Ecology of the calling song of two Namibian armoured ground crickets, Acanthoplus longipes and Acanthoproctus diadematus (Orthoptera Tettigoniidae Hetrodinae)

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2 authors:

Erminia Conti
University of Catania

Fabio Viglianisi
University of Catania

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Ecology of the calling song of two Namibian armoured ground crickets, *Acanthoplus longipes* and *Acanthoproctus diadematus* (Orthoptera Tettigoniidae Hetrodinae)

E. CONTI and F.M. VIGLIANISI

Dipartimento di Biologia Animale "Marcello La Greca", Università di Catania, Via Androne 81, 95124 Catania, Italy

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The calling songs of the Namibian armoured ground crickets *Acanthoplus longipes* and *Acanthoproctus diadematus* were analysed and described for the first time. Some differences in the length of the cuticular file and the number of the teeth of the pars stridens are also described. The different song patterns are related to differences in the autecology of the two species. Both utilise a broad frequency bandwidth, but the rare and endemic *Acanthoproctus diadematus*, which lives in interdunal areas of the desert, emits lower frequency signals. These consist of a repetitive sequence of very simple echemes. In contrast the widespread and invasive *Acanthoplus longipes*, which inhabits open grasslands, emits complex sequences of high-frequency diplosyllabic echemes. Other ecological features, related to the songs of the two species, are discussed.

KEY WORDS: calling song, stridulatory organ, armoured ground crickets, behavioural ecology.

INTRODUCTION

Sound production is used for communication by a variety of animals. Among Orthoptera, in particular, song plays a leading role in behaviour. Crickets and grasshoppers produce different acoustic signals according to varying situations and behavioural contexts (DUMORTIER 1963). The most common signal is the calling song. This is produced by males as a means of attracting a partner. If a female is receptive, she approaches the male and, when they meet, mating takes place. The song is species specific and can be produced by males that have never heard it before (ALEXANDER 1968). Thus it is a fundamental mechanism that prevents hybridisation. Such intraspecific communication is especially necessary for species that live in harsh environments, including deserts or semi-desert areas, where the extreme conditions require an optimisation of the meetings to guarantee reproductive fitness. As these songs are the result of environmental adaptation, their features, as well as the underlying structures of the stridulatory apparatus have been analysed. As it is of primary importance in reproductive behaviour, the calling song lends itself especially well to adaptive analysis.

METHODS

Study species

Both *Acanthoplus longipes* and *Acanthoproctus diadematus* are armoured ground crickets (Orthoptera Tettigoniidae). They are included in the same subfamily Hetrodinae, which is endemic to Africa (Caudell 1914; Peringuey 1928; Weidner 1941, 1955; Skaife 1953; La Greca & Messina 1989; Irish 1992). According to Weidner (1941) the geographical distribution of the genus *Acanthoplus* is restricted to Africa south of the Sahara. *A. longipes* ranges from the Congo to Namibia and Angola (Irish 1992), where it inhabits semi-desert bush areas. In contrast, *Acanthoproctus diadematus* is endemic to the Namib Desert where its presence is limited to a few dune and interdunal areas near the Kuiseb River within the Namib-Naukluft Park.

A. longipes is a large (30-50 mm long), black, flightless bushcricket. It is sexually dimorphic and the female is larger than the male. As with other congener species, *A. longipes* shows impressive seasonal explosions in number and is a pest of agricultural crops. *A. discoidalis* is an even more serious pest and causes severe damage to maize crops in the Omaruru area of Namibia (Berthold Wohlleber, Subdivision of Law Enforcement, Government of Namibia, pers. comm.), while *Acanthoplus speiseri*, seriously harms maize and sorghum crops in Zambia (Mbata 1992). These species also eat other crops and even feed on dead members of their own species which have been killed on the road by passing vehicles.

Very little is known about the behaviour of *A. longipes*. We noted that stridulation by males takes place both during the day and at night. In the sibling species *A. discoidalis,* Bateman & Ferguson (2004) recently found that, when mating, the males are able to discriminate between virgin and pregnant females, based on their weights. They show a preference for females with an intermediate weight.

A. diadematus is known as 'the *!nara* cricket' because it feeds on *Acanthosicyos horrida*, a thorny endemic cucumber which is called *!nara* by the Topnaar Hottentots (Craven & Marais 1986, Seely 1987). It is also a large, flightless bush cricket (50-60 mm long). It shows marked sexual dimorphism and its pale colour is homochromous with that of the sand surface over which it is active. Even less is known about the biology of this species, and its reproductive behaviour has not been described. Day-time activity takes place within *!nara* bushes, but the crickets move from one bush to another at night. Stridulation can be heard both during the day and at night.

