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Bioacoustics and Niche Differentiation in Two Cicada Species from Bornean Lowland Forest

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Abstract. Calling songs and disturbance squawks of two abundant Bornean cicada species, *Dundubia vaginata* (FABRICIUS 1787) and *Pomponia imperatoria* (WESTWOOD 1842) were recorded and analyzed, to be used for further ecological studies. Songs of both species are characterized by constant carrier frequencies with higher harmonics and exhibit a species-specific temporal structure. The elementary sound pulses, produced by tymbal clicks, are damped in *D. vaginata*, while they are coherent in *Pomponia imperatoria*. On the abdomen of *D. vaginata*, thin transparent cuticular areas are described which could serve as additional sound radiators. Power spectra of disturbance squawks show only one dominant frequency, coinciding with the fundamental frequency of the respective calling songs, but without its higher harmonics. Their species-specific calling songs are easy to recognize in the field. Acoustic monitoring of song activity revealed that *P. imperatoria* sings only at dusk, while *D. vaginata* can be heard during the day and at dusk. These results show that acoustic monitoring is a valuable tool to study the composition and regional distribution of species-rich tropical cicada communities.

Key words. Cicadidae, behaviour, bioacoustics, South East Asia, niche differentiation

1. INTRODUCTION

Among the numerous voices within tropical rainforests, cicada songs are the most intense and complex sounds to be heard during daytime from dawn to dusk. As in many other insect groups, diversity of Cicadidae is highest in tropical forests: 142 species are reported from Malaysia (MOULTON 1923). The taxonomy of these generally large insects is comparatively well known, though some genera are in need of revision. Songs are species-specific, and once identified their analysis could facilitate taxonomic studies of morphologically similar species, as for example the genus *Dundubia* (OVERMEER & DUFFELS 1967). Based on comparative studies of cicada songs, PRINGLE (1955) and HAGIWARA & OGURA (1960) began to correlate the structure of songs with current taxonomic schemes. Unfortunately, this approach has not been pursued, though the large number of tropical cicada species provides ample opportunity to continue this comparative approach. In the field, identified songs

could be of immense value for inventorying and monitoring tropical cicada species without the necessity of capturing specimens (RIEDE 1993). The knowledge of songs is of great value to collect data on life history and diel periodicity of these large but cryptic tropical forest insects. In spite of these advantages, only few studies on tropical cicada songs exist (PRINGLE 1954; ENGER et al. 1969 DUFFELS 1988). This might be due to the extreme difficulties in spotting songsters in their forest habitat. A possible solution could be a somewhat indirect approach, i.e., to correlate disturbance squawks of captured specimens with calling songs taped at the respective localities. The present paper investigates if such an inference is possible by comparing disturbance squawks and the fine structure of calling songs from two common Bornean cicada species, *Dundubia vaginata* (FABRICIUS 1787) and *Pomponia imperatoria* (WESTWOOD 1842). A further aim of this study is to provide information on their ecology and phenology by evaluating sound recordings from different sites and seasons.

2. MATERIAL AND METHODS

2.1. Study sites and periods

Investigations were made at Mt. Kinabalu National Park, Sabah, Malaysia, in a lowland mixed dipterocarp forest at Poring Hot Springs (500-900 m asl), along Langanan river trail and Langanan waterfall (500-1100 m asl), at mountain forest around Park Headquarters (1500 -2300 m asl) and sub-montane forest at Sayap (900m); for a general description of habitats see KITAYAMA (1992). A canopy walkway system with a total length of 900 m was available at Poring. Observations were made from April to June 1991, February until April and August 1992, March until May and October 1993, thereby covering different seasons and weather conditions.

2.2. Recording

Individual songsters were recorded and localized by a custom-made highly directional microphone consisting of an electret microphone capsule with inbuilt FET-amplifier (type MCE-2000, frequency range 30-20.000 Hz, ±2dB) mounted into a parabolic perspex reflector (PBR-330, Sony, diameter 33 cm) and recorded by a stereo cassette recorder (Sony TCD5-PRO, frequency response 40-16000 Hz ±3dB [NAB]). Sound intensity was measured by a soundlevel meter (Noris NM-3) with a dB(A) frequency weighting.
Animals were collected at night where they gathered at artificial lights. *D. vaginata* occured in great numbers, while *P. imperatoria* was rarer and was only observed after the middle of march. Disturbance squawks could be elicited easily by slight touch in freshly caught specimens. In general, caged specimens do not sing. Fortunately, in a few cases songs could be recorded from caged specimens, especially when exposed to songs from congeners. This allowed unequivocal correlation of songs to voucher specimens which are deposited in the collection of K.R. Recordings used for frequency analysis were made without parabolic reflector, to avoid frequency distortions.

