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The courtship behaviour of *Calliptamus wattenwylianus* Pantel, 1896 (Orthoptera, Catantopinae)

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Summary

The courtship behaviour and sound production of *Calliptamus wattenwylianus* Pantel, 1896 (Orthoptera, Catantopinae) has been studied for the first time. Ten behavioural units (BUs) have been established. Three different types of sound produced by males (male alone, chorus or interaction and courtship) as well as the sound produced by females have been recorded and analyzed. Behavioural data point to an active attitude of males and a passive one of females during intersexual relationships. Obtained results are compared with those from literature on other species of genus *Calliptamus* (*C. italicus, C. barbarus* and *C. plebeius*). Although all the species display and use in a more or less similar way the same BUs, some differences found in the whole behaviour or in some of its elements, as well as in the sound emitted, point to the possibility of the reproductive behaviour is acting as a reproductive barrier, especially among sympatric species.

Zusammenfassung

Erstmalig wurde das Balzverhalten und die Stridulation von *Calliptamus wattenwylianus* Pantel, 1896 (Orthoptera, Catantopinae) untersucht. Es wurden zehn Verhaltenselemente differenziert. Drei verschiedene Gesangstypen der Männchen (Spontangesang, Wechsel-/Rivalengesang und Balz) sowie die Stridulation der Weibchen wurden aufgenommen und analysiert. Das beobachtete Paarungsverhalten deuten auf eine aktive Rolle der Männchen und eine eher passive der Weibchen hin. Die Untersuchungsergebnisse wurden mit Literaturangaben zu anderen Arten der Gattung *Calliptamus* (*C. italicus, C. barbarus* and *C. plebeius*) verglichen. Demnach zeigen alle diese Arten mehr oder weniger ähnliche Verhaltenselemente. Einige Unterschiede in Teilen dieser Elemente und in der Lautproduktion weisen darauf hin, dass diese insbesondere bei Arten innerhalb eines gemeinsamen Verbreitungsraumes als interspezifische Reproduktionsbarriere dienen.

Introduction

Genus *Calliptamus* Serville, 1831 is widely distributed, covering large areas of Europe, Asia and Africa. The species usually live in arid places, full sunny areas or fixed dunes, and some species are able to reach high altitudes. The individuals of some species can aggregate in large groups leading to form a pest (JAGO 1963).

Three species inhabit the Iberian Peninsula: *Calliptamus italicus* Linneo 1758, *Calliptamus barbarus* Costa, 1836 and *Calliptamus wattenwylianus* Pantel, 1896 (PRESA et al. 2007). All three species are able to form pests of different magnitude, depending on the geographical area where they reside. However, in areas of the Mediterranean basin, where the abandonment of agricultural practices is expanding the potential areas for pests, there has been an increased interest on their biological aspects (ANTONATOS & EMMANOUEL 2014; BLANCHET et al. 2010a, 2010b, 2012a, 2012b, COCA-ABIA et al. 2010, LLORENTE 1982, PYRIDON et al. 2013,TERMIER 1991).

Despite such interest, there is not much information on the behaviour and sound production of the *Calliptamus* species. UVAROV (1977) noted that males move toward females producing short sounds with the mandibles while moving the hind femora. When males were close to females, they slowly approach the female while curving the abdomen and moving the hind femora. This opinion is based almost exclusively on studies conducted on *C. italicus*, and contributed by FABER (1953) and JACOBS (1950,1953). KÖHLER (2010) provides some information about these same behaviours in *Calliptamus plebeius* (Walker, 1870) endemic in the Canary Islands. As it concerns *C. barbarus*, LARROSA et al. (2004) described the "active pursuit of female" and "satellite" behaviours, with the first definition being similar to the descriptions of courtship behaviour of *C. italicus* provided by FABER (1953). In *C. italicus* JACOBS (1950, 1953) and FABER (1953) indicate the existence of different types of sounds during the confrontation between individuals of this species and gave them different names: rivalry, jump, courtship, defence, etc. LARROSA et al. (2008) described different acoustic productions, such as courtship, chorus and interaction sounds.

KÖHLER (2010) comments about *C. plebeius* (Walker, 1870) "*it is neither clear from the ephemeral present observations (1) if mandibles or post-femur stridulation ocurred nor (2) whether male or female singing was heard*". The same author described the erection of a pistil-like structure between the ventral valvae of the female, which he interprets as a behaviour for attracting males, and that in that case most likely involved pheromone emission. UVAROV (1966) comments the presence of *Comstock-Kellog* glands in the same position, in members of the Acrididae. These glands are eversible and have glandular epithelium and possibily play some part in the attraction of the male by the female. However, up to date, there has not been any information on these aspects of the biology concerning other species of *Calliptamus.*

In this paper, the courtship patterns, as well as the sounds produced by *C. wattenwylianus* were studied, because of the increasing importance of this species as a pest in the Iberian Peninsula (COCA-ABIA et al. 2010). These data can be compared with those of other species with an attempt to establish relationships among them and enlarging the knowledge on these species.

Materials and Methods

The specimens used in this study (5 males and 5 females) were collected in the Segóbriga Roman site, in Saelices, Cuenca province (Spain) on the 28th June, 2001. The specimens were separated by sex in the laboratory, and held in wood cages with glass front and metal mesh top, 40x34x40 cm, exposed to artificial light provided by a 25 W bulb 12 hours per day. Diverse food and water were provided daily.

To study behaviour, specimens were identified by a nail spot on the pronotum and, then, placed in a cage 32x42x32 cm. The cage had a glass front that allowed video recordings, and a little mesh on the top. The floor was covered by a graph paper with a square of 1 cm, making possible to estimate distances. Light and heat were provided by a 60 W bulb. Temperature was continuously monitored with a thermometer Datron HC520 Shenzhen Datron Electronics Co. Ltd. held inside the cage; it remained stable between 30 and 38 ºC. Since it is known that isolated specimens do not carry out any activities other than those spontaneously performed, several specimens, males and females were placed together.