Methodology

Specimens of *A. longipes* were collected between Karibib and Usakos in the west-central part of Namibia during August 2000. Populations of *Acanthoplus* spp. usually peak there during the summer, from March to May (B. Wohlleber pers. comm.). Because of heavy rainfall at the end of March 2000, however, many adults shifted their life-cycle and males were singing later than usual in the reproductive season.

This study was carried out in a laboratory in Walvis Bay, 206 km from the area in which the insects had been collected. Fourteen specimens were kept in two cardboard boxes (60 × 40 × 35 cm) each containing 3 males and 4 females. They were maintained at 15 °C under a regime L:D/10:14. For food, they were provided with the same species of Gramineae that were present in their natural habitats. Two other males were maintained separately in different cages far from each other and from the other specimens. In the laboratory, stridulation took place at dawn, as it had in the field at the time of capture. It frequently persisted throughout the night. The songs produced by different stridulating males were recorded during the second half of August 2000.

Six specimens of *A. diadematus* (3 males and 3 females) were collected in the Namib Naukluft Park near Gobabeb on 15 September 1991. They were kept outdoors at the Desert Ecological Research Unit of Namibia, in three different terraria, each containing a pair of crickets. Another male was maintained separately in a different cage far from the other specimens. Stridulation was recorded from 18 to 23 September 1991.

Recordings were made with a Superscope tape recorder using TDK (IECI/TYPE I) sound cassettes and a Pioneer DM-31 microphone placed 20 cm away from the animals. Recordings lasted for 15 min. This equipment cut off all sounds above 16-20 kHz, so the song analyses were limited to frequencies below 16 kHz. It was considered acceptable to eliminate frequencies below 100 Hz (these are the noises usually heard under laboratory conditions). The songs were later analysed at the Department of Animal Biology, University of Catania. They were sampled digitally at 44 kHz and 16 bit resolution, using a Sound Blaster AWE32 sound card. They were then processed by wave editor Cooledit Pro ver 2.0 (Syntrillium Software). The two calling songs were compared with previously published digital recordings of other tettigoniids (Ragge & Reynolds 1998).

The structure of the stridulatory organs of the two species was observed using a Hitachi S4000 scanning electron microscope (SEM). We measured the length of the pars stridens and counted the number of teeth. Because the pars stridens is curved (Fig. 3), we measured both its total length and the distance between its two extreme points.

The terminology used here follows that of Ragge & Reynolds (1998), according to whom the main call unit consists of a syllable, that is, the sound produced by one to-and-fro movement of the stridulatory apparatus. The songs are shown as oscillograms at speeds of 15 mm/sec, 70 mm/sec and 135 mm/sec. A frequency spectrum is also shown.

RESULTS

Patterns of the calling song

Acanthoplus longipes. The call of *A. longipes* consists of a long sequence of echemes (Fig. 1A). (On occasion it can last for some minutes.) The echemes are repeated at the rate of about 6/sec and the interval between two successive echemes is about 80-90 msec. Each echeme, in turn, is made up of two syllables close together (a disyllabic echeme) whose total duration is 60 msec. The echeme is formed by two different syllables: the first syllable having a duration of 15 to 17 msec and the second one of 26 to 30 msec. A gap of 16 msec to 18 msec occurs between the two syllables. Each syllable is broken up into a constant number of discrete pulses. These have the same oscillographic form (each pulse shows a regularly decreasing frequency). With a duration of about 7 msec, the pulse is repeated twice in the first syllable and from 4 to 5 times in the second one. In addition, a gap of 1 msec is present inside the first syllable; no gap is present in the second hemi-syllable where the pulses are very close together. The frequency spectrum shows maximum amplitude from 7 to 16 kHz and peaks at 10 kHz (Fig. 2A).

