

The reproductive behaviour of the cricket *Lebinthus santoensis* Robillard, 2009 (Grylloidea, Eneopterinae, Lebinthini)

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ABSTRACT

We describe and quantify the mating behavioural sequence of *Lebinthus santoensis* Robillard, 2009, a cricket species from Espiritu Santo Island (Vanuatu) characterised by ultrasonic calling songs reaching 26 kHz. In trials carried out in laboratory we observed the complete mating sequence for two couples. We observed sequences of multiple copulations of short duration repeated at constant intervals, characterised by high rates of tremulation and acoustic activity, and showing an overlapping between the inter-copulation guarding and courtship. We analysed the durations of the production, transfer and retract of successive spermatophores and described the male and female behaviours during courtship and mating.

KEY WORDS

Insecta,
Orthoptera,
courtship,
mating behaviour,
copulation,
ethogram,
Vanuatu.

RÉSUMÉ

Le comportement reproducteur du grillon Lebinthus santoensis Robillard, 2009 (Grylloidea, Eneopterinae, Lebinthini).

Nous décrivons et quantifions la séquence de comportement reproducteur chez *Lebinthus santoensis* Robillard, 2009, une espèce de grillon originaire de l'île d'Espiritu Santo (Vanuatu) caractérisée par un chant d'appel ultrasonore dont la fréquence atteint 26 kHz. La séquence complète de reproduction a été observée en laboratoire pour deux couples. Nous avons observé des séquences de copulations multiples courtes et régulières, caractérisées par des trémulations fréquentes et une importante activité acoustique, et présentant un chevauchement entre la garde et la cour entre les copulations. Les durées de production, de transfert et de retrait des spermatophores successifs sont analysées et les comportements mâles et femelles durant les phases de cour et d'accouplement décrits.

MOTS CLÉS

Insecte,
orthoptère,
cour,
comportement
reproducteur,
copulation,
éthogramme,
Vanuatu.

INTRODUCTION

The crickets of the subfamily Eneopterinae Saussure, 1874 *sensu* Robillard & Desutter-Grandcolas 2008 are now well known for their diversity of stridulatory structures (Robillard & Desutter-Grandcolas 2004a) and for their calling signal diversity which combines the usual diversity of cricket songs, especially for temporal dimension (Robillard & Desutter-Grandcolas 2011a), with original traits at the level of the frequency domain (Desutter-Grandcolas 1998; Robillard & Desutter-Grandcolas 2004b; Robillard *et al.* 2007; Robillard 2009). Among eneopterines, the Lebinthini Robillard, 2004 tribe occupies an important part in this acoustic diversity. Previous studies have shown that they use high frequency signals (Robillard & Desutter-Grandcolas 2004b). Strikingly, whereas crickets usually sing with dominant frequencies corresponding to the fundamental frequency, the high frequencies dominating Lebinthini's songs correspond to the second or third peak of their song's spectrum (Robillard *et al.* 2007). In the most contrasted cases, the calling song is so particular that it can no more be associated with a common "field cricket-like" communicatory system. In these conditions, drastic changes of the courtship and copulatory behaviours may be expected in response, especially when the song becomes ultrasonic, as in *Lebinthus santoensis* Robillard, 2009.

Crickets exhibit exceptional diversity in mating behaviour and have provided a valuable system for examining evolutionary questions about reproductive strategies (e.g., Alexander & Otte 1967; Evans 1988; Vahed 1998). In most true cricket species, pair formation is initiated by the male calling song followed by female phonotaxis (e.g., Alexander 1962; Robinson & Hall 2002). The basic sequence of cricket mating behaviour then involves the production of a spermatophore by the male (Alexander & Otte 1967), its transfer to the female with a female-upon-male copulatory position, and the retract and consumption of the spermatophore by the female after a variable time of spermatophore attachment. Multiple copulations between the same partners during a mating sequence is common in crickets and it

usually involves specific inter-copulation guarding and courtship behaviours (Preston-Mafham 2000; deCarvalho & Shaw 2010). Intraspecific communication in crickets is most often multimodal, including chemical, visual, vibrational and/or acoustic signals (Alexander 1962), which can occur during each part of the mating sequence.