The experiments were conducted from June 29th to July 3rd, 2001, following the same methodology described by LARROSA et al. (2004). Each experiment lasted approximately 2 hours during which the activity was registered by an observer, who took notes, and by a camera JVC GR-ax70.

More than 100 minutes of video recording of interactions between specimens were analyzed with a video player JVC HR-57851 and a monitor Samsung CB-20P0BZ. Each video tape was repeatedly visualized at different playback speeds. First, a preliminary observation was carried out briefly describing each intra- and intersexual conduct, as well as the circumstances under which it appeared. This first visualization serves to become familiar with the behaviour of the species, and for identifying the different sequences between males and females. The following visualizations were analysed at 1/6 the rate. When necessary, the image was slowed down to allow moving frame by frame.

Detailed notes were taken of the identified parts. Specific actions carried out by each specimen were annotated, as well as the approximate location relative to each other, and a description of the displayed behavior. With such information, behavioural units (BUs) were established. These BUs reflect the actions that were always performed with the same movements, and which all fit together the behaviour of each individual, both at the beginning and the end of the courtship sequence.

1.- Raise and lower one of the hind femora (1F); 2.- Raise and lower both hind femora (2F); 3.- Kicking with extension of tibia (ET); 4.- Knock (G); 5.- Progress (AV): 6.- Rest (Q); 7.- Fore legs kicking (PTL); 8.- Cleanness (AS); 9.- Chas and 10.- Assault.

Furthermore, the start and the end of the courtship sequence were established. It was considered that the sequence begins with the male approaching a female and trying to occupy one of the starting positions around the female (perpendicular, behind, in front, or parallel with her) or when the male realizes the presence of the female and, being already in one of these positions, continues with any of the BUs of the courtship.

For the quantitative analysis of the results, those BUs that occurred with a frequency of less than 0.05 in all individuals and all situations were eliminated. A Chi-square test was used to determine if the behaviours of males and females occurred randomly. Afterwards, the behavioural sequences were established through crosstabs which illustrate the number of transitions between each unit of behaviour. After converting these data to conditional frequencies (LARROSA et al. 2004, LEONARD & RINGO 1978), cinematic diagrams (or "flow diagrams") were developed. In these diagrams, the arrows represent transitions between BUs, symbolized by squares (males) or circles (females). The thickness of the arrows is proportional to the conditional frequency with which that transition appeared.

To simplify the process, transitions were subjected to a Chi-square test (95% significance level and 6 degrees of freedom). Only non-random transitions and those for which the probability were also greater than if it occurred randomly (LARROSA PÉREZ 2002) were included.

Sound study

Sounds were recorded with a Tascam DA-P1 analogical recorder attached to an AVL 600 omnidirectional microphone, which was placed inside the cage. The frequency response was 20 Hz–20 KHz ± 0.5 db. Sounds were studied with a Mingograph 420 system attached to a digital oscilloscope (Tektronix 2211) and to a Krohn Hite 3550 filter (pass band filter 2 Hz–200 KHz). To study the physical characteristics of the sound, the analogical signal was digitized with a Sound Blaster (R) Audio PCI with Advance Processor Upgrade, and then studied using the Avisof® Lab Pro 3.8. The tool FIR-filter (Finite Impulse Response), applying the high pass filter (1000–2000 Hz), was use to improve the signal/noise ratio. To study the frequency spectrum of the signal, the FFT tool (Fast Fourier Transform) was applied (window width: 256 poins).

The terminology used to describe the acoustic signals is the following:

Song: Acoustic output of the particular species or individual (RAGGE & REYNOLDS 1998).

Courtship song: Song produced by a male when next to a female (RAGGE & REYNOLDS 1998).

Chorus song: Songs produced alternately by a group of males (EWING 1989).

Interaction song: Sound produced by a specimen as a consequence of apparent perturbation generally due to other specimens walking nearby (GARCÍA et al. 2001).

Syllable: Sound produced during a complete cycle of movement of the stridulatory apparatus or the sound producing apparatus (RAGGE & REYNOLDS 1998).

Pulse: Simple and homogeneous group of oscillations delimited by silent intervals (CHAVASSE et al. 1954)

Echeme: A first order train of syllables (RAGGE & REYNOLDS 1998).

76 songs were selected for statistical analysis. In view of previous studies in *Calliptamus* species (LARROSA et al. 2008) and the features of the recorded songs, the comparative study of sound produced under different conditions (male alone, courtship and interaction and female) concerned the syllable length and the number of pulses per syllable. For the statistical analysis and comparison, the statistical analysis software SPSS 15 was used. The specimens studied, as well as the sound recordings are kept in the Área de Zoología of the Universidad de Murcia.

Results

The following behavioural units were established: 1.- Elevation and lowering of one of the hind femora (1F); 2.- Elevation and lowering of both hind femora (2F); 3.- Kicking with extension of tibia (ET); 4.- Knock (G); 5.- Progress (AV): 6.- Rest (Q); 7.- Fore legs kicking (PTL); 8.- Cleanness (AS); 9.- Chas and 10.- Assault.

Raising and lowering of one of the hind femora (1F)

One of the hind legs moves up and the other moves down, with the tibia folded, so it cannot be seen. The speed of the movement varies. The femur reaches an angle of 45–90º with respect to the ground, although in females it can reach up to 180º. The movement can be repeated, but courting males tend not to repeat it.

Females perform this movement when males get as close as 2–3 cm. Males perform it when courting after a resting period or when moving around the female and may keep the knee in the air for a period of time before lowering.

Raising and lowering of both hind femora (2F)

Both hind legs move up and down, with the tibia folded. The speed of the movement varies. As previously described, the width of the movement can be up to 45–90º although in the case of the females it can reach 180º. The legs can move synchronously or alternately. The specimen can repeat the movement several times. This behavioural unit is not often associated, neither in males nor in females. Females can perform it when the male approaches, but there is not a clear pattern associated with its performance by males.