Acanthoproctus diadematus. The calling song of *Acanthoproctus diadematus* is less complex; it is formed by a series of regular syllables whose duration is about

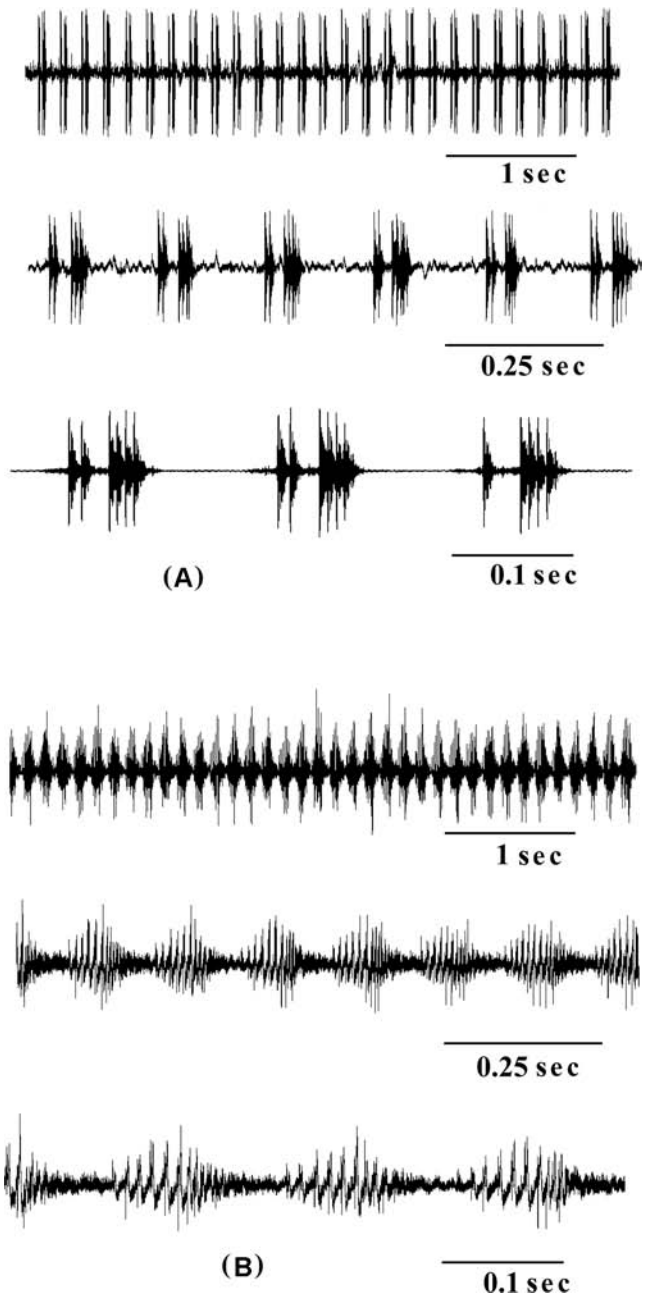

Fig. 1. — Oscillograms of the calling songs of the two armoured ground crickets studied. (A) *Acanthoplus longipes*, (B) *Acanthoproctus diadematus*: the speeds of the traces from top to bottom are 15 mm/sec, 70 mm/sec and 135 mm/sec respectively.

130 msec (Fig. 1B). Unlike those of *A. longipes,* the syllables have a standard structure, being similar to one another and repeated at the rate of 7/sec without gaps. Each syllable includes from 9 to 11 pulses. The song frequency shows maximum amplitude from 150 Hz to 250 Hz with a peak at 195 Hz (Fig. 2B).