The island of Espiritu Santo was extensively sampled during the SANTO 2006 expedition (for a narrative and background of the expedition, see Bouchet *et al.* [2011a], and for a review of the geography and natural history of Santo, see Bouchet *et al.* [2011b]) and many new data were published on orthopteran taxonomy and ecology (see Desutter-Grandcolas 2009, 2012; Desutter-Grandcolas *et al.* 2011; Hugel 2009, 2012; Robillard 2009). Among the new cricket species described from the Vanuatu archipelago, *Lebinthus santoensis* is currently the species which song has the highest dominant frequency ever documented for crickets, with a dominant frequency reaching 26 kHz. This nocturnal species is largely distributed in Espiritu Santo, inhabiting coastal areas, near river banks or along beaches. It lives in open forested areas, where it is found in dense populations in wet leaf litter, generally on or under large dead leaves.

In this paper, we characterise and quantify the mating behaviour of *L. santoensis* and discuss the observations in the context of ultrasonic calling. *Lebinthus santoensis* behavioural sequence is also compared to other cricket species previously documented.

MATERIAL AND METHODS

OBSERVED SPECIMENS

Extensive fieldwork was made in many localities in Espiritu Santo with Laure Desutter-Grandcolas and Sylvain Hugel, within the "Forests, Mountains, Rivers" theme of SANTO 2006 expedition. Wild specimens of *L. santoensis* were collected and brought to the laboratory, where a small colony was maintained for a few generations. Specimens were reared at 20-25°C with a 12 h:12 h day:night cycle, on a diet of ivy leaves, rodent food and water in cotton-plugged vials.

TABLE 1. — Periods of events and duration of states in the mating behaviour of *Lebinthus santoensis* Robillard, 2009 as documented by JWatcher. The upper part indicates the interval between two successive occurrences of the same event, and the lower part the duration of each state. Abbreviation: n, number of states which could be measured despite missing observations.

	Couple 1		Couple 2	
Behavioural events	n	intervals (min)	n	intervals (min)
Spermatophore transfer	3	47.3 ± 0.1	7	56.9 ± 28.5
Female retracts spermatophore	3	46.9 ± 1.8	5	58.1 ± 16.9
Male starts spermatophore production	3	47.5 ± 0.7	5	50.7 ± 5.9
Behavioural states	n	duration (min)	n	duration (min)
Initial courtship	1	36.85	0	?
Mating (mounting duration)	3	1.11 ± 0.37	7	0.25 ± 0.09
Inter-copulation	3	115.8 ± 38.6	7	41.0 ± 26.8
Inter-copulation guarding	3	16.45 ± 0.7	5	23.21 ± 4.13
Inter-copulation courtship	3	24.71 ± 0.30	5	54.43 ± 70.89
Production of spermatophore	3	17.8 ± 4.8	4	11.81 ± 11.08

BEHAVIOURAL TRIALS AND OBSERVATIONS

We used specimens of F1 and F2 generations for trials. We could record the complete sequence of reproductive behaviour for two couples under the following conditions: virgin individuals of both sexes were separated as sub-adults. After about two weeks of maturation after final moult, we placed a couple of crickets in a glass container for observation under normal artificial room light, the lateral parts of the container replaced by mosquito net to allow sound recording. Video recordings were done using a Sony Handycam HDR-HC3 video recorder.

BEHAVIOURAL ANALYSIS AND QUANTIFICATION

The software Ulead Video Studio version 11 was used for video extractions. Behavioural sequences were analysed using the program JWatcher version 1.0 (Blumstein *et al.* 2000-2012). An ethogram was constructed based on video analyses, describing the behavioural sequence as a succession of states (behavioural acts defined by their duration, with a clear beginning and end) and events (considered as instantaneous behaviours within states) (Blumstein & Daniel 2007). The ethogram describes male and female behaviours from the initial courtship (time between first male-female antennal contact and first time when female gets over male to copulate) and behavioural cycles for reproduction (production, transfer and retract of one spermatophore). The cycles were divided in two parts: mating (time between female gets over male until she gets down) and inter-copulation period (time between two successive matings).