Kicking with extension of tibia (ET)

It is the result of raising the hind femur in combination with an extension of the tibia, producing an effect similar to a kick. The femur can move 45–90º with respect to the ground, although in the case of females it can reach 180º. The tibia moves between 45 and 90º from the femur. The movement of the tibia can be repeated once o more times before the specimen folds it and lowers the femur.

Males perform it rarely and, usually, they raise the legs at a certain distance from the female. They can maintain the legs on the air, even with a movement of the tarsus. Females perform it when males are close (1–1,5 cm), or when the male abruptly approaches, moving only one or both legs, in the last case almost always alternately. It is possible that one leg extends the tibia, and that the other one does not. The unit is usually performed together with movements of the antenna, the mouthparts and, even, forelegs kicking.

Knock (G)

To perform this behavioural unit the specimen raises both hind legs with the tibia unfolded up to 45º to the ground. Afterwards, the legs are suddenly lowered causing the tarsi to knock the ground. The movement is not gradual but convulsive: the legs act synchronously and move very rapidly. It appears to be a defensive movement. It was observed in females when males got too close to them after ignoring other rejection signals.

Progress (AV)

The progress unit includes any type of displacement whether it is walking or jumping. Females can display certain agonistic movements of hind femur and/or the fore legs movement when rejecting a male.

Rest (Q)

The specimens remain inactive for three or more seconds.

Fore legs kicking (PTL)

Fore and/or medium legs from one side of the body kick the substrate for one or two seconds. This behaviour has been observed in very perturbed females during or after rejecting a male.

Cleanness (AS)

This unit comprises all behaviour associated with cleanness of eyes, antenna, legs and wings.

Chas

It is an onomatopoeic name for a very rapid unfolding of the tegmen and wings producing a red flash visible to the human eye and a little noise that can be phonetically transcribed as /tʃæs/, but which, for convenience, we shall write as "chas". It is made by both sexes, but never during the courtship. It was observed that when females produced a Chas, males that were resting would approach them appearing to answer the signal. When males produced a Chas, no response was observed in either females or other males.

Assault

To perform an assault, the male positions behind the female and parallels her body. Then, the male extends and curves his abdomen toward the female and tries to hold her with his cercus in order to be able to jump on her.

Data analysis

After analyzing the data, the Chas unit was eliminated because of its low frequency and because it never appeared during courtship. Chi-square test showed that behaviours do not appear randomly in males (Table 1) or females (Table 2) ($X^2 > X^2_{0.05,6}$), although transitions between AS and the other BUs (Tables 3 and 6) are random (Tables 5 and 8). For females, transitions between PTL and the rest of BUs are not significant (Table 8). Cinematic diagrams (Figs. 1 and 6) were designed from conditioned frequencies crosstabs (Tables 4 and 7), taking into account all transitions, even those not significant.

Table 1: BUs (Behavioural units) of males. Remarks: Number of remarks of every BUs. (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (G) Knock; (AV) Progress; (Q) Rest; (PTL) Fore legs kicking; (AS) Cleanness.

BUs	**1F**	**2F**	**ET**	**G**	**AV**	**Q**	**PTL**	**AS**
Remarks	15	5	9	0	65	54	0	1
%	10,1	3,4	6	0	43,6	36,2	0	0,7

Table 2: BUs of females. Remarks: Number of remarks of every BUs. (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (G) Knock ; (AV) Progress : (Q) Rest ; (PTL) Fore legs kicking; (AS) Cleanness.

BUs	**1F**	**2F**	**ET**	**G**	**AV**	**Q**	**PTL**	**AS**
Remarks	40	7	68	25	36	64	7	7
%	15,7	2,8	26,8	9,8	14,2	25,2	2,8	2,8

Table 3: Transitions between BUs in males. (from file to column). (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (G) Knock; (AV) Progress; (Q) Rest; (PTL) Fore legs kicking; (As) Cleanness.

	1F	**2F**	**ET**	**G**	**AV**	**Q**	**PTL**	**AS**
1F		1	1		4	9		
2F					4	1		
ET	1				3	5		
G								
AV	6	1	4			35		
Q	6	3	3		24			1
PTL								
AS					1			

Table 4: Conditional frequency of transitions between BUs in males. (from file to column). (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (G) Knock; (AV) Progress; (Q) Rest; (PTL) Fore legs kicking; (AS) Cleanness.

	1F	**2F**	**ET**	**G**	**AV**	**Q**	**PTL**	**AS**
1F		0.07	0.07		0.27	0.60		
2F					0.80	0.20		
ET	0.11				0.33	0.56		
G								
AV	0.13	0.02	0.09			0.76		
Q	0.16	0.08	0.08		0.65			0.03
PTL								
AS					1.00			

Table 5: Significance of transitions between BUs in males. (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (AV) Progress; (Q) Rest; (AS) Cleanness.

	X^2>or< $X^2_{0.05,6}$	**Are the transitions random?**
1F → other BUs	31.202>12.5916	No
2F → other BUs	18.801>12.5916	No
ET → other BUs	18.223>12.5916	No
AV → other BUs	148.486>12.5916	No
Q → other BUs	82.382>12.5916	No
AS → other BUs	6.000<12.5916	Yes

Table 6: Transitions between BUs in females. (from file to column). (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (G) Knock; (AV) Progress; (Q) Rest; (PTL) Fore legs kicking; (AS) Cleanness.

	1F	2F	ET	G	AV	Q	PTL	AS
1F			10	1	5	20	1	
2F	1		1					
ET	7	2		22	14	18	1	
G			24		1			
AV	6		5	1		9	4	
Q	21	2	19	1	4		1	4
PTL			1		3	3		
AS	1		2			1	3	

Table 7: Conditional frequency of transitions between BUs in males. (from file to column). (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (G) Knock; (AV) Progress; (Q) Rest; (PTL) Fore legs kicking; (AS) Cleanness.

