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Intraspecific and interspecific variation in drumming signals in the genus *Capnioneura* (Plecoptera: Capniidae)

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The male drumming calls of four species of the genus *Capnioneura*, and for the first time, the female answer signal from one species of this genus are described. Only the male call of *C. mitis* from a southern Iberian Peninsula is known. In the current study, the male calls of three additional *C. mitis* populations from two different mountain drainages and the male calls of *C. gelesae*, *C. libera* and *C. petitpierreae* are described and analysed. The calls were near-ancestral and percussive signals with variable numbers of beats and approximately constant, monophasic beat intervals. The mean interbeat intervals were species specific, ranging from 250 to 1500 ms. The *C. mitis* female answer interbeat intervals were similar to the call but composed of 3–4 beats. Intraspecific and interspecific variation is discussed and these results support the hypothesis that stonefly drumming plays an important role as a reproductive isolating mechanism.

Keywords: stoneflies; *Capnioneura gelesae*; *Capnioneura libera*; *Capnioneura mitis*; *Capnioneura petitpierreae*; vibrational communication

Introduction

Intersexual vibrational communication in Plecoptera, mainly produced by drumming, is the most important mode to bring the sexes sufficiently close enough together to accommodate mate-finding (Stewart and Sandberg 2006). The importance of drumming, or communication used in mate location, has been studied under laboratory conditions using an artificial substrate (Abbott and Stewart 1993) and a natural substrate (Alexander and Stewart 1996). The role of species-specific drumming signals used as a reproductive isolation mechanism has been proposed in Plecoptera that drum, and has been used for resolving systematic questions (Maketon and Stewart 1984; Stewart and Zeigler 1984b; Tierno de Figueroa and Sánchez-Ortega 1999). The ability of an unmated female to recognise a call signal from a male of the same species appears to be based on the interbeat intervals (Stewart and Zeigler 1984a; Zeigler and Stewart 1985). Of particular interest is the hypothesis that the effects of evolutionary pressures on the

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diversification of vibrational calls among related species (within the same genus and between related genera) sharing the same geographical distribution area are expected to have substantially different calls than those that do not coincide in the same geographical area (Tierno de Figueroa, Luzón-Ortega and Stewart 2002).

To support this hypothesis, calls of different species (and of different populations of a same species) of the genus *Capnioneura* Ris, 1905 are described and compared in this paper. Some of these species share the same distribution area, while others never inhabit together. *Capnioneura* is distributed in the West-Palaeartic region, from Caucasus to the Iberian Peninsula, including the Maghreb region. The genus includes 14 species, 11 of them present in Europe and six of them present in the Iberian Peninsula (Tierno de Figueroa, Sánchez-Ortega, Membiela-Iglesia and Luzón-Ortega 2003; Fochetti and Tierno de Figueroa 2006; Vinçon and Sivec 2011). Currently, the drumming call of only one species, *C. mitis* Despax, 1932 has been described from a population from Sierra Nevada (S Spain) recorded at two different temperatures (Tierno de Figueroa, Luzón-Ortega and López-Rodríguez 2009): the male call consisted of a highly variable number of beats (2–32) with interbeat intervals approximately constant along the call, but temperature dependent. At 13°C the mean interbeat interval was 1397 ms (SD = 50) while at 21°C it was 1139 ms (SD = 93). The interbeat interval call pattern exhibited by this species, as those of the majority of previously studied Capniidae species, was a near-ancestral percussive monophasic signal (Tierno de Figueroa et al. 2009).

Materials and methods

Adults of six populations belonging to four species of *Capnioneura* Ris were collected in the field from vegetation, stones or snow on the riverbanks:

