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ACOUSTIC CHARACTERISTICS OF DYNASTID BEETLE STRIDULATIONS

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Abstract

Oryctes rhinoceros (L.) (Coleoptera: Scarabaeidae: Dynastinae) causes economically important damage to ornamental and commercial coconut palm trees in the western Pacific region that could be mitigated significantly by early detection and treatment. Adults are difficult to detect visually because they attack the crowns of the trees and feed internally before mating and dispersing to new hosts. Visual inspection is nevertheless the most widely used detection method, augmented with pheromone traps. This species is an ideal candidate for acoustic detection because the adults are large, active borers that produce stridulations during courtship and mating. The stridulations have distinct, easily recognized temporal patterns. Larvae and pupae also produce stridulations. To assist in development of new detection methods, acoustic characteristics of the adult and larval stridulations have been quantified and compared with stridulations produced by larvae of other dynastids recorded in the western Pacific region.

Key Words: *Oryctes rhinoceros*, *Dermolepida albohirtum*, *Dasygnathus*, communication, stridulation, acoustic detection

Resumen

El *Oryctes rhinoceros* (L.) (Coleoptera: Scarabaeidae: Dynastinae) causa daño económico importante a las palmas de coco ornamentales y comerciales en la región occidental del Pacifico del oeste que podría ser mitigada significativamente por la detección temprana y tratamiento. Los adultos son difíciles de detectar visualmente por que ellos atacan la corona de las palmas y se alimentan internamente antes de aparearse y de ahi se dispersan a nuevos hospederos. Sin embargo, la inspección visual es el método de detección usado mas extensamente, aumentada con el uso de trampas de feromonas. Esta especie es un candidato ideal para la detección acústica por que los adultos son grandes, barrenadores activos que producen estridulaciones durante el cortejo sexual y el apareamiento. Las estridulaciones tienen un patrón temporal distinto y reconocido fácilmente. Las larvas y pupas también producen estridulaciones. Para ayudar en el desarrollo de nuevos métodos de detección, las características acústicas de las estridulaciones de los adultos y larvas han sido cuantificadas y comparadas con las estridulaciones producidas por las larvas de otros dinástidos reportados en la región occidental del Pacifico.

Stridulation has been identified in many coleopteran families (Wessel 2006) but relatively more is known about the morphology of the stridulatory organs in most of these species than about the acoustic characteristics and behavioral roles of the signals. It has long been known, for example, that adults, pupae, and larvae of the coconut rhinoceros beetle, *Oryctes rhinoceros* (L.), produce audible stridulations (Darwin 1871; Gressitt 1953). Mini & Prabhu (1990) described the stridulatory structures of adult *O. rhinoceros* and observed males that stridulated during courtship and mating, as well as during aggressive encounters with other males. It was not specified whether the stridulations produced in the different contexts were similar or different. Mated females stridulated occasionally, usually during interactions with males, but the function of these stridulations was unknown. Larvae and pupae of other beetle species also produce stridulations in response to disturbance (Palestrini et al. 1990), and stridulations have been shown to repel predators (Masters 1979; Hill 2007). However, the acoustic characteristics and much of the behavioral role of stridulations in *O. rhinoceros* and other beetles remain to be analyzed.

Because *O. rhinoceros* is a large insect that causes extensive damage to coconut (*Cocos nucifera* L.) and other palms (Gressitt 1953;

Hinckley 1973; Bedford 1980), acoustic characterization of its stridulations is of considerable practical use above and beyond any behavioral, physiological, or evolutionary considerations. Adults bore into and feed on the folded emerging fronds at the crowns of the palm trees, and frequent attacks by several adults eventually kill the tree (Gressitt 1953). It would be ideal to remove the insects, treat with pesticide or viruses, or cut down a tree soon after the first attacker enters the tree (Jackson & Klein 2006), but beetle attacks cannot be easily detected from the ground until well after significant damage has occurred. Visual inspection of frond and trunk damage is nevertheless the most commonly method of detection, augmented by traps baited with aggregation pheromone (Hallett et al. 1995; Ramle et al. 2005). Acoustic techniques have potential to detect adults that are moving and feeding in the crowns, as well as larvae that feed in standing dead trunks of previously killed palms (Mankin et al. 2000, 2002, 2008a, b). The reliability of acoustic methods improves considerably when stridulations and other behaviors can be detected and distinguished from background noise by automated digital signal processing tools. Here we describe stridulations recorded during acoustic detection studies conducted in Guam and Australia to provide basic information about stridulation behavior in *O. rhinoceros* and other dynastids, and also to assist efforts to detect *O. rhinoceros* in coconut trees in urban Guam and other areas with high background noise.

MATERIALS AND METHODS

Insects and Recording Procedures

In laboratory studies, *O. rhinoceros* adults and larvae were obtained from a rearing facility at the University of Guam. Recordings were done on different days from 3 separate groups of 10, 3, and 5 adults, respectively, held in different 30 × 24 × 24-cm plastic rearing cages containing short pieces of coconut palm trunk and fronds, and on 3 separate days from multiple larvae (numbers unknown) in other cages containing decaying pieces of palm trunk and detritus. Temperatures were ca. 24-26°C. Field re-