	1F	2F	ET	G	AV	Q	PTL	AS
1F			0.27	0.03	0.14	0.54	0.03	
2F	0.14		0.14			0.71		
ET	0.11	0.03		0.34	0.22	0.28	0.02	
G			0.96		0.04			
AV	0.24		0.20	0.04		0.36	0.16	
Q	0.40	0.04	0.37	0.02	0.08		0.02	0.08
PTL			0.14		0.43	0.43		
AS	0.14		0.29		0.14	0.43		

Table 8: Significance of transitions between BUs in females. (1F) Raising and lowering of one of the hind femora; (2F) Raising and lowering of both hind femora; (ET) Kicking with extension of tibia; (G) Knock; (AV) Progress; (Q) Rest; (PTL) Fore legs kicking; (AS) Cleanness.

	X^2>or< $X^2_{0.05,6}$	**Are the transitions random?**
1F → other BUs	60.706>12.5916	No
2F → other BUs	20.001>12.5916	No
ET → other BUs	51.721>12.5916	No
G → other BUs	104.216>12.5916	No
AV → other BUs	19.521>12.5916	No
Q → other BUs	61.080>12.5916	No
PTL → other BUs	12.001<12.5916	Yes
AS → other BUs	8.000<12.5916	Yes

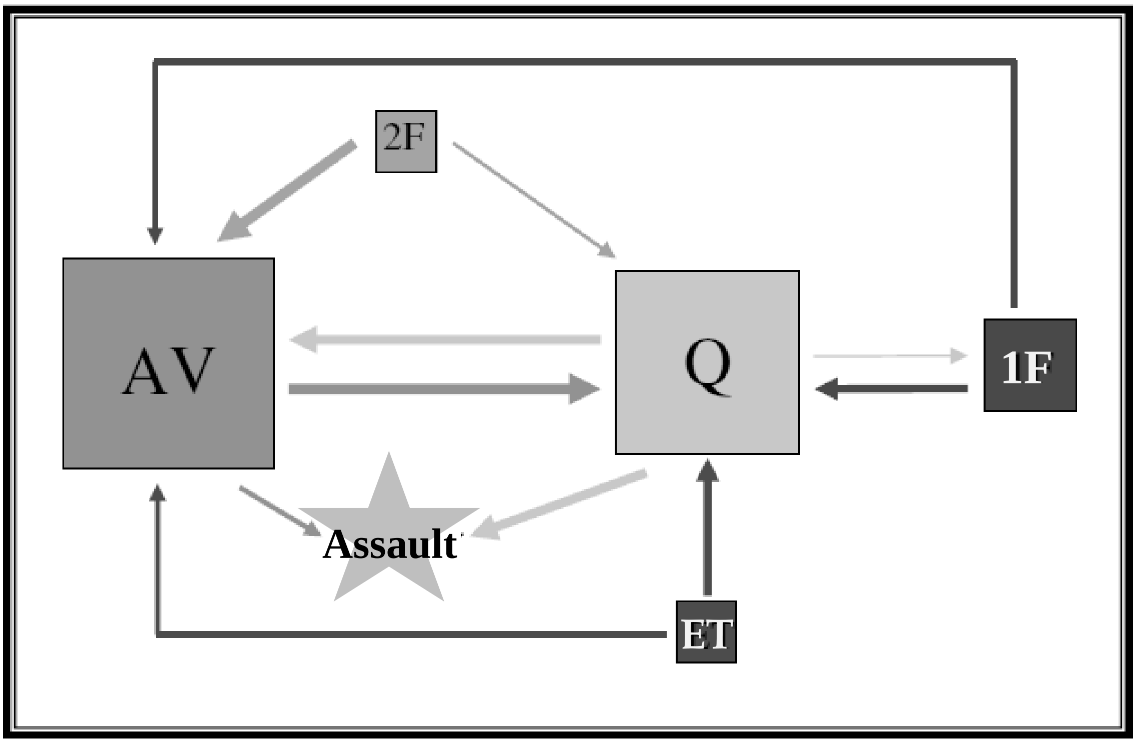

Figure 1: Cinematic diagram performed by males. (1F): Raising and lowering of one of the hind femora ; (2F): Raising and lowering of both hind femora; (ET): Kicking with extension of tibia; (G): Knock; (AV): Progress; (Q): Rest.

Male courtship behaviour

Figure 1 presents the cinematic diagram of courting males. The male starts with a Progress. This unit frequently alternates with Rest. Both units are the most common in male courtship since the male spends most of the time either approaching the female or resting. Approaching occurs in a more or less fixed way. The male detects a female and moves towards her until being at a few centimetres in distance.

The male usually approaches the female at a right angle, with his body perpendicular to hers. Then the male stops and starts moving slowly around the female, always facing her, until positioning behind her. It was observed that males moving rapidly provoked an immediate reject of the female. Males of *Calliptamus* are able to recognize the female body hind tip, most likely because of the tibia coloration (UVAROV 1977, OTTE 1970) and, when necessary, they correct their position.

In the next step, the male is close to the female, as much as 1 cm, with his body parallel to her and his head facing the female body hind third. His head and antennae are directed towards the female. From that position, it gets closer to the female. Usually, the female performs defence movements which make the male to stop and wait resting until the female stops moving. However, some males ignore such female movements and continue approaching her. If the female advances, the male pursuits her trying to maintain his position.

The male can stop at each position and rest, usually for 3 seconds (maximum 30 sec). When resting, the knees are usually in normal position, at about in line with the tegmens. When the male gets close enough to the female for attempting an assault, it keeps the body close to the substrate, and extends his abdomen, and curves it towards the female, trying to hold the end of the abdomen of the female with the cerci, starting the assault. However, the male may extend his abdomen without curving it, and continuing pursuing the female, although in other cases, he picks it and interacts with the female.

In addition to the units described above, others such as "elevation and lowering of one hind femur" (1F), "elevation and lowering of both hind femur" (2F) and "Kicking with extension of tibia" (ET) are commonly found.

Unit 1F usually follows and is followed by Rest, although it can be followed by Progress. Males appear to perform it when the female does not respond (female staying at rest) or when they are moving around the female (after a Progress).