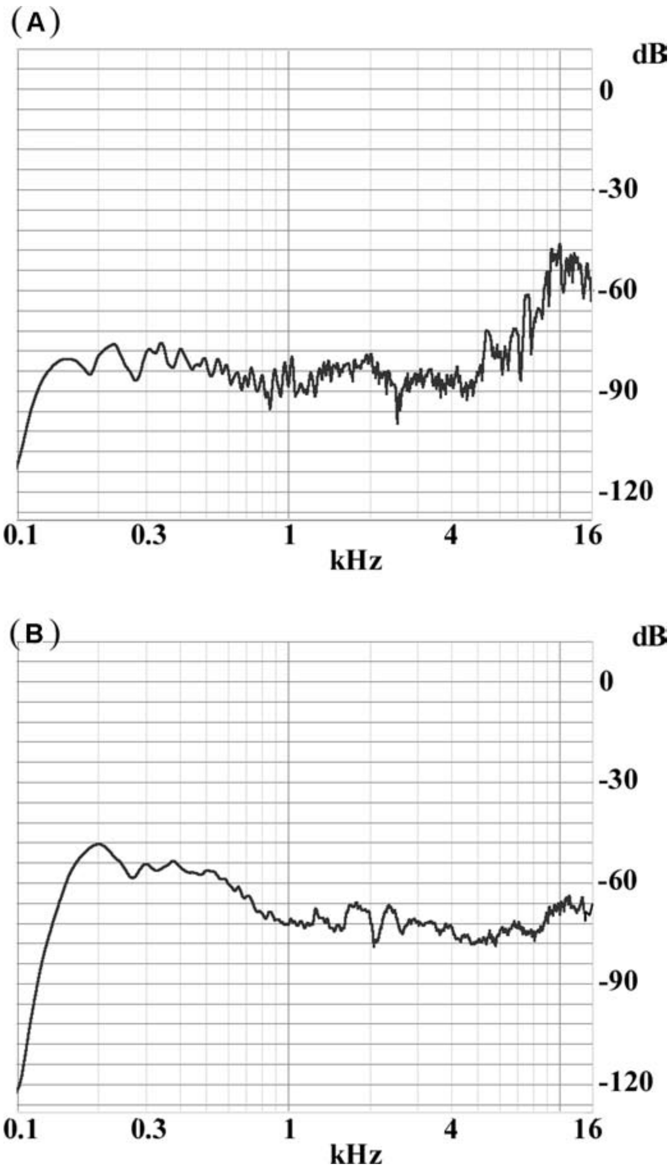

Fig. 2. — Frequency spectrum of the calling song of the two armoured ground crickets in the range 0.1-16 kHz; the x-axis represents a logarithmic scale of frequencies, the y-axis the amplitude of the frequency: (A) *Acanthoplus longipes*; (B) *Acanthoproctus diadematus*.

Structure of the stridulatory organ

Stridulation is performed by rubbing the reduced mesothoracic wings under the pronotum. The left tegmen overlaps the right, both during stridulation and when at rest. The pars stridens consists of a series of teeth running along the lower surface of the left wing. These are rubbed to and fro against the right tegmen to produce the song.

The fine organisation of the stridulatory organ of the two crickets is very similar. Analysis by SEM shows the presence of similar structures although some differences are visible. The dimensions and the numbers of the teeth on the pars stridens are variable and may well have taxonomic value. Moreover, in both species, tooth size gradually decreases towards the ends of the cuticular file.

Fig. 3 shows the pars stridens of *A. longipes* and *A. diadematus* as they appear under a SEM at 25×. In *A. longipes* the total length of the cuticular file is 3.4 mm,

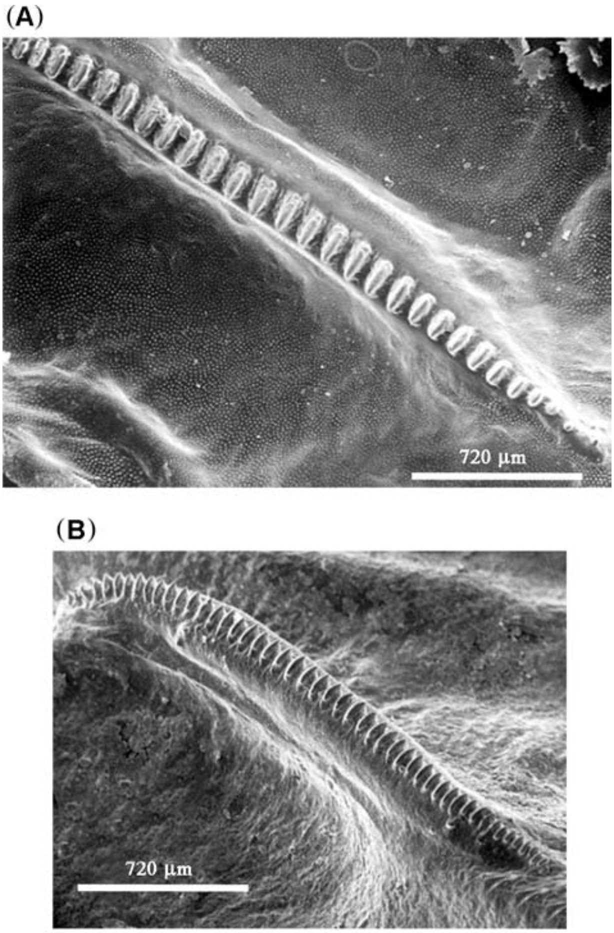

Fig. 3. — Scanning electron micrograph of the underside of a male forewing showing the stridulatory file. Magnification ×25: (A) *Acanthoplus longipes*; (B) *Acanthoproctus diadematus*.