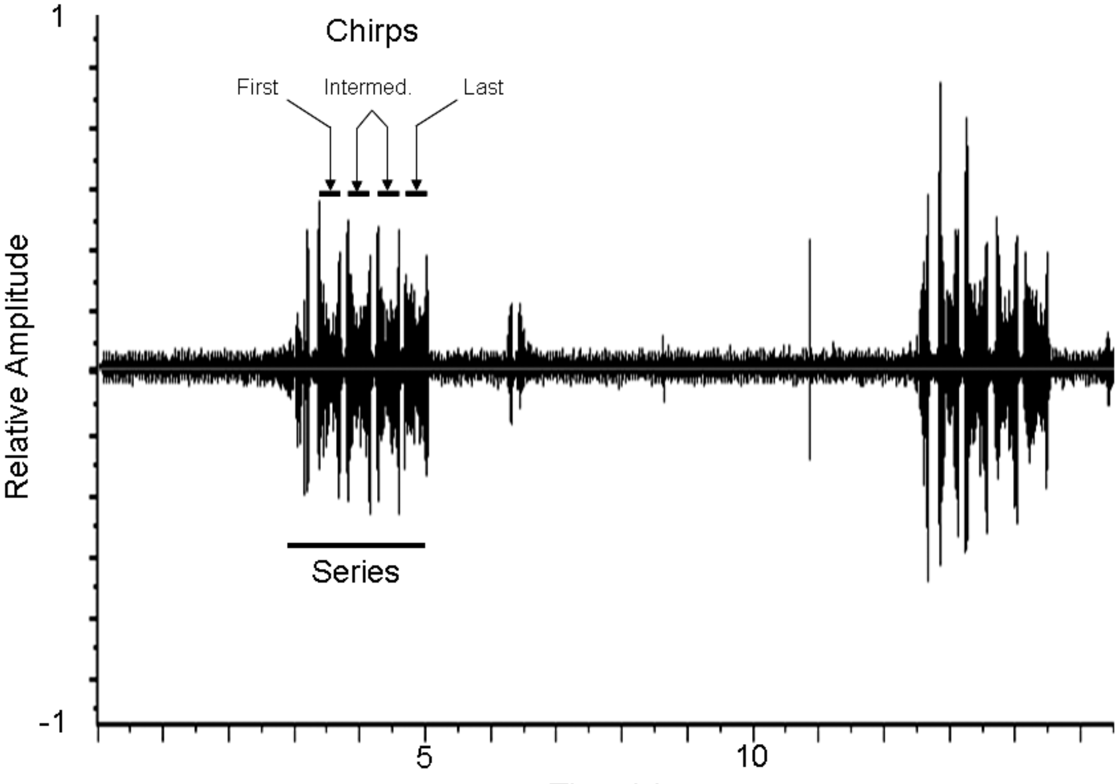

Fig. 1. Two series of 4 chirps recorded from a microphone placed over a plastic rearing cage holding 10 adult *O. rhinoceros*. Positions of chirps within a series are noted as first, intermediate, and last.

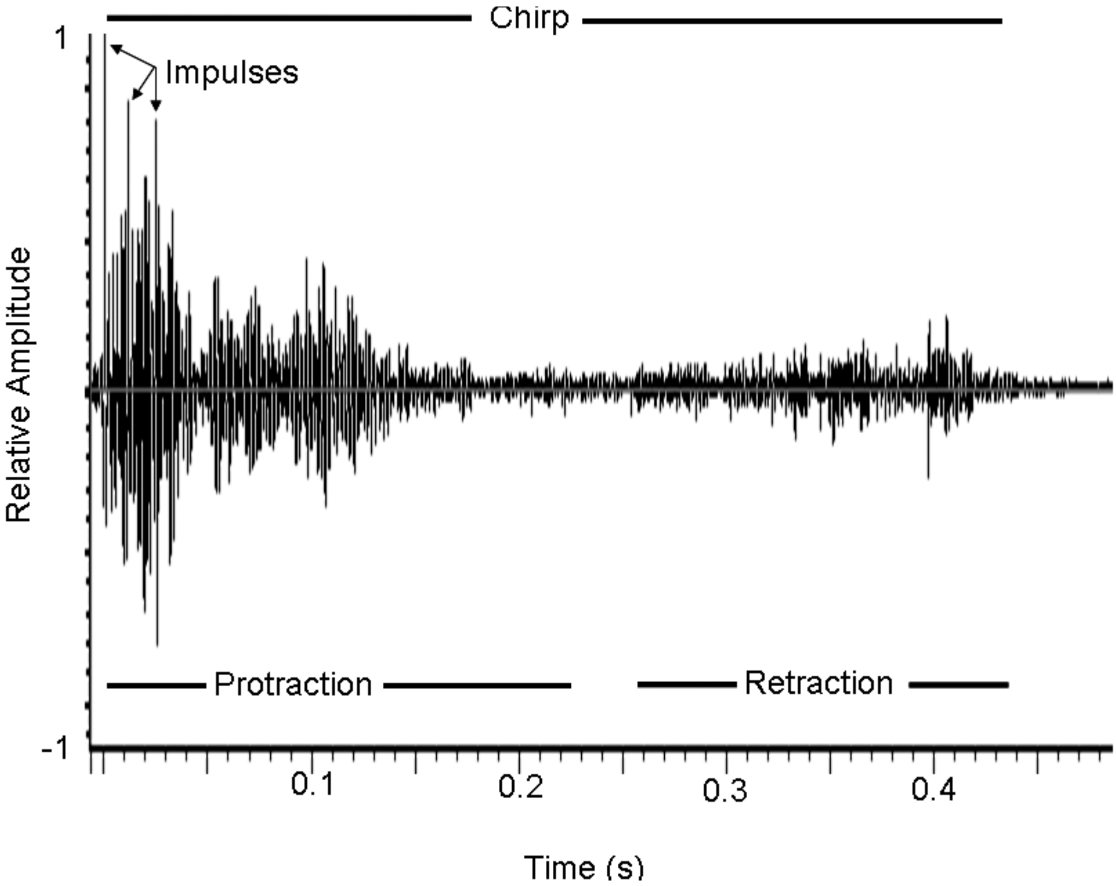

Fig. 2. Chirp recorded from an accelerometer attached to a second rearing cage holding 5 adults. As in most chirps, the impulses were variable in amplitude and temporal pattern, but generally highest in amplitude at the beginning and end. The protraction and retraction phases of the chirp were separated by a brief pause.