Specimens randomly achieve 2F and ET, and both units can be followed by either Q or AV. ET seems to involve an identification behaviour: specimens arise their hind legs and quietly extend the tibiae keeping them there (even moving the tarsi), thus showing the coloration of the inner side of the hind femur in a similar manner to what has been observed in Oedipodini (OTTE 1984).

In two occasions the Assault was preceded by Rest and once by Progress, and always performed by the same couple (male and female). Mating was twice interrupted by other males, and two other times by the movements of the female.

Sound production

The sound produced by males was monitored under three different conditions: 1) when the male was at a certain distance from other individuals and not interacting with them; 2) during agonistic interaction with other individuals, either males or females and 3) when courting a female. It was also observed that when several males were kept together in the recording cage, sounds were alternately emitted in chorus song.

The sound produced by isolated males consists of echemes of 2–3 syllables, each syllable lasting 96 ± 46 ms (mean; range 55–158). Syllables are composed of 12.6 ± 5.2 pulses (mean; range 8–21; median=11). The number of pulses and syllable length are strongly related (Pearson's correlation index: 0.945). (Fig. 2). The sound produced by courting males also consists of echemes of 3–5 syllables lasting 88 ± 44 ms (mean; range 12–214) and is composed of 12.6 ± 5.4 pulses (mean; range 3–24; median=14). In this case, the number of pulses and syllable length are also strongly related (Pearson's correlation index: 0.882) (Fig. 3).

When interacting, males can perform long sequences of alternated echemes of similar characteristics to the above (echemes 2–3 syllables). Syllables last 101 ± 35 ms (mean; range 43–158) and are composed of 14.2 ± 4.5 pulses (mean; range 7–24; median=14.5; mode 17). Syllable length and number of pulses are also correlated (Pearson's correlation index: 0.740). Sometimes, echemes overlap, and this prevents their features from being identified (Fig. 4).

The intervals distance between pulses are not uniform. At the beginning of the syllable the pulses are usually more separated, becoming closer as the syllable progresses (Fig. 2). The first pulses of the syllable can be so far away that they appear to perform as isolated short syllables (Fig. 4B).

The Student's test of comparison of means applied taking into account some features of the song on the time domain shows that the sounds produced in all behavioural contexts are quite similar. No significant differences were observed. In the frequency domain, all these sounds show similar characteristics. Thus, they show a main peak between 7–8 kHz; the minimum and maximum frequencies falling at around 3–4 and 12–20 kHz respectively (Fig. 5A-C).

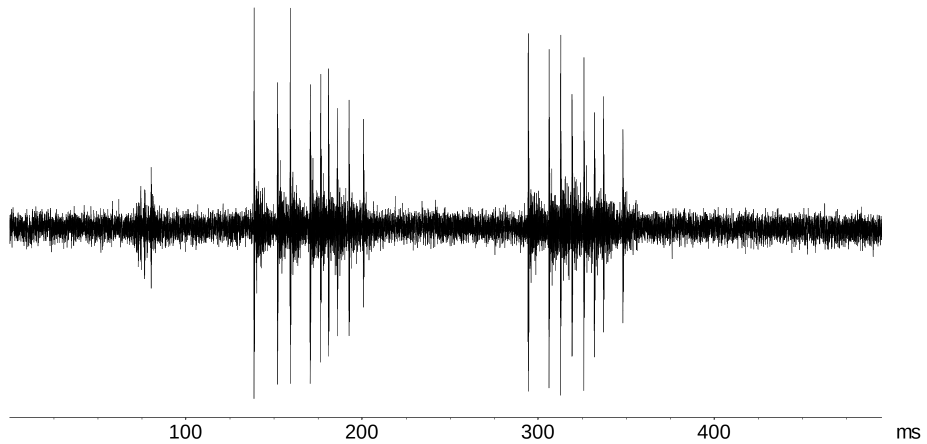

Figure 2: Song of a male alone: Two syllables echeme.

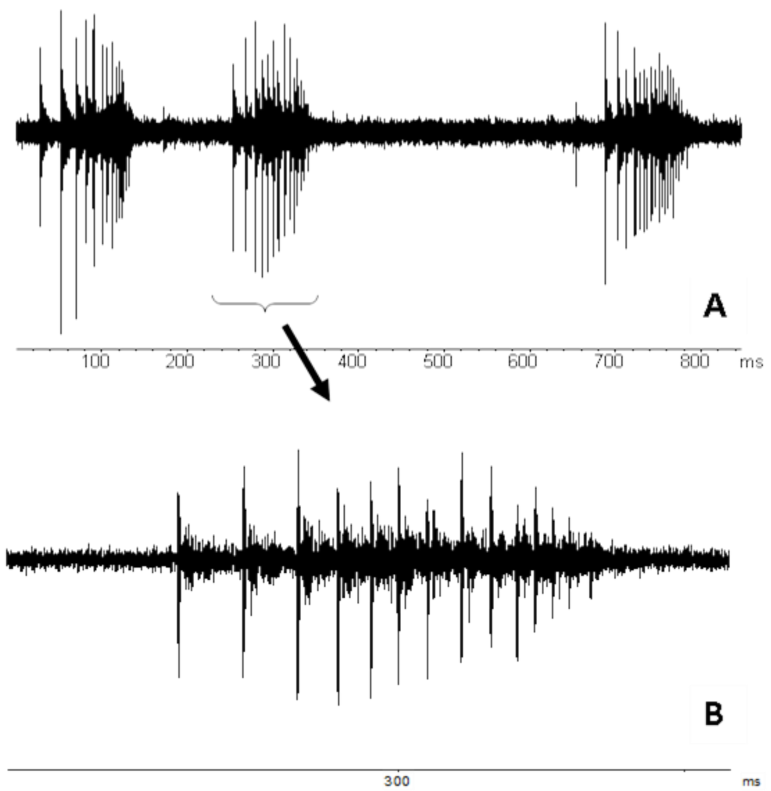

Figure 3: A: A three syllables echeme of a courtship song.
B. Detail of a syllable.