Identified states are initial courtship, mating, inter-copulation guarding and inter-copulation courtship; their duration have to be quantified using JWatcher. Identified events are spermatophore production, transfers and retract by the female, male tremulations. We described male and female behaviours within each state and quantified the occurrences of events for the entire sequence and for each behavioural cycle.

ACOUSTIC ANALYSIS

We recorded the courtship/inter-copulation songs at 25 °C during video recording for comparison with the calling song of the species using a Condenser Microphone Capsule CM16 (Avisoft), with a flat frequency response from 5 to 250 kHz (R. Specht, pers. comm.), connected to a TASCAM HD-P2 digital recorder (96 kHz sampling frequency, 16 bit). Acoustic analyses were performed using the computer software Avisoft-SASLab Pro version 5.1.22 (Specht 2011). Song features were measured using the automatic commands under Avisoft-SASLab Pro.

RESULTS

MATING BEHAVIOUR (Figs 1, 2)

We analysed the mating behaviour for two couples of *L. santoensis* (males: MNHN-ENSIF 2550, 2554; females: MNHN-ENSIF 2958, 2959).

Both couples showed multiple copulations of short duration repeated at constant intervals and

TABLE 2. — Number and frequency of tremulations of *Lebinthus santoensis* Robillard, 2009 per behavioural cycle (three in couple 1, seven in couple 2) and per behavioural state (inter-copulation guarding, inter-copulation courtship).

Behavioural states	Couple 1					Couple 2								
	Behavioural cycles				Nb per minute	Behavioural cycles							Nb per minute	
	1	2	3	Mean		1	2	3	4	5	6	7		Mean
Initial courtship	0	–	–	0	0	?	–	–	–	–	–	–	–	–
Mating (mounting)	0	0	0	0	0	–	0	0	0	0	0	0	0	0
Inter-copulation			121											
Total per behavioural cycle	73	150	121	115 ± 21	1	–	136	148	147	125	13	131	117 ± 30	3
Inter-copulation guarding	65	122	–	103 ± 19	6	–	119	131	–	118	–	106	119 ± 5	5
Inter-copulation courtship	8	28	–	18 ± 7	< 1	–	19	17	147	7	13	25	38 ± 31	2

characterised by high rates of tremulation. Observed sequences include behavioural cycles consisting of production, transfer and retract of three and seven spermatophores respectively, for a total duration of 134 and 241 minutes (Table 1). Durations and periods of behavioural cycles, states and events per couple, and frequency and number of tremulations per behavioural state are reported in Tables 2 and 3.

During the initial courtship, the male sings in front of the female with the forewings raised at less than 45°. Male and female continuously antennate, moving their antennae in an upward or forward position, the antennae of each individual making an angle of approximately 45°. The subsequent courtships correspond to inter-copulation courtships and take place between the retract of the previous spermatophore and the transfer of the next one (next mounting): from the face-to-face position, the male begins to produce a spermatophore, which takes 13.9 ± 8.4 minutes ($n = 10$ cycles). During inter-copulation courtship, the male sings almost continuously, tremulates, waves his antennae against the female, and individuals interact using the palpi (possibly visual and tactile signals).

Mating starts with the male turning back and walking backward toward the female, who touches the male's tergites with her palpi before mounting the male. Then the copulation takes place, resulting in the transfer of the spermatophore; copulation ends with the male moving forward. While getting down from the male's back, the female sometimes keeps touching the last tergites of the male with her palpi. The male then slightly turns around, while staying before the female in a back-to-face position, with one antenna oriented backward

toward the female and the other antenna oriented forward. The male keeps this guarding position for 20.6 ± 4.5 minutes ($n = 9$ cycles) while tremulating intensely, until the female retracts the spermatophore. When a new spermatophore production begins, the male turns around completely to place himself in a face-to-face position with the female, antennates, tremulates and sings. In most cases, the female retracts the spermatophore when the production of a new one has already started, which means that there is a slight overlap between the inter-copulation guarding and the time of production of a new spermatophore; however, in one of the observed couples, the first spermatophore was retracted by the female before the production of the next one.