cordings of larval activity were obtained from dead coconut palm trees in the Tumon Bay hotel district of Guam at temperatures of 28-31°C (stridulations were detected at 2 of the 3 sites where larvae were recovered). The numbers of larvae recovered from the trees after recordings were obtained ranged from 3 to >50. In Australia, recordings of dynastids other than *O. rhinoceros* were obtained from sugarcane fields near the BSES laboratories in Mackay and Bundaberg, Queensland. Temperatures were 27-32°C.

Adult- and larval-produced vibrations were recorded by inserting a 30-cm-long steel probe into the substrate, usually a trunk or a section of a log, and magnetically attaching an accelerometer (model 4370, Brüel and Kjær [B & K], Nærum Denmark) connected to a charge amplifier (model 2365, B & K), as in Mankin et al. (2000, 2001, 2002). For detection of white grubs in Australian sugarcane fields, probes were inserted into the soil next to a sugarcane stool. Signals were stored on a digital audio recorder (model HD-P2, Tascam, Montebello, CA) at a 44.1 kHz-, 24-bit sampling rate and subsequently copied to a computer.

Adult stridulations of *O. rhinoceros* also were recorded from a rearing cage containing 10 adults by setting a MP3 recorder with an internal microphone on top of the cage.

Signal Processing

Digitized signals were analyzed with Raven 1.2 software (Cornell Lab of Ornithology, Ithaca, NY) and other dedicated signal sampling software developed in Matlab (MathWorks, Inc., Natick, MA), or with the customized software program, DAVIS (Mankin 1994; Mankin et al. 2000, 2008b). Signals were band-pass filtered between 0.5 and 5 kHz to eliminate low- and high-frequency background noise. Fast Fourier Transforms for spectrogram displays were calculated

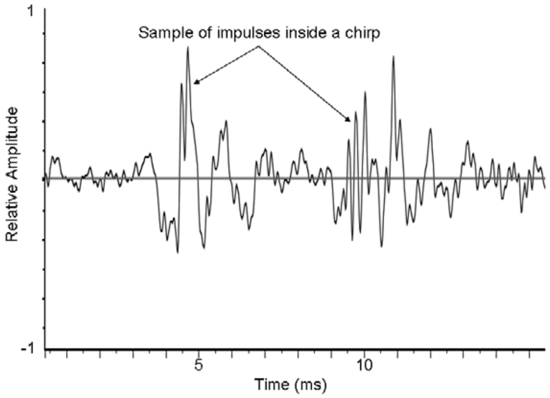

Fig. 3. Two consecutive impulses sampled from chirp in previous figure, showing typical variations of shape and duration.

on 64-point (1.5 ms-) time-slices of the waveforms in a Hamming window, and spectrograms were calculated by sections with 90 per cent overlap. Transforms for spectral comparisons were calculated on 512-point (11.6 ms-) time-slices, and all spectrum levels were referenced to the maximum acceleration, A_{max}, in the 0.5-5 kHz reference range, i.e., dB = 20 $\log_{10}(A/A_{max})$ (Mankin & Benshemesh 2006).

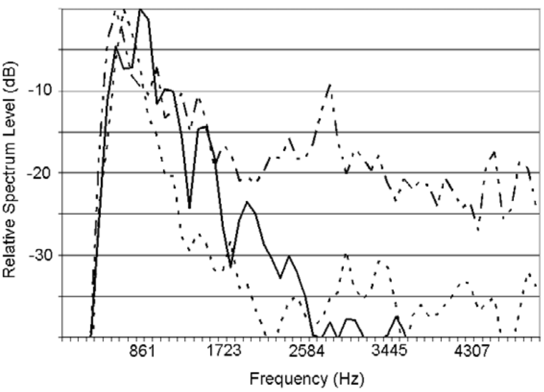

Fig. 4. Spectra of 0.1-s signals in chirps from 3 different adults in rearing cage containing various pieces of coconut palm tree trunks. The vertical axis indicates spectrum level relative to the highest level between 500 and 5000 Hz and the horizontal axis indicates frequency.

The DAVIS program identified and timed groups (trains) of impulses with interpulse intervals less than a preset duration, I_i, storing the beginning and end times of these trains in a spreadsheet along with the times of individual impulses and the numbers of impulses in each train. Im-

TABLE 1. MEAN DURATIONS AND STANDARD ERRORS OF THE PROTRACTION, PAUSE, AND RETRACTION PHASES OF THE FIRST, INTERMEDIATE, AND LAST CHIRP IN SERIES RECORDED FROM CAGED ADULT *O. RHINOCEROS*

	Mean (± SE) duration (ms) of phase of chirp at specified position			
Phase of chirp	First (*n* = 24)	Intermediate (*n* = 53)	Last (*n* = 24)	*P*1
Protraction	135.2 ± 16.0	169.4 ± 9.3	170.0 ± 15.0	0.0474
Pause	63.2 ± 10.8	54.1 ± 6.2	42.1 ± 7.3	NS
Retraction	153.6 ± 14.3	182.3 ± 8.7	188.8 ± 17.5	NS

[1] Probability under the Kruskal-Wallis test (*df* = 2) that the median durations for the specified phase of the first, intermediate (i.e., second up to penultimate), and last chirp in each series of chirps were equal; NS = Not Significant, mull hypothesis that median durations were equal was not rejected.