2.3. Sound analysis and classification

Sounds were visualized with a spectrum analyzer (Spectro 2000, MEDAV) which produced an on-line Fast Fourier Transformation visible on a colour monitor. For further analysis, records were sampled into a computer (Tandon 486/33, Compaq) via an analog-digital converter (DT2821, Data Translation) at a sampling frequency of 30 kHz and analyzed with a signal processing software (Hypersignal Acoustic, Hyperception Inc.).

2.4. Morphology

Cuticular thickness of distinct parts of the abdomen of *D. vaginata* was measured with a dial gauge (Mitutoyo) with an accuracy of 1 μm, using small rectangular pieces of cuticula cut from dried specimens. Drawings were made from transverse cuts of dried specimens under a dissection microscope.

3. RESULTS

3.1. Song structure

3.1.1. *Dundubia vaginata*, calling song. Compared to other cicada species from the area, the song structure is quite simple (fig. 1a,b). The basic elements are phrases composed of two easily distinguishable parts (A and B). Phrases are separated by pauses of 85 ms (mean duration 85 ms, s.d. 18 ms, n=170 phrases from 10 animals). From the same data, the mean duration of the shorter starting sequence (A-part) was determined to be 139±31 ms, and the mean duration of the much longer main sequence (B-part) with 1656±327 ms. At a higher time resolution clearly separable chirps of 9 ms length, separated by 2.5 ms intervals, are visible within the B-part. In the middle of the B-part chirps are grouped into hyperstructures consisting of three elements, the triplets. This rigid song structure is maintained uninterruptedly up to several minutes. Songs start with a prelude of up to 40 s length, and terminate with a coda around 20 s long. Both prelude and coda resemble part B and are made up of chirps of similar length, but triplets are formed only irregularly, so that they resemble a stuttering motor.

The fine structure of single chirps from the B-part (fig. 1d) suggests that each chirp corresponds to the sound pulses generated by the inward tymbal movement, while the interchirp interval probably corresponds to the toneless outward movement of the tymbal (cf. HENNIG et al. 1994). In contrast, the underlying waveform of the A-part is a continuous train of damped pulses (fig. 1c). The power spectrum of a phrase (fig. 1e) consists of a fundamental frequency of 940 Hz and higher harmonics, revealing prominent peaks around 2.6 and 3.7 kHz. A comparison of power spectra from A- and B-part (fig. 1f,g) shows impurities within part B, due to modulation with the chirp repetition rate of 80 Hz, while the continuous wave form within part A results in sharper frequency bands (see discussion). Fundamental and carrier frequency is slightly lower within part A.