its linear length is 3.2 mm and it contains 28 to 30 teeth. The pars stridens of *A. diadematus* is shorter. Its total length is 2.1 mm and its linear length is 2.0 mm. It has 48 to 49 teeth. The difference between the sizes of the stridulatory organs of the two species indicates a different distribution of teeth inside the two files. *A. diadematus* has a short pars stridens with many teeth which are close together. In the contrast, the cuticular file of *A. longipes* is longer and has relatively few teeth which are more widely spaced. The mean distance between teeth is 120 µm in *A. longipes* and 44.4 µm in *A. diadematus*.

DISCUSSION

The oscillograms presented here are the first to be published of the two species considered. The calling song of *A. diadematus* falls into category 1 according to the classification by RAGGE & REYNOLDS (1998): 'Continuous trains of rapidly repeated, ungrouped syllables, lasting indefinitely (often more than a minute)'. It is similar to others described for many bushcrickets and molecrickets. Moreover, as the train has a regular syllable repetition rate, it can be included in the subcategory 1a.

The relative simplicity of the song structure of *A. diadematus* (a long train of simple syllables) suggests that it might be an ancestral form of calling song, according to the classification by RAGGE & REYNOLDS (1998) of the songs of European Ensifera. This is supported by the fact that the *!nara* cricket inhabits very limited areas of desert where there are no other congeneric species to engender selective pressure. The frequency spectrum of the calling song of *A. diadematus* presents a maximum amplitude among low values. Emission of low frequencies can be well justified by the large size of the crickets (BENNET-CLARK 1998). A peak as low as 195 Hz has not previously been recorded among Tettigoniidae. Indeed, the principal carrier frequencies used by these insects are generally above 6-10 kHz (DUMORTIER 1963, BELWOOD 1990, BAILEY et al. 1993, BENNET-CLARK 1998, OLIVEIRA et al. 2001). The low frequency of the song of *A. diadematus* probably forwards an unambiguous acoustic signal, without loss of frequency components, to females far from the sender. It has been demonstrated that higher frequencies are attenuated more by distance than are lower frequencies (KEUPER & KÜHNE 1983, KEUPER et al. 1986, RÖMER & BAILEY 1986), and *!nara* bushes are widely scattered in the Namib dunal areas. The distance between one and the next often exceeds tens of metres. In contrast, in other Orthoptera such as katydids, populations living at high densities tend to use higher frequencies than those dispersed with greater individual distances (DUBROVIN & ZHANTIEV 1970).

Secondly, *A. diadematus* spends most of its life close to the ground deep within its host plant (G. COSTA & E. CONTI unpublished). Here, low frequency emissions are particularly effective (BRADBURY & VEHRENCAMP 1998). At the same time, while insect calls are scarce in the Namib interdunal environment, the noise of the wind is the major source of low-frequency sounds in open sandy areas (BRADBURY & VEHRENCAMP 1998). It is probably significant that *A. diadematus* stridulates very early in the morning, a time when the wind speed tends to drop. Moreover, the risk of predation is less during the hours of darkness when the female cricket has to cross open desert to reach her potential mate.

A. longipes emits a much more complex calling song than does *A. diadematus*. This song can be classified as category 5 'Separately audible dense echemes in a series lasting indefinitely (often more than a minute)', and belongs to the subcategory 5a, since it includes disyllabic echemes. According to RAGGE & REYNOLDS (1998) such complexity results from intense selection. This may be correlated with dense populations where an elaborate male song pattern may allow females to detect the quality and fitness of their potential mates. No doubt, only males endowed with good health will perform perfect songs.

Very little is known about the biology of the congeneric species *A. discoidalis* which occupies the same habitat, but it is likely that its reproductive behaviour is similar, as is the male calling song. In this situation, the development of a more complex, species-specific signal would be a means of preventing interbreeding. In Zimbabwe, MBATA (1992) reported both silent males and males singing in chorus in *A. speiseri*. A male, ready to mate, first begins to stridulate. This attracts conspecific adults of both sexes. The silent males stop at short distance from the singing male and either attempt to mate with a female that has been attracted to it or else begins to stridulate too. Clearly, the reproductive behaviour of the genus *Acanthoplus* reflects an interplay of complex relationships.

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