TABLE 2. MEAN AND STANDARD ERRORS OF NUMBERS OF IMPULSES IN THE PROTRACTION, RETRACTION, AND TOTAL PHASES OF THE FIRST, INTERMEDIATE, AND LAST CHIRP IN SERIES RECORDED FROM CAGED ADULT *O. RHINOCEROS*.

	Mean (± SE) number of impulses in phase			
Phase of Chirp	First (*n* = 24)	Intermediate (*n* = 53)	Last (*n* = 24)	*P*1
Protraction	14.8 ± 1.8	19.6 ± 1.2	19.3 ± 2.3	0.0441
Retraction	17.3 ± 2.1	21.0 ± 1.5	19.1 ± 2.3	NS
Total	32.1 ± 3.1	40.6 ± 2.3	38.5 ± 4.4	NS

[1] Probability under the Kruskal-Wallis test (*df* =2) that the median No. of impulses for the specified phase of the first, intermediate (i.e., second up to penultimate), and last chirp in each series were equal; NS = Not Significant. Null hypothesis that median numbers were equal was not rejected.

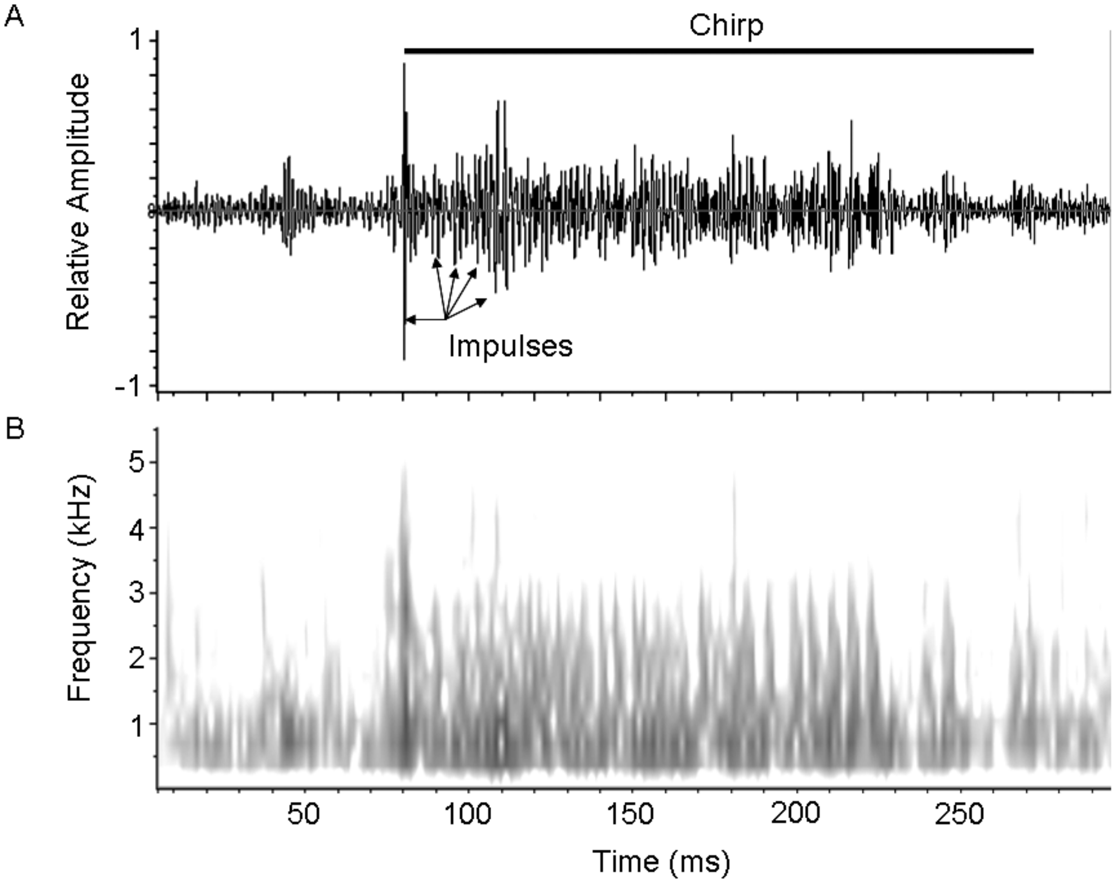

Fig. 5. Oscillogram (A) and spectrogram (B) of a chirp recorded from an *O. rhinoceros* larva in a palm tree trunk. The first 5 impulses in the chirp are marked by arrows. Darker shading in spectrogram indicates higher relative spectrum level.

pulses that failed to match 1 or more specified insect sound profiles (Mankin et al. 2000, 2007, 2008b) were discarded. The beginning of a train was set as the beginning of the first impulse after a period where the interpulse interval was > I_i, and the end was set as the end of the last impulse whose interpulse interval was < I_i. For this study, we set I_i = 250 ms, which resulted in trains that closely matched the timing of distinct sounds identified when the recordings were played back.

Comparisons among temporal and signal patterns of trains and impulses were conducted with nonparametric (NPAR1WAY) analyses in SAS (2004).