- *C. gelesae* Berthélemy and Baena, 1984. Arroyo del Rey, Sierra Morena, Spain, 560 m a.s.l., UTM: 30S 455320 4247374, 24 November 2010, 3 males, Luzón-Ortega leg.
- *C. libera* (Navás, 1909). Arroyo Bodurria, Sierra de Baza, Spain, 1500 m a.s.l., UTM: 30S 517043 4129264, 3 January 2010, 6 males, 7 females, Luzón-Ortega and Tierno de Figueroa leg.
- *C. mitis* Despax, 1932. Río Gor, Sierra de Baza, Spain, 1820 m a.s.l., UTM: 30S 513197 4132961; 3 January 2010, 5 males, 5 females, Luzón-Ortega and Tierno de Figueroa leg.
- *C. mitis* Despax, 1932. Arroyo Bodurria, Sierra de Baza, Spain, 1500 m a.s.l., UTM: 30S 517043 4129264, 3 January 2010, 3 males, Luzón-Ortega and Tierno de Figueroa leg.
- *C. mitis* Despax, 1932. Arroyo de Fuente Grande, Sierra de Huétor, Spain, 1460 m a.s.l., UTM: 30S 458779 4130958, 15 March 2009, 3 males, 2 females, Luzón-Ortega leg.
- *C. petitpierreae* Aubert, 1961. Arroyo Bolaje, Sierra Bermeja, Spain, 660 m a.s.l., UTM: 30S 308355 4054330, 27 April 2009, 2 males, Luzón-Ortega, López-Rodríguez and Tierno de Figueroa leg.

The methods for recording and analysis of drumming signals in Tierno de Figueroa et al. (2009) were used. Drumming signal recordings were made the following two days after collection in the field, in a room with incandescent light and a constant

temperature of 20°C. As previously reported in this genus, call interbeat intervals can be influenced by the effect of ambient temperatures (Tierno de Figueroa et al. 2009). The calls were recorded using a microphone (100–16,000 Hz, 44 dB V/Pa) placed in contact with the paper of the recording chamber, and attached to a computer. Audacity v1.2.6 software (<http://audacity.sourceforge.net/>; Free Software Foundation, Boston, MA, USA) was used for recording and analysing the calls. For each call, the number of beats, interbeat interval, and total call duration were analysed and reported in milliseconds.

For *C. mitis* a Kruskal–Wallis ANOVA was used to determine if the drumming calls of individuals from different populations differed significantly. This non-parametric ANOVA was used due to data not being normally distributed (Kolmogorov–Smirnov $p < 0.05$).

Results and discussion

The number of male calls recorded for each species, mean interbeat intervals and signal durations are presented in Table 1. All the populations show a same near-ancestral percussive monophasic signal pattern consisting of a highly variable number of beats with interbeat intervals approximately constant along the call (e.g. Figure 1); however, the interbeat intervals were species-specific.

The mean interbeat intervals of two *C. mitis* populations from the same mountain system (Río Gor and Arroyo Bodurria, both from Sierra de Baza) were nearly identical but differed slightly from the Arroyo de Fuente Grande (Sierra de Huétor) population [Kruskal–Wallis $H(2, 100) = 16.104$, $p < 0.05$]. Additionally, the three populations from this study and the population from Sierra Nevada previously studied by Tierno de Figueroa et al. (2009) had overlapping mean interbeat intervals. The mean interval was 1397 ms at 13°C and 1139 ms at 21°C for the Sierra Nevada population, while it was 1449, 1454 and 1349 ms for the three studied populations.

Capnioneura libera had the highest mean beats per signal, $\bar{x} = 32.000 \pm 34.764$ (Table 1) and the shortest interbeat interval $\bar{x} = 256$ ms (Figure 2) which differed from *C. mitis*. Both species can coexist in the same stream (Sánchez-Ortega, Alba-Tercedor and Tierno de Figueroa 2002), as is the case in our study. The same situation occurs with *C. petitpierreae*, whose mean interbeat interval also differed from *C. mitis* (Figure 2), and also both species can coexist in nature (Sánchez-Ortega et al. 2002), although it is not the case in our study. Finally, although the mean interbeat interval of *C. gelesae* does not overlap with *C. petitpierreae*, they present values very close. Nevertheless, *C. gelesae* is geographically isolated from *C. petitpierreae* and it is the only one of these four species that has never been found coexisting with other *Capnioneura* species (Sánchez-Ortega et al. 2002). These data support the possible role of the male drumming calls acting as a reproductive isolating mechanism, leaving the female to recognise the male call to its species when other species of the same genera are present in the same area. This is particularly important considering that the four species have an overlapped flight period in the southern Iberian Peninsula that spans from the end of autumn to the beginning of spring (Tierno de Figueroa et al. 2003). Although the call patterns of *Capnioneura* species are much more homogeneous (only differing in mean interbeat intervals), this situation is similar to the one found in the genus *Isoperla* Banks, 1906 in the same geographical area (Tierno de Figueroa et al. 2002). Our data also support the

Table 1. Vibrational male call description of the studied *Capitoneura* spp. from Spain.