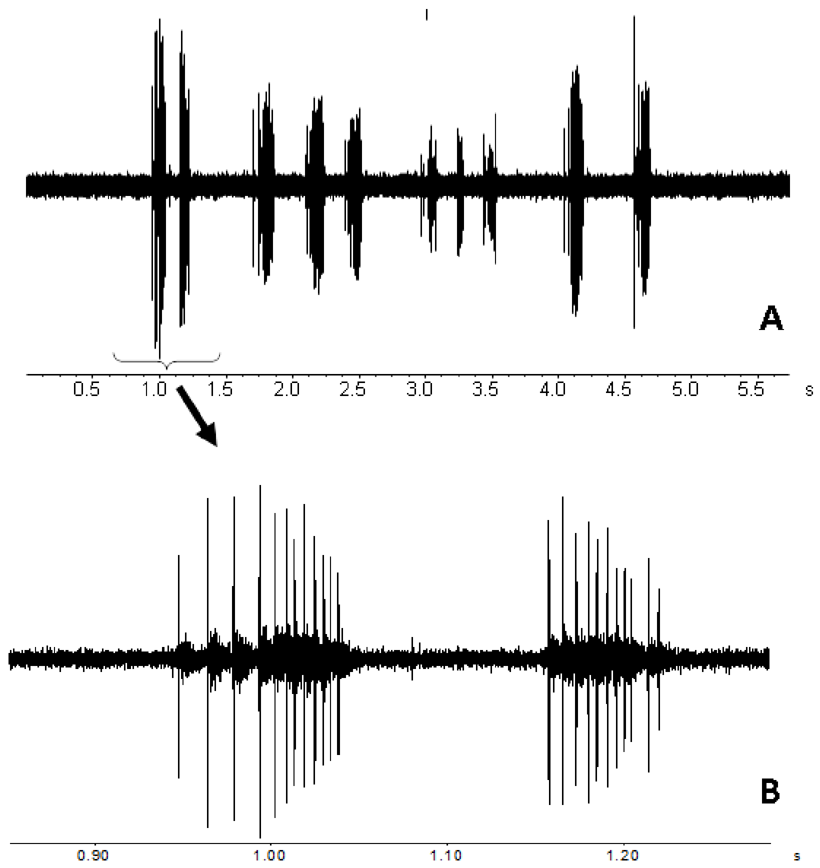

Figure 4: A: Fragment of a sequence of males chorusing / interacting.
B. Detail of two syllables.

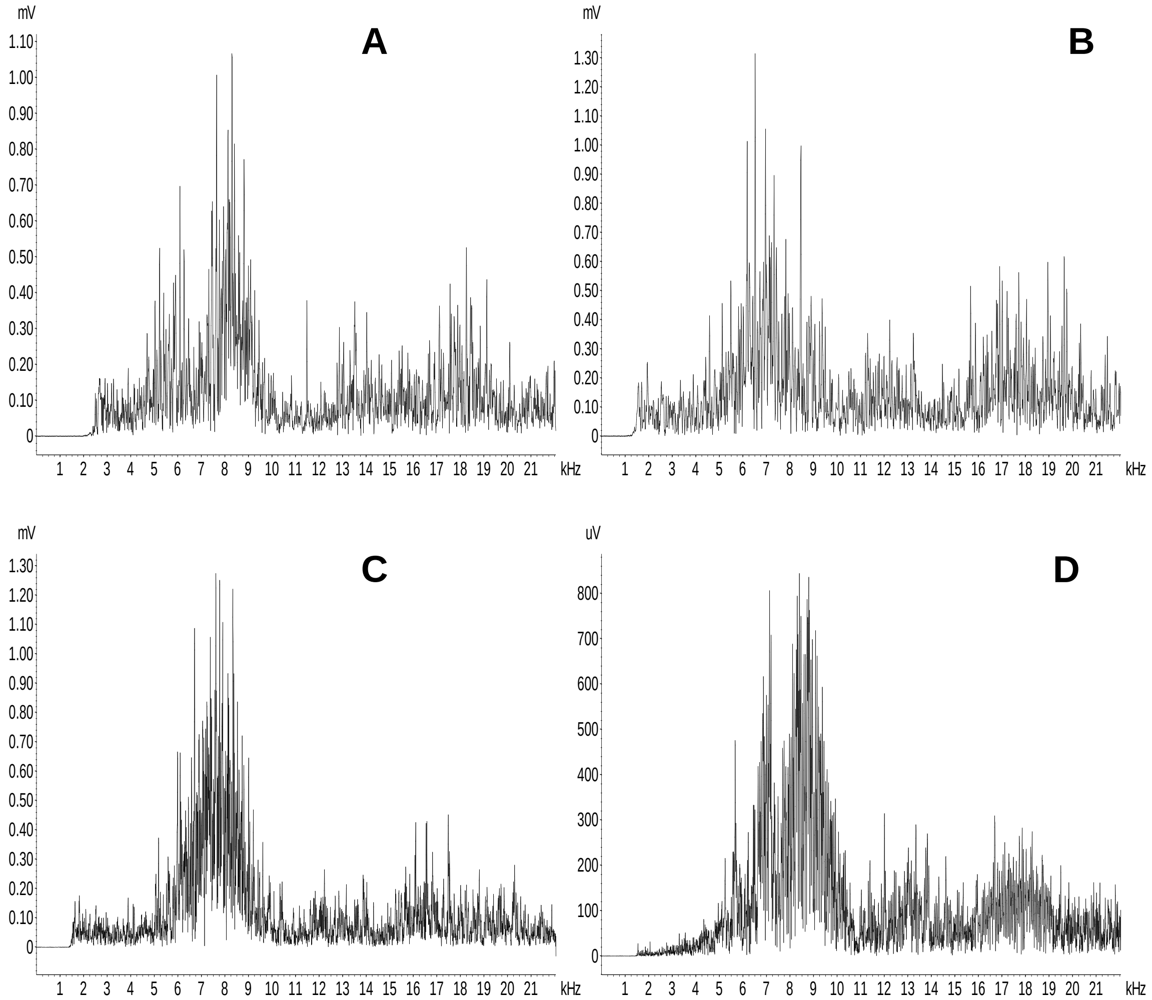

Figure 5: Frequency spectra of *Calliptamus wattenwylianus* songs: A: male singing alone; B. courtship song; C: chorus song; D: female song.