RESULTS

Adult Stridulations

Adult *O. rhinoceros* in rearing cages produced frequent, audible stridulations in multiple series of 3 to 6 (most frequently 4) chirps separated by variable intervals (Fig. 1). Individual chirps within a series contained a 3-phase sequence of protraction, pause, and retraction. The protraction phase (Fig. 2) contained high-amplitude, irregularly-timed impulses. As the protraction phase proceeded, the impulse amplitudes usually decreased. After a brief pause, the impulses then increased in amplitude until the end of the chirp (retraction phase, Fig. 2). In the example of Fig. 2, the rise in amplitude at the end of the chirp is not as pronounced as in most of the chirps in Fig. 1, and considerable variation was observed in amplitudes overall. Individual impulses within a chirp were variable in shape as well as amplitude, and ranged typically from 1 to 4 ms in duration (Fig. 3).

As observed in other studies of insect vibrations in different substrates (Markl 1983; Hirschberger 2001; Mankin et al. 2008a, b; Joyce et al. 2008), the spectral characteristics of the signals

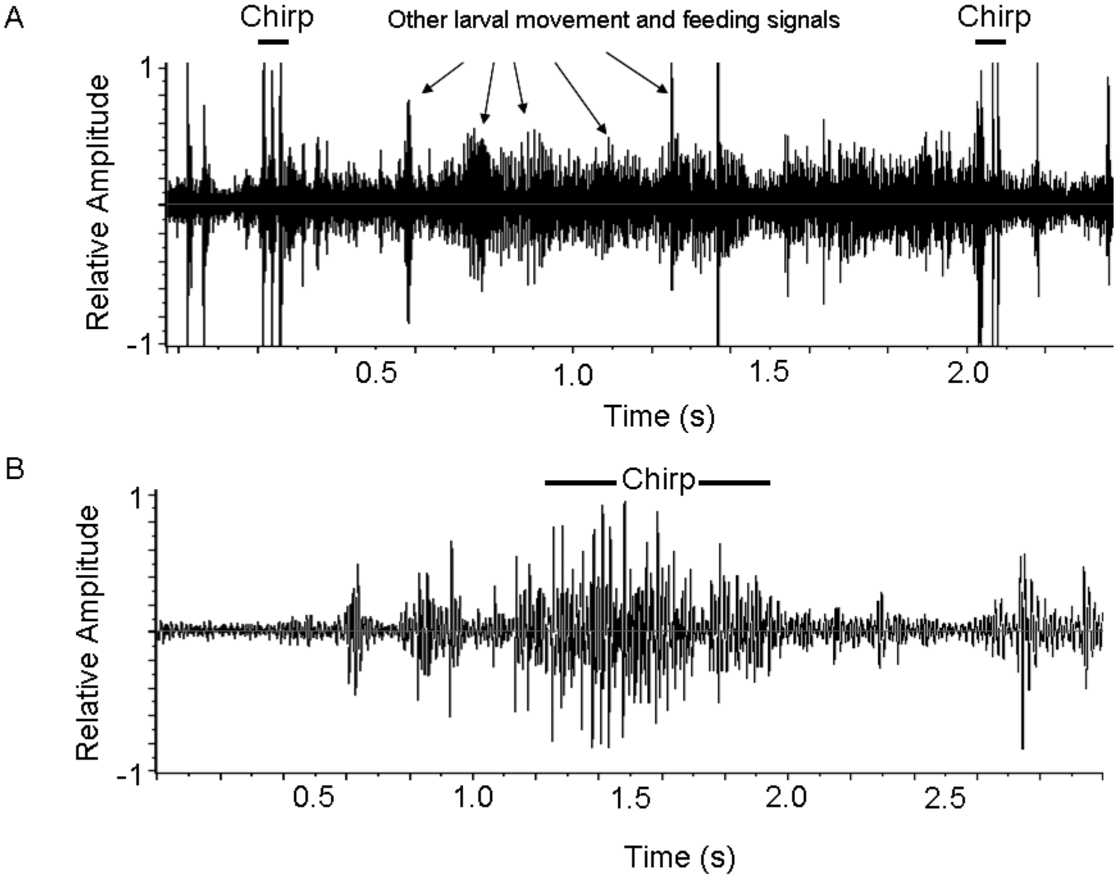

Fig. 6. Oscillograms of 2 short chirps (A) and a longer chirp (B) recorded from multiple *O. rhinoceros* larvae in a rearing cage. The chirps are embedded in other larval movement and feeding signals of similar amplitude.

recorded in the rearing cages depended on the resonance properties of the palm tree trunks or other substrates in which the adults were moving and feeding. Stridulations from males recorded on different substrates in the cage were distinctively different to the human ear and also had distinct frequency spectra, examples of which are shown in Fig. 4. These differences enabled listeners (and possibly the beetles themselves) to establish that different adults were stridulating at different times. It should be noted, however, that this is not a totally unambiguous method of identifying different individuals. Two adults stridulating within the same substrate might not produce distinctively different spectra. Also, they may not be distinguishable on the basis of chirp impulse rate. The 3 different adults whose stridulation spectra are shown in Fig. 4, for example, produced impulses at intervals whose medians were not significantly different under the Kruskal-Wallis *H*-test ($\chi^2 = 2.71$, $P = 0.25$, $df = 2$). The means and standard errors of the interpulse intervals of the second chirp (i.e., the first intermediate chirp) in the first series recorded from each adult were 11.2 ± 0.8 ($n = 32$), 11.9 ± 0.8 ($n = 30$), and 10.5 ± 1.3 ms ($n = 29$).