Species (stream)	Number of signals analysed	Interbeat interval (ms)		Call duration (ms)		Number of beats	
		Mean \pm SD	(min-max)	Mean \pm SD	(min-max)	Mean \pm SD	(min-max)
<i>C. gelesae</i> (A. del Rey)	5	689 \pm 7	(684-697)	10,614 \pm 6,180	(2784-18,127)	16.2 \pm 8.8	(5-27)
<i>C. libera</i> (A. Bodurria)	12	256 \pm 42	(197-340)	8417 \pm 9475	(986-29,085)	32.0 \pm 34.8	(5-104)
<i>C. mitis</i> (R. Gor)	7	1449 \pm 102	(1319-1622)	16,995 \pm 11,516	(6594-38,916)	11.7 \pm 6.8	(5-24)
<i>C. mitis</i> (A. Bodurria)	25	1,454 \pm 58	(1320-1539)	20,465 \pm 7708	(9241-38,485)	14.0 \pm 4.9	(7-26)
<i>C. mitis</i> (A. de Fuente Grande)	18	1,349 \pm 80	(1170-1452)	11,366 \pm 3616	(5581-17,182)	8.3 \pm 2.3	(5-12)
<i>C. pettipierreae</i> (A. Bolaje)	3	602 \pm 20	(582-622)	13,681 \pm 9050	(3610-21,133)	23.3 \pm 15.3	(6-35)

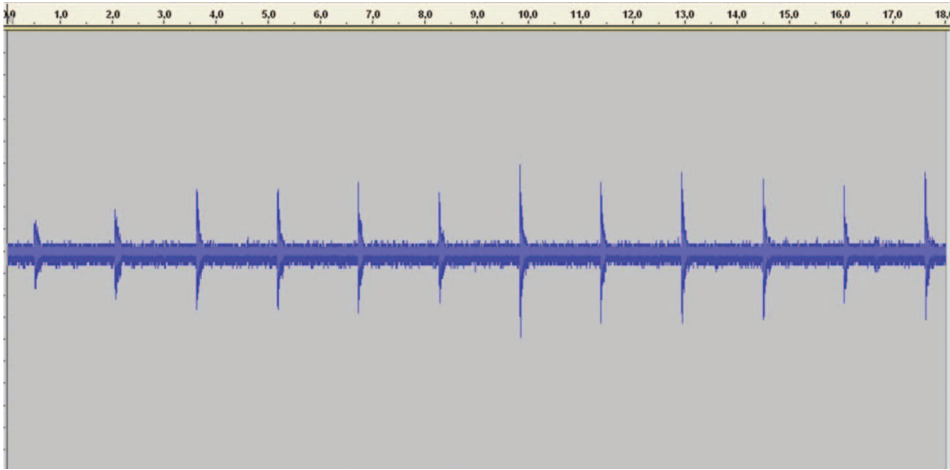


Figure 1. Sonogram of a male drumming call of *Capnioneura mitis* (in seconds).