Female courtship behaviour

The female usually reject courtship of the male (Fig. 6). The female changes from Rest to movements of hind legs, with a frequency similar to 1F and ET, when she discovers a male's presence. From each unit, the female can return to Rest if the male refuses to approach. If the male continues approaching, the females respond to this behaviour. The unit that follows Rest depends on conditions such as the distance between male and female and the speed by which the male approaches and the previous female stage.

Males slowly approaching and stopping 2–3 cm from the female incite a low intensity response (1F) that can change to a high intensity response (ET) if they disturb more. Less careful males can provoke an intense response from the beginning. Females perform ET at high frequency. If the courtship continues, the female can respond strongly: intercalating kicking and knocking the substrate (G) and/or moving away (AV).

The female can escape from the male or rotate towards him. The escape must be fast in order to get away from the male pursuer. If the female rotates to face the male, she continues with rejection movements (1F, ET and PTL) until the male stops courting and rests. Nevertheless, confrontation is not often reached since the male moves away and prevents it; the couple is in perpendicular position with a different orientation.

In general, the female does not move spontaneously during the courtship, just reacting to the male's approach. Among the defensive responses there are resting movements (the unit Q occurs at a high frequency, as indicated above) that also occur when the male is behind the female and she does not see him. The females can feel attacked by the male while resting and, in that case they can change their attitude raising the body. UVAROV (1977) called this attitude "stilt posture" in contrast with the positions "resting" and "squatting". It allows the female to improve the effectiveness of her kicks and knocks.

Female sound production

In females, sound production was observed during interaction between them and when they were pursued by a male. The sound produced by the female seems to be less structured than that of the male. Every syllable, during 67 ms (mean; range 26–102), is composed of 4 pulses as a mean (2–6) (Fig. 7). The syllable length and the number of pulses are not strongly related (Pearson's correlation index: 0,45). In fact, pulses are not uniformly separated in all the studied syllables. In some syllables they appear more or less separated independently of the part of the syllable. The length of the sequences and the number of syllables emitted vary depending on the context, but it is difficult to determine them quantitatively since the intensity of the sounds is very low, being hardly listened and recordable, sound records usually offering a bad sound/noise ratio. The frequency spectrum of the sound produced by females is similar to that of the sound produced by males (Fig. 5D).

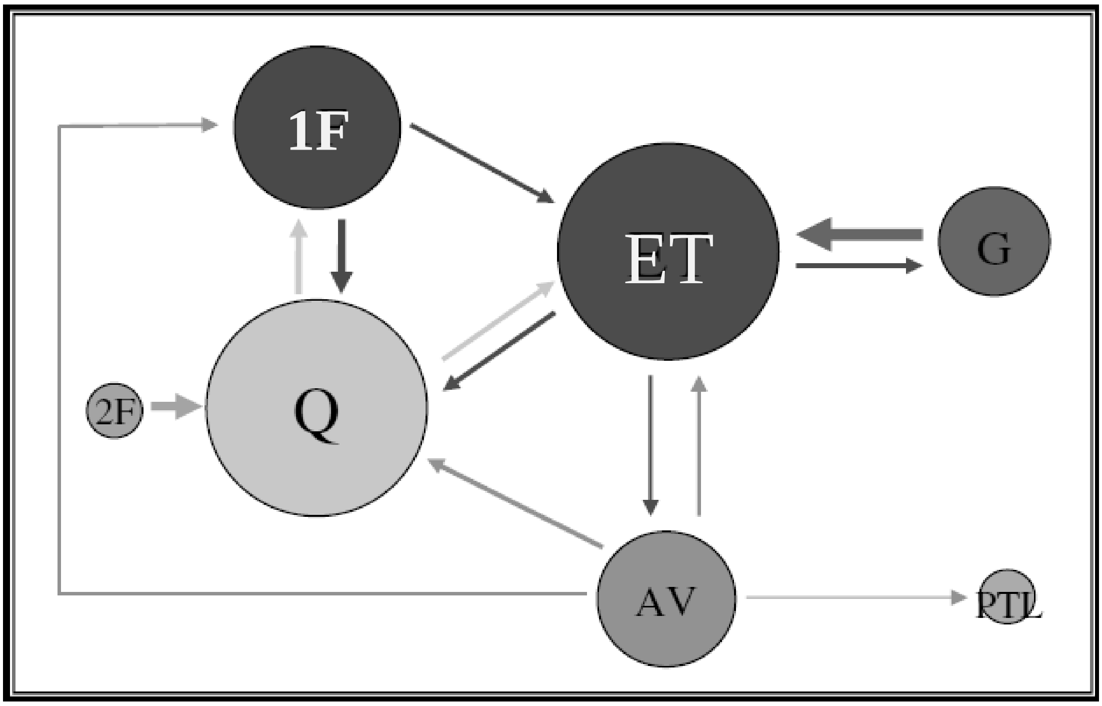

Figure 6: Cinematic diagram performed by females. (1F): Raising and lowering of one of the hind femora; (2F): Raising and lowering of both hind femora; (ET): Kicking with extension of tibia; (G): Knock; (AV): Progress; (Q): Rest.

