indicated by computer-simulation models (Stewart and Maketon, 1990), then this 2-beat call of *G. franzi* would represent the simplest possible percussion-produced call that could be effectively derived from monophasic ancestral signals in a drumming mode of communication.

One-beat answers of females, such as here in *G. franzi*, are possible because such a simple female answer conveys information to the male only that she is responding with location to her recognition that he is a conspecific caller.

Table 1. Vibrational call description of seven Southern Iberian Perlodid species. Seq= sequence; Ph= phase; N= number; T= time; Int= interval. * For *I. grammatica*, we have considered the Membiela & Vidal (1998) (*) description based in Spanish *I. grammatica* specimens, but Rupprecht (1968, 1984) (**) pointed a highly variable drumming call for this species in Central Europe.

	males								**females**		
Species	**Call production**	**N. seq/ call**	**N. ph/ seq**	**T. seq & ph (msec) Mean (range)**	**N. beats or rubs/seq & ph Mean (range)**	**Beat Int. reduction**	**Seq Int. Mean (range)**	**Final beat**	**Call production**	**N. beats Mean (range)**	**Beat Int Mean (range)**
G. franzi	Drumming	1	1	182.32 (165–227)	2	–	–	No	Drumming	1	–
H. flaviventris	Drumming	1	1	204.64 (176–261)	3	Yes	–	No	Drumming	1.41 (1–3)	100.91 (68–227)
I. bipartita	Rubbing	6.73 (3–10)	1	257.74 (24–594)	3.11 (1–4)	Yes	180.75 (142–290)	No	Drumming Rubbing	1 beat + 1 rub	479.09 (258–544)
I. curtata	Drumming	1	2	792.9 (228–1312) Phase I: 649.9 (149–1140) Interphase: 17 (13–24) Phase II: 118.2 (37–185)	17.3 (8–27) Phase I: 9.5 (5–17) Phase II: 8.1 (3–12)	Phase I: yes Phase II: No	–	No	Tremulation?	–	–
I. grammatica	Drumming	6.70 (5–8)* 14 (2–15)**	2	123 (25–334)* Phase I: 65 (25–122)* Phase II: 58 (0–212)*	7.48 (2–11)* Phase I: 2* Phase II: 5.48 (0–9)*	Phase I: yes* Phase II: No*	173.6 (68–469)*	No*	No detected	No detected	No detected
I. nevada	Drumming	2.73 (1–5)	2	1595–4028 **Seq I** Phase I: 3446 Interphase: 19 Phase II: 563 **Seq II-V** Phase I: 853–1089 Interphase: 23–36 Phase II: 719–827	**Seq I** Phase I: 43.3 Phase II: 54.9 **Seq II-V** Phase I: 13–22 Phase II: 50–62	No	134–236	Yes (1–12)	No detected	No detected	No detected
I. pallida	Drumming	1	1	1462.69 (548–1835)	65.94 (25–83)	–	–	No	No detected	No detected	No detected

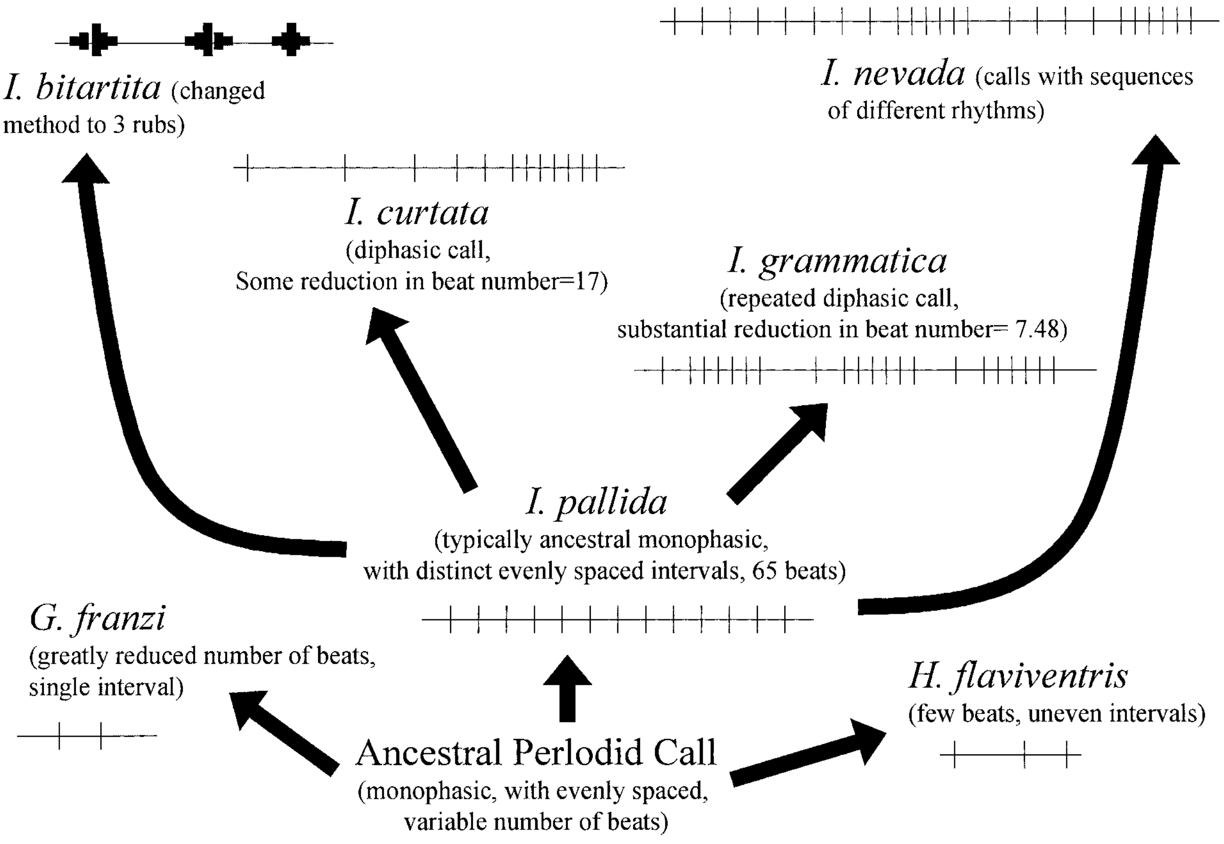

Fig. 3. Possible evolution of vibrational call complexity in Southern Iberian Perlodids.

She is not required to give more complex information on her species identity, and in fact such derivation toward simpler answer is less energy demanding, thus saving resources for egg-yolking and oviposition activity. The duet descriptions (Table 1) show for regional species a simplification of female answer (*H. flaviventris* 1-3 beats; *G. franzi* 1-beat) or change in method of answering (*I. bipartita* 1 beat + 1 rub; *I. curtata* possible tremulation). In other species, no answer has been successfully detected or recorded.

In Central Europe, where *Hemimelaena* and *Guadalgenus* genera are not present, there are some *Isoperla* species (such as *I. rivulorum* in Rupprecht, 1969, or *I. difformis* in Rupprecht, 1981) whose males show a similar call pattern to them, supporting the importance of the reproductive isolating mechanism among sympatric species. Likewise, in the pointed Central Europe species, female answers have been detected that show relatively similar patterns to those of *Hemimelaena* and *Guadalgenus.*

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