To consider the range of chirp durations and interpulse intervals that can be expected in different *O. rhinoceros* recordings, we examined chirps collected over approximately 1 h from 3 different rearing cages containing a total of 18 adults. When possible, we selected signals from separate adults, based on audible and spectral differences between chirps evaluated by playback of the recordings in the Raven signal analysis program. Comparisons of the durations of chirps in different series suggested that the durations of the first and subsequent chirps in a series were variable (Table 1, Fig. 1). However, the difference was statistically significant only for the protraction phase of the chirp. As with the durations, there were statistically significant differences in the

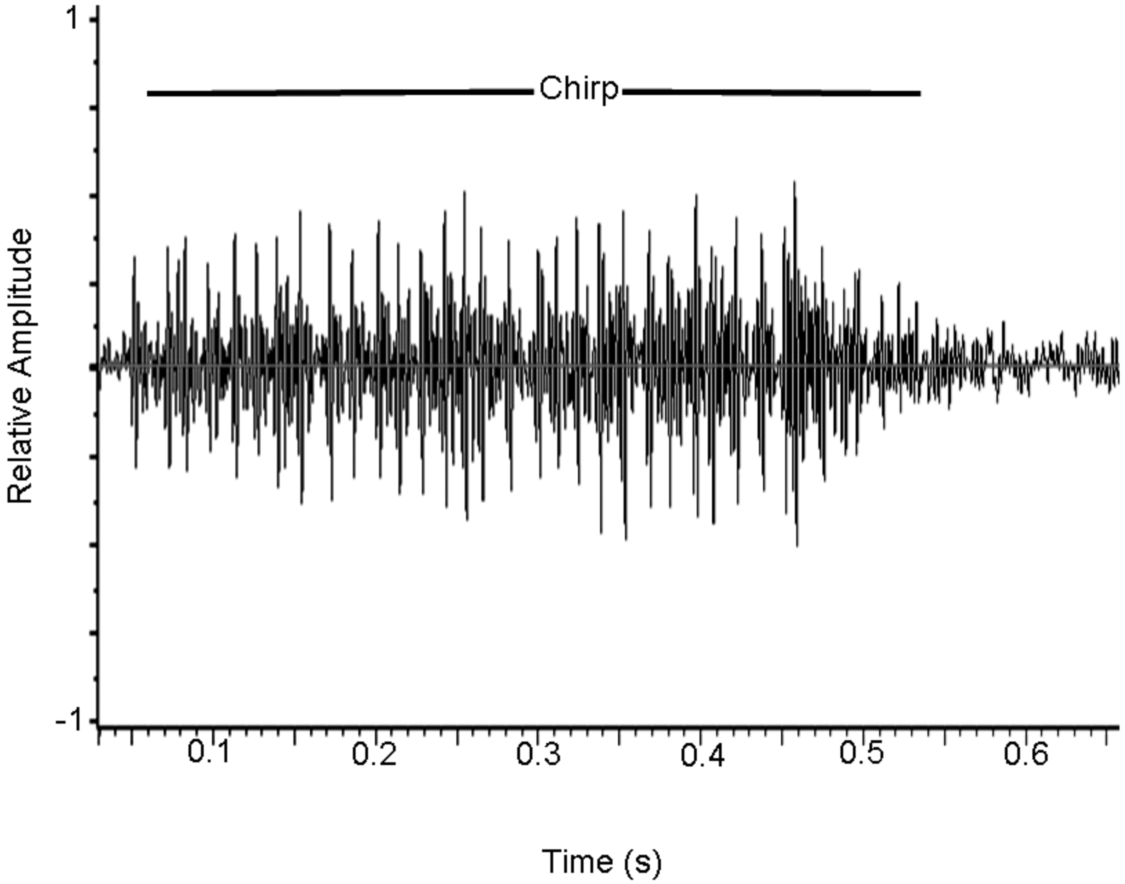

Fig. 7. Short, unpatterned chirp recorded from a dynastid larva in sugarcane field near Bundaberg, Australia.

mean numbers of impulses occurring in the protraction phases of the first and subsequent chirps in a series (Table 2). The mean interval between chirps within a series was 77.2 ± 6.0 ms, similar to the mean pause between the protraction and retraction phases of the chirps.

Larval Stridulations

Stridulations from *O. rhinoceros* larvae were detected in field recordings from palm trees (Fig. 5) and in 1 of 6 recordings from rearing cages containing multiple larvae feeding on pieces of palm tree fronds and trunk (Fig. 6). Unlike the chirps produced by adults, the larval chirps did not occur in a series and had no discernible pattern of amplitudes. The chirp durations were highly variable, and the amplitudes were lower than for adults.