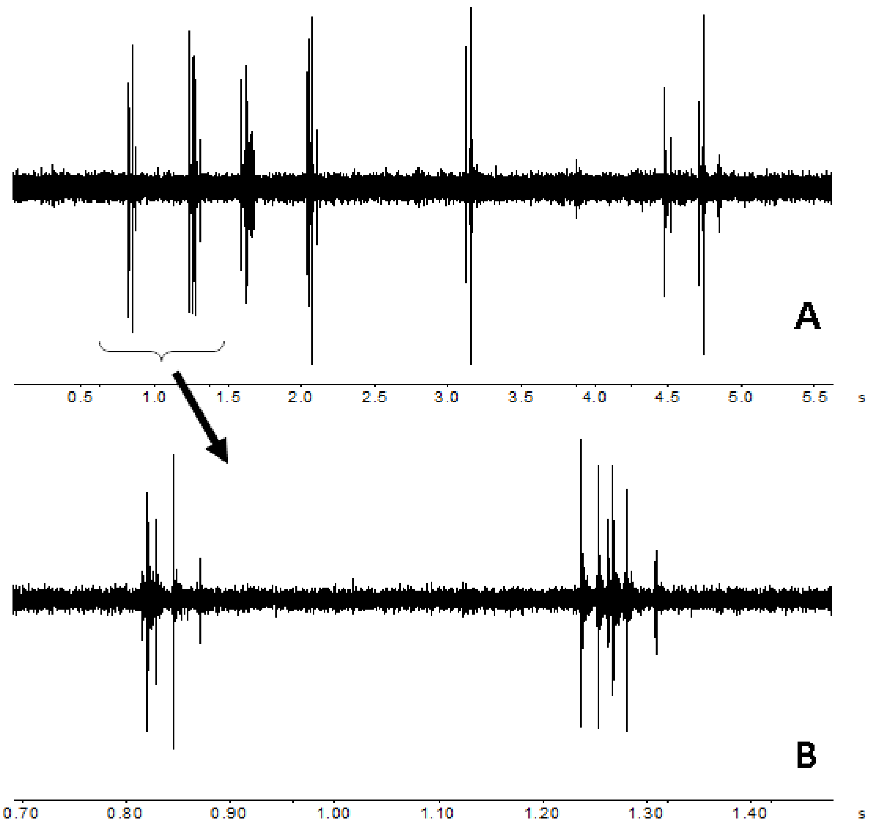

Figure 7: A: Phragment of a sequence of female songs.
B. Detail of two syllables

Discussion

The established behavioural units are similar to those proposed by LARROSA et al. (2004) for *C. barbarus*, althougt there are certain differences concerning hind legs movements. In *C. barbarus,* the Knock was not observed; nevertheless they present hind femora convulse movements, both synchronous and alternate, in addition to 1F and 2F. The same behaviour, femora convulse movements, has been described in *C. plebeius* by KÖHLER (2010).

The courtship sequences of all species have also similarities and differences. For *C. barbarus*, two courtship sequences were described: active pursuit of female and satellite behaviour (LARROSA PÉREZ 2002, LARROSA et al. 2004). In active pursuit, the male stands behind the female. If the female stands still, the male progresses, stops and progresses again, etc. If the female progresses, the male follows her from behind. A similar behaviour in *C. wattenwylianus* can be identified, although the male initial position is usually perpendicular to the female and not behind her. In this case, the active pursuit would be represented by the male avoidance of confrontation positioning behind the female, but parallel to her.

This behaviour coincides with that of *C. italicus*, except that in this species the final approach of the male to the female is done with very slow, almost invaluable movements (0.5 mm/2 seconds) (FABER 1953). Thus, active pursuit is a behaviour shared by these species, although with differences in the initial orientation of the male with respect to the female.

It is discussed as the sequence of units performed by the males when approaching the female, and being an alternative between Rest and Progress. All species also share the male rejection by the female.

Despite these similarities, some differences can be observed, such as, in the case of *C. italicus, C. plebeius* and *C. wattenwylianus* which do not perform any satellite behaviour similar to that displayed by *C. barbarus*. (LARROSA PÉREZ 2002, LARROSA et al. 2004). At least twice it was observed that the female did not run away from the male when he tried to assault her. On these occasions, the female also performed movements with the leaflets of the ovopositor, as if she tried laying eggs. These movements are similar to the behaviour indicated by KÖHLER (2010) in the female of *C. plebeius* when she lifted a structure with the form of pistil between the ventral valves with the function of emitting pheromones. It is not possible to define the presence or absence of this structure in *C. wattenwylianus*, because its existence has not been investigated.

As it concerns the studied songs, those produced by males of *C. wattenwylianus* are similar regardless of the condition in which they are emitted. Moreover, they are similar in the time domain to those produced by 1S males of *C. barbarus* (LARROSA et al. 2008). In the case of females, syllable does not seem to follow a clearly arranged pattern as occurs in *C. barbarus* females. In the frequency domain, their features are similar to those of *C. barbarus*. Thus, the sound produced by *C. wattenwylianus* follows the pattern already known for *Calliptamus* species (FABER 1953, JACOBS 1950). This was expected taking into account the sound production organ (mandibles) and its possibilities of action.

In general it can be observed that the courtship behaviour of all *Calliptamus* species is quite similar. The presence in *C. barbarus* of "satellite" behaviour, which differs from the remaining, may be related to two features of this species. During the active pursuit, the female sometimes seems to discover the males since she turns back, facing the male, and begins to perform movements with both hind femora. Then, the males also perform movements, such as raising and lowering one of the hind femora or both hind femora, kicking with extension of tibia and alternating movements of both hind femora. If female stops, male also stops but continues performing convulsive movements with both hind femora accompanied by acoustic emission. This sequence, performed by the male when the female is facing him, is called satellite behaviour (LARROSA et al. 2004, 2008). Afterwards, the male tries again to stand behind the female to restart active pursuit. On the contrary, in *C. wattenwylianus,* when a female detects a male close to her, begins to reject him. Then, males usually do not perform any movements of hind femora. The most common answers are: 1) resting until female stops moving; 2) moving slightly backwards and staying restful; 3) walking away. Nevertheless, sometimes the male rapes the female despite her rejection or performs active pursuit.

The two features mentioned above are, first of all, the great morphological variability that the species display, and secondly, their wide distribution, that can be considered transpalaeartic (JAGO 1963). These two features could lead to a possible confusion with the majority of the species of the genus, which are syntopic with it and could explain the use of the courtship behaviour as a reproductive barrier. Therefore, it will be necessary to know the courtship behaviour of the remaining species of *Calliptamus* to confirm this hypothesis.

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