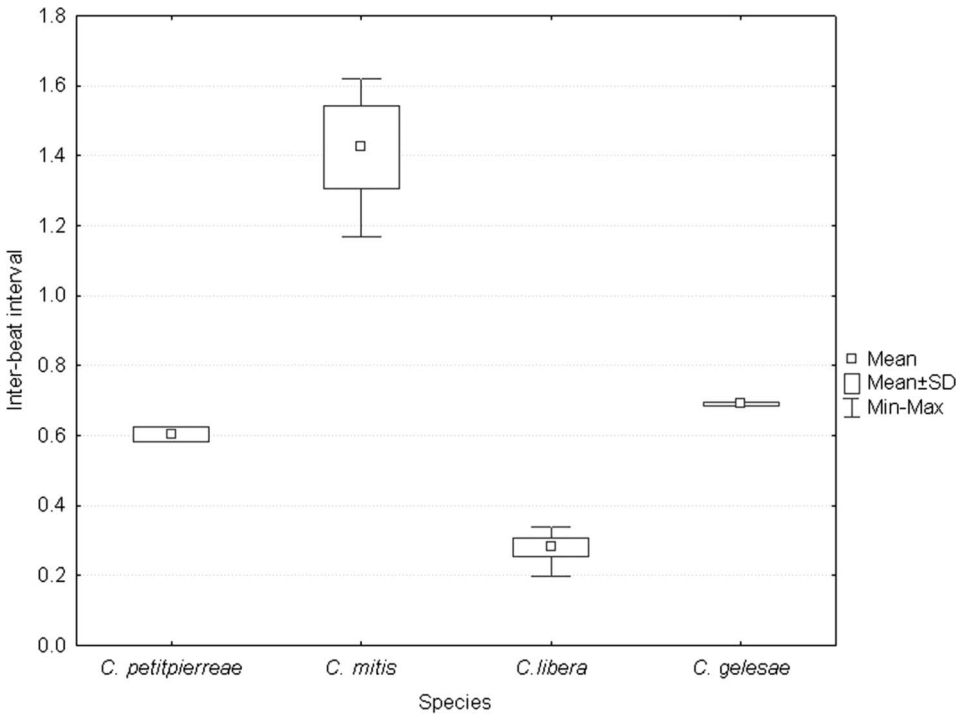


Figure 2. Graphical comparison of interbeat intervals of the studied *Capnioneura* species.

statements pointed out by Stewart and Zeigler (1984a) and Zeigler and Stewart (1985) that species recognition appears to be chiefly based on the beat intervals.

The female answer of *C. mitis* (population from Fuente Grande, $n = 13$ recorded answers) consists in a sequence of 3.692 ± 0.480 beats (from 3 to 4 beats), with an

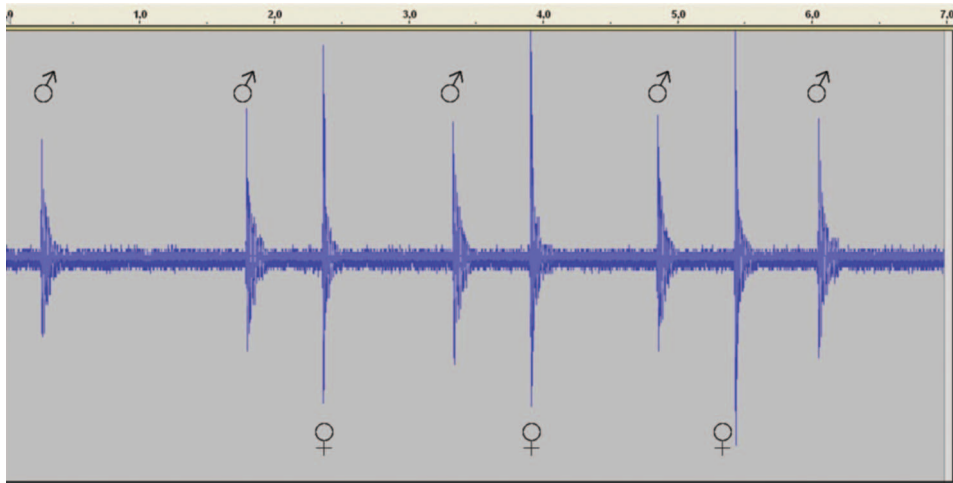


Figure 3. Sonogram of a duet of *C. mitis* from Fuente Grande (in seconds).

interbeat interval of $1130 \text{ ms} \pm 72$ (from 1006 to 1207 ms) and a total signal duration of $4204 \text{ ms} \pm 777$ (from 3018 to 4829 ms). The female answer begins after the first few beats of the male call (4.231 ± 1.481 beats; between the second and the eighth beat; $n = 13$) and they overlap with a regular interval between male and female beats of $622 \text{ ms} \pm 42$ (from 557 to 766 ms; $n = 48$) (Figure 3). When a duet is established, the male finishes the call with a single beat after the end of the female answer. However, this was not interpreted as a complex three-way exchange. The fact that the female starts to answer after a variable number of beats of the male call supports the idea that the interbeat interval of the male's call is the key to recognition by females (Stewart and Zeigler 1984a; Zeigler and Stewart 1985).

There were no new call signal types detected in this study for Capniidae. The male calls of the *Capnioneura* species studied, as well as those of other Capniidae except *Mesocapnia lapwae* (Baumann and Gaufin, 1970) and *M. yoloensis* (Baumann and Gaufin, 1970) (Abbott and Stewart 1997, Rupperecht 1997), are relatively simple, monophasic signals, representing a near-ancestral pattern.

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