The *O. rhinoceros* signals were similar in many respects to larval stridulations of other dynastids recorded in a recent survey conducted in Australia to detect root-feeding melolonthines (Agnew 1997; Miller & Allsopp 2000) in sugarcane. Stridulations were recorded at a site near Bundaberg, AU (Fig. 7), from which a dynastid larva was excavated. Stridulations also were recorded at a site near Mackay, AU (Figs. 8 and 9), from which a larva subsequently identified as *Dasygnathus* sp. was recovered along with several nonstridulating invertebrates, including 2 earthworms, a cockroach, a tenebrionid larva, and a larva of an economically important root-feeding melolonthine scarab, *Dermolepida albohirtum* (Waterhouse). Some of the chirps (Figs. 8 and 9A) had an amplitude pattern similar to that seen for adult *O. rhinoceros* in Fig. 1. Other chirps appeared to be without pattern (Fig 9B) similar to those detected from *O. rhinoceros* larvae (Figs. 5 and 6). The mean interpulse in a randomly sampled Dynastinae chirp recorded at Mackay was 4.0 ± 0.4 ms (*n* = 27), and was similar to the mean interpulse in-

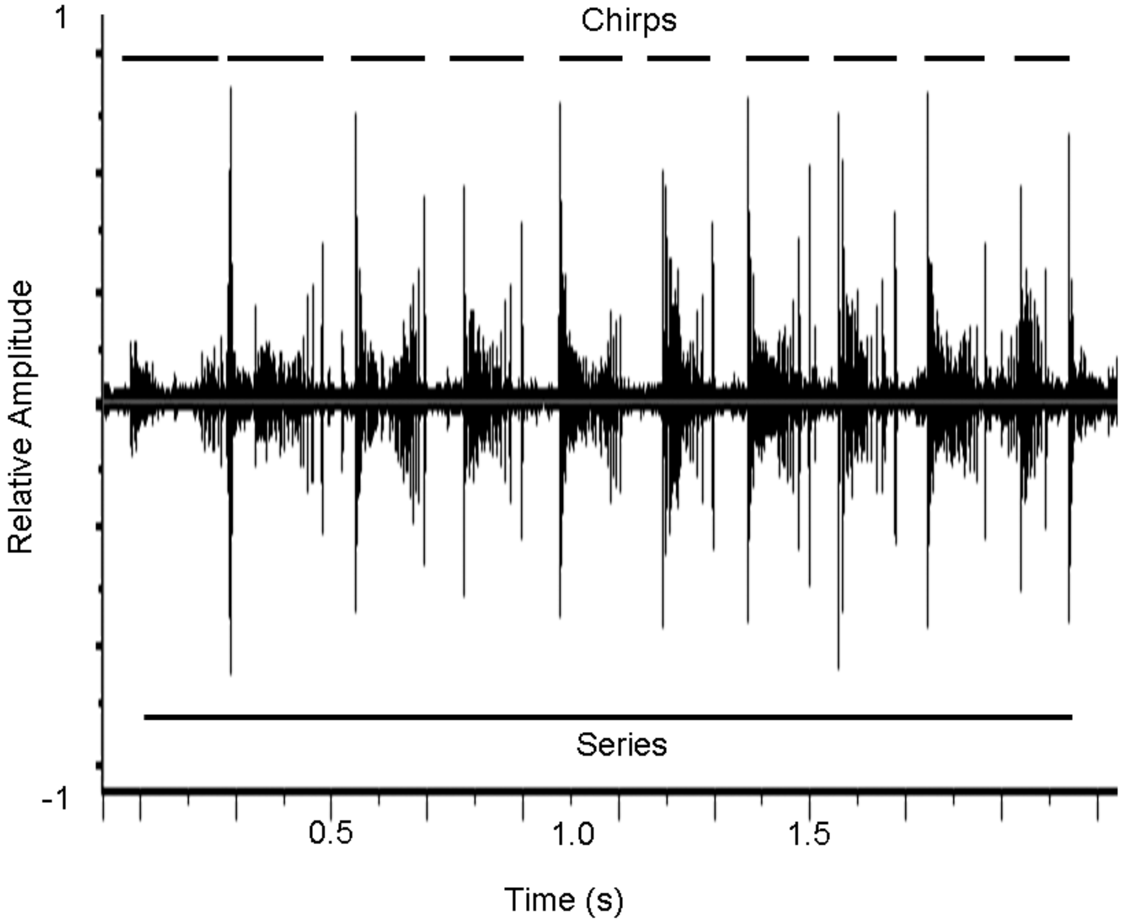

Fig. 8. Sample series of chirps recorded from a *Dasygnathus* sp. rhinoceros beetle larva in a sugarcane field near Mackay, Australia.

terval of a chirp sampled at random from a cage with *O. rhinoceros* larvae in Guam (3.44 ± 0.4 ms, $n = 16$). The median interpulse intervals were not different in a Mann Whitney U test ($U = 299$, $Z = -1.38$, $P = 0.17$). In general, the amplitudes of impulses in chirps were smaller and the intervals between impulses were shorter for the Australian dynastid larvae and the *O. rhinoceros* larvae than for the adult *O. rhinoceros*.

DISCUSSION

The occurrence in this study of several periods when a series of chirps produced by 1 adult was followed immediately by series produced by other adults supports previous hypotheses that stridulation may play an important role in intraspecific communication of this and other scarabaeoids in hidden environments (Mini & Prabhu 1990; Hirschberger 2001; Carisio et al. 2004; Kasper & Hirschberger 2006). Also, the similarities of disturbance stridulations among rhinoceros beetle larvae in Guam and Australia suggest that similarities may be found as well among stridulations produced by other dynastid larvae. It is likely that *O. rhinoceros* stridulations will remain of interest in future basic studies of insect communication behavior.