INTER-COPULATION SONG (Table 3)

The inter-copulation song is produced almost continuously after the female has removed the spermatophore; at that stage, the male is also producing a new spermatophore. The inter-copulation song is produced with the forewings less raised than for the calling song, which results in a less intense signal than the calling song. The frequency of the inter-copulation song is more broadband than the calling song, between *c.* 25–45 kHz with no clear dominant peak. The temporal pattern is very similar to that of the calling song: at 25°C the inter-copulation song consists of long two-part echemes separated by a short silence (630 ± 180 ms), with a sub-echeme made of widely spaced syllables (mean = 3.3 ± 0.1 syllables per second), followed by a sub-echeme where syllables are shorter and more rapidly emitted (mean = 42.7 ± 0.6 syllables per second).

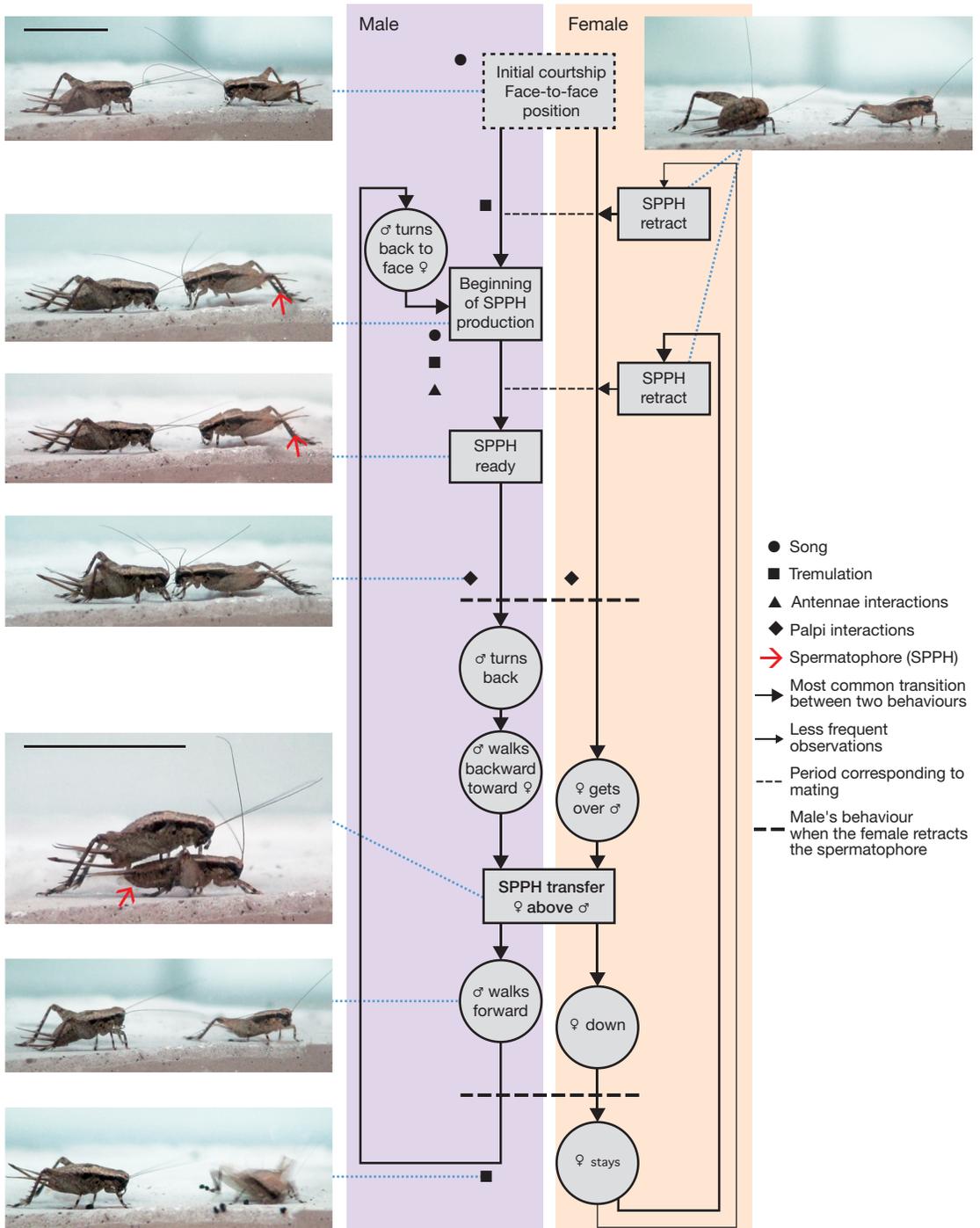


FIG. 1. — Ethogram of *Lebinthus santoensis* Robillard, 2009. The left panel concerns the male's behaviours and the right panel the female's behaviours, displayed in chronological order from top (initial courtship) to bottom (after spermatochore transfer), with rising lateral arrows ending the cycle for each individual. Scale bars: 1 cm.

TABLE 3. — Inter-copulation courtship song parameters of *Lebinthus santoensis* Robillard, 2009.

Song	Slow sub-echeme		Syllables in slow sub-echeme		
	Duration (s)	Syllable number	Duration (ms)	Period (ms)	Rate (/s)
Calling (n = 5)	13.7 ± 5	42.3 ± 8.5	11 ± 1.9	302 ± 73	3.5 ± 0.9
Inter-copulation (n = 1)	12.3 ± 1.3	41.3 ± 5	9.8 ± 0.5	301 ± 9	3.3 ± 0.1
Song	Fast sub-echeme		Syllables in fast sub-echeme		
	Duration (s)	Syllable number	Duration (ms)	Period (ms)	Rate (/s)
Calling (n = 5)	10.8 ± 2.8	451 ± 57	9.9 ± 3.3	23.6 ± 4.5	43.4 ± 7.6
Inter-copulation (n = 1)	8.8 ± 1.1 s	373 ± 37	7.1 ± 0.7	23.1 ± 0.2	42.7 ± 0.6

DISCUSSION

The large naturalist expeditions for surveying biodiversity in far places like Espiritu Santo not only permit massive systematic revisions, description of new species and quick faunistic/floristic surveys; provided adequate observation protocols are allowed, they may also give access to a world of original information about biodiversity itself, especially in terms of ecology and habitats of the species, and in some instances, about their behaviour.