In addition, the relative uniformity of interpulse intervals and chirp amplitude patterns observed during stridulatory behavior may be of practical interest in future acoustic monitoring of *O. rhinoceros* in coconut palm trees. If stridulations similar to those recorded here from adults were detected at the base of a live tree, it could be predicted that adults (most likely males, Mini & Prabhu 1990) were present in the crown. Similarly, if stridulations similar to those recorded here from larvae were detected at the base of a standing dead tree, it would predict that larvae were present in the rotten part of the upper trunk. However, the larval stridulations would

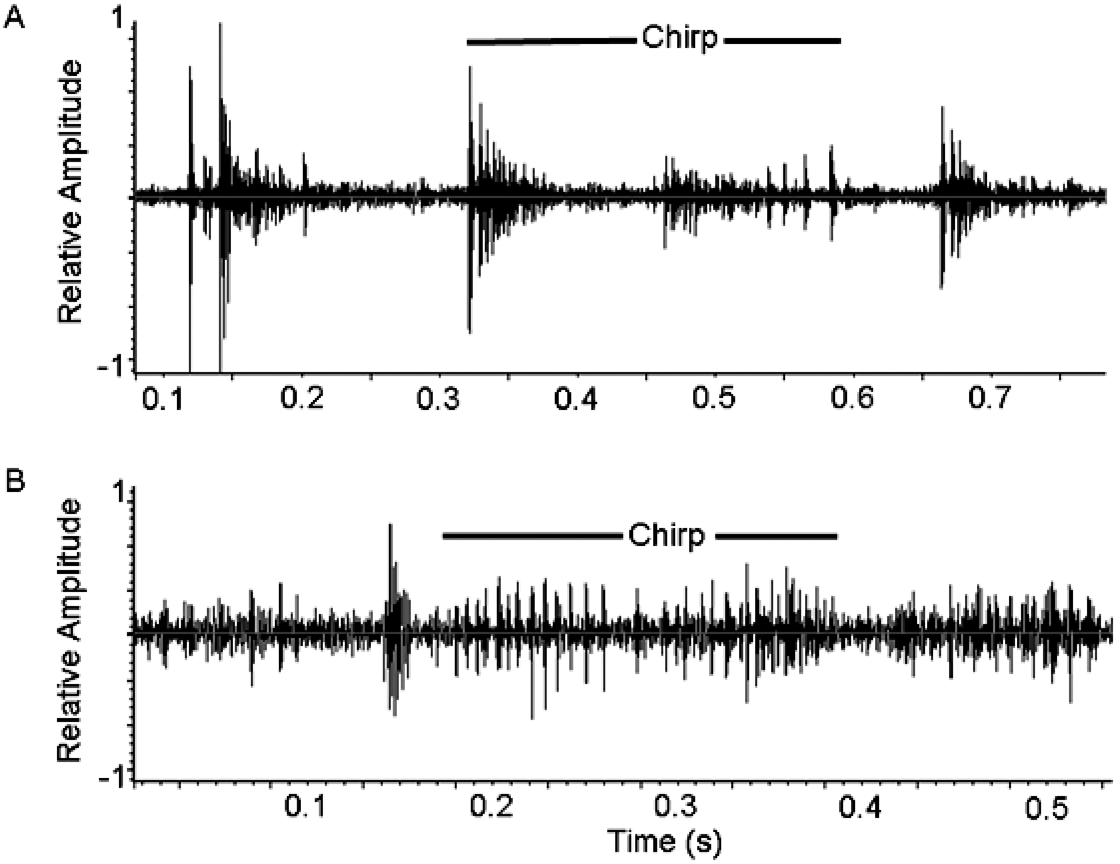

Fig. 9A. Expanded version of a single chirp from Figs. 8 and 9B. Sample chirp of a different pattern appearing at a later time in recording from same site in a sugarcane field near Mackay, Australia.

not be expected to occur as frequently or as loudly as with adults in the crown of a live tree. Either adult or larval stridulations would be easier to detect than unpatterned movement and feeding sounds because the occurrence of a pattern in the target signal enables unpatterned nontarget signals to be averaged out over time (Mankin et al. 2000, 2008b).

We noted with interest the numbers of impulses that occurred within adult *O. rhinoceros* chirps and the durations of intervals between chirps within series. In previous acoustic studies of larvae of the red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Mankin et al. 2008a) and the Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Mankin et al. 2008b), it had been determined that particular classes of impulse trains, denoted as bursts, were good predictors of the presence of insect infestation at a recording site. For *R. ferrugineus*, the bursts were defined as trains with >6, but <200 impulses, separated by intervals <500 ms. For *A. glabripennis,* bursts were defined as trains with >6, but <50 impulses, separated by intervals <250 ms. For this study, the results in Table 2 suggest that a series of chirps could be defined as a burst, in which case the minimum number of impulses could be as few as 6, as in the examples above, and the maximum could be the number of impulses in a series of 5 chirps of 40 impulses, or ca. 200 impulses, as with *R. ferrugineus.* In this case, and perhaps also with *R. ferrugineus* and *A. glabripennis*, the acoustic feature defined as a burst may be interpretable as a sound produced by stereotyped behaviors such as abdominal movements or the movement of legs or other body parts.

The stridulating dynastids detected in sugarcane fields near Bundaberg and Mackay were not considered pests because they fed primarily on decaying vegetation and detritus. At the Mackay site, however, the dynastid was present with a root-feeding larval pest, *D. albohirtum*. To unambiguously identify both insects in this case would require knowledge also of a signal feature that is associated with the presence of *D. albohirtum*, perhaps a specific behavior performed only by this pest. Indeed, a grand challenge of acoustic detection surveys is to identify and characterize multiple features of pest and nonpest signals, like the dynastid larval stridulations, or previously described termite head-bangs and ant stridulations (Connétable et al. 1999; Rauth & Vinson 2006; Mankin & Benshemesh 2006), and use these features to identify and discriminate target pests from nontarget organisms.

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