Cricket calling songs are characterised by their diversity and species-specificity (Alexander 1962). They are however only the first step of a series of filters playing a role in the reproductive isolation of species. Each species is not only characterised by a specific calling song, but also by diverse sequences of courtship and copulatory behaviours (Alexander & Otte 1967). Evolutionary correlations between song and behavioural diversity have long been hypothesised in terms of sexual selection, and mutual benefits for males and females to avoid costly interspecific reproduction. Such correlations should be studied in a phylogenetic context to understand their role in the mechanisms of species diversification. The first step to achieve this goal is to acquire basic knowledge about the behaviour of as many species as possible representative of the diversity in a diverse monophyletic group (Grandcolas *et al.* 2001).

It has been shown that eneopterine diversity deals mostly with acoustic communication, and both the stridulatory apparatus (Robillard & Desutter-Grandcolas 2004a) and the calling songs (Robillard & Desutter-Grandcolas 2011a) have been studied in a comparative way. To further understand the

diversification of acoustic communication in this clade, it is now necessary to study how the original properties of the songs may have modified the courtship patterns. Here we document the mating behaviours in *Lebinthus santoensis*, a species with the highest dominant frequency ever found in a cricket.

Despite the original features of the calling song, the basic acts of the mating sequence described here for *L. santoensis* are similar to those documented up to now in other true crickets (Grylloidea Laicharting, 1781), including antennation, courtship involving tremulation (body jerking), movements of antennae and palpi, stridulation and copulation in female-above-male position and transfer of a reproductive spermatophore to the female (e.g., Alexander & Otte 1967; Evans 1988; deCarvalho & Shaw 2010).

The originalities of *L. santoensis* behavioural sequence stand in the multiple copulations, which is also documented in other cricket species including eneopterines (Preston-Mafham 2000), but also in the intense tremulation during guarding after spermatophore transfer, as well as in the intense acoustic activity during inter-copulation courtship. The contrast between these two parts of each inter-copulation period for using different modalities of communication is clearly established in the two couples under study (Table 3). Similar interactions have to be tracked amongst other *Lebinthus* Stål, 1877 species to understand the evolution of communication systems in mating behaviours.

All the Lebinthini species documented so far, including *Lebinthus santoensis*, lack glands on male metanotum, contrary to most other eneopterine species (Robillard & Desutter-Grandcolas 2004a). According to the phylogeny of the subfamily, this loss of male glands and the associated behaviours

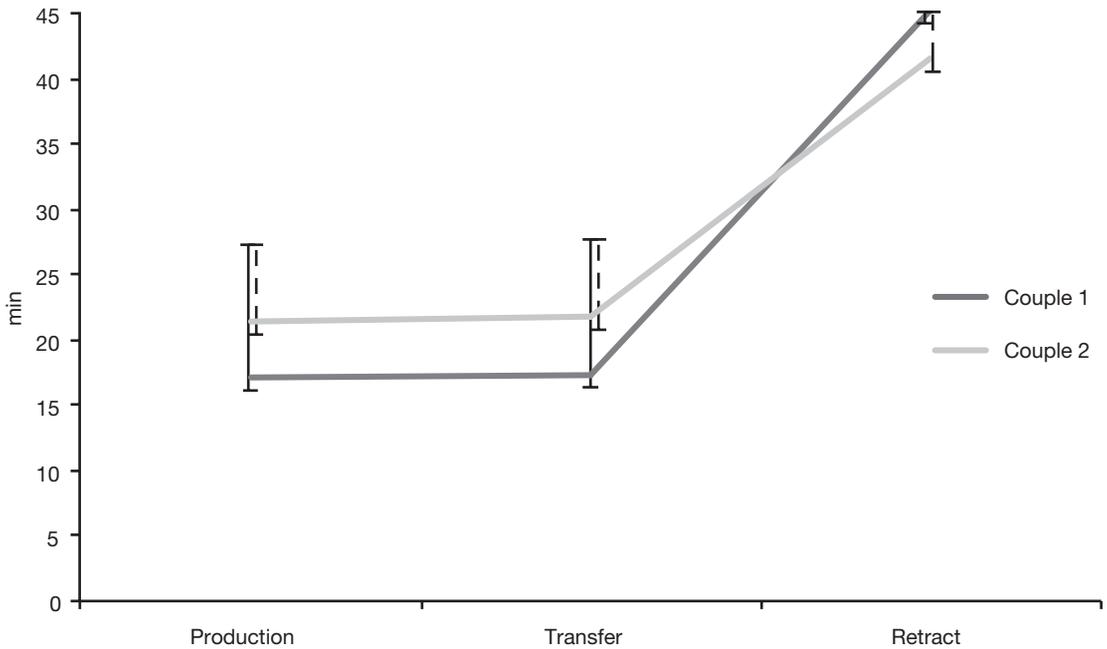


FIG. 2. — Mean duration of spermatophore production, transfer and retract within behavioural cycles of *Lebinthus santoensis* Robillard, 2009 based on three complete cycles for each couple. Standard deviation: solid line for couple 1, broken line for couple 2.

during mating may in some manner be associated with the use of high frequency signals for calling.

Although most individual behaviours seem to be shared by other species (songs, tremulations, antennations, etc.) in terms of raw presence/absence pattern, their sequences and quantification prove rich in information in terms of male-female body and antennae positions, durations of each part of the mating sequence, and diversity of communication modalities during mating. This suggests that behavioural sequences should indeed be highly informative to understand the evolution of eneopterine species in a comparative and phylogenetic context.

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