***Dundubia vaginata*, disturbance squawk.** The disturbance squawk consists of short chirp sequences which are remarkably similar in length to the chirps making up the B-part of the calling song, but differ in frequency composition (fig. 2a, b). As shown by the power spectrum (fig. 2c), they contain mainly the fundamental frequency of 900 Hz, without any higher harmonics. The underlying wave train of each pulse clearly reveals seven peaks (fig. 2d), which could correspond to the successive stimulation of seven sclerotized tymbal ribs during inward buckling of the tymbal.
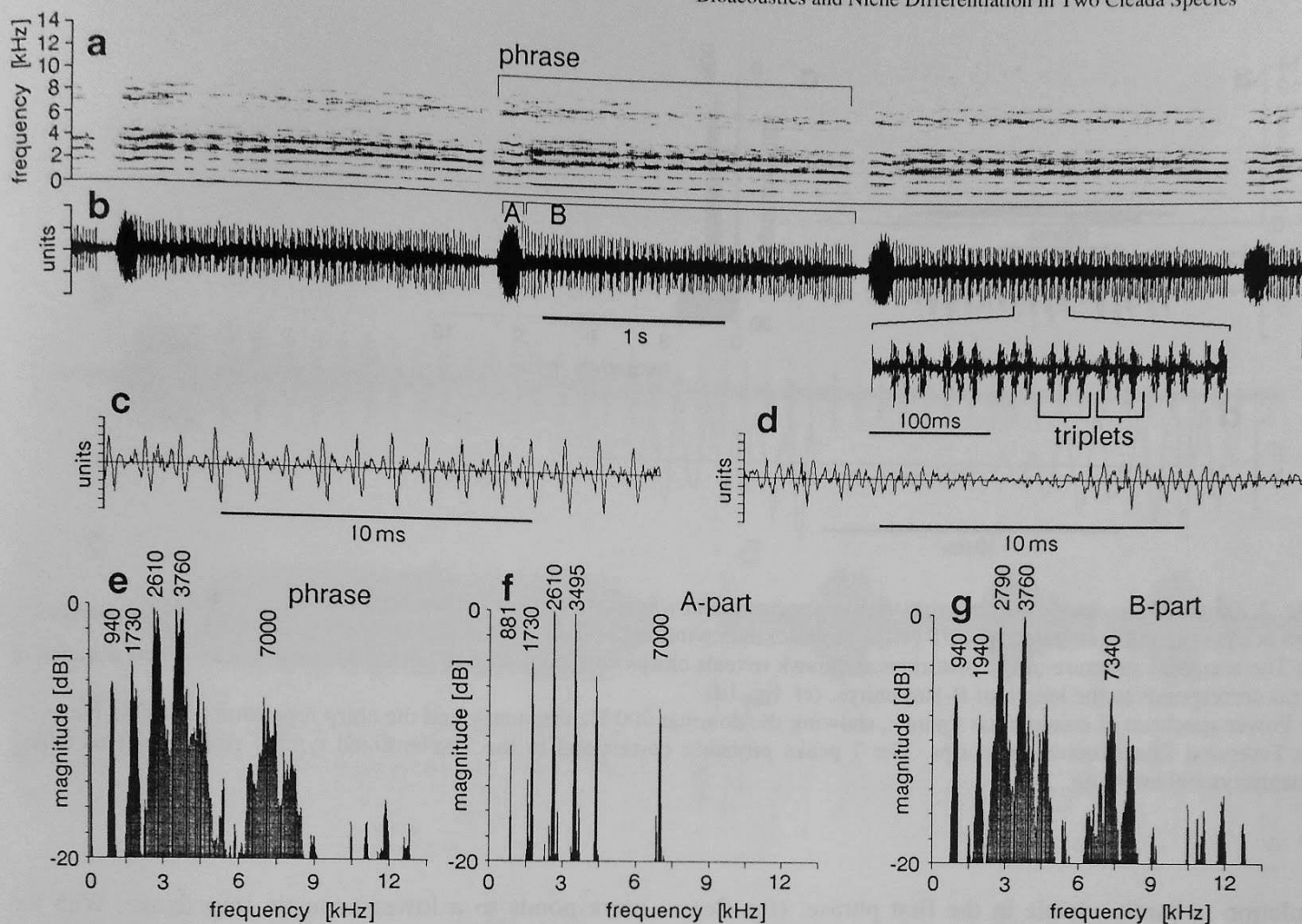
Fig. 1. *Dundubia vaginata*: Spectrogram, waveforms and power spectra of the calling song.

a) Spectrogram of two phrases generated by Fast Fourier Transformation (FFT;1024 pt, Blackman window). The starting chirp (A-part) is characterized by clearly separated frequency bands, while the following B-part consists of short chirps and a rougher spectrum.

b) Temporal structure of calling song at low time resolution revealing the structure of chirps. The A-part consists of one longer chirp , while the B-part consists of much shorter chirps arranged in groups of three ("triplets") during the middle part.

c) Temporal structure of A-part at high time resolution, showing highly damped continuous wave trains.

d) Temporal structure of a chirp from a triplet at high time resolution. Chirps are clearly separated, pauses probably correspond to a toneless outward tymbal oscillation.

e) Power spectrum of a whole phrase, revealing maxima at 2610 and 3760 Hz. The prominent side bands at 1.8 and 3.5 kHz can be explained by modulation of the 2.6 carrier frequency by the 940 Hz fundamental frequency.

f) Power spectrum of the A-part, revealing much sharper frequency bands due to a less deep modulation by the slightly lowered fundamental frequency of 880 Hz.

g) Power spectrum from 300 ms sequence of triplets, showing more impurities due to an additional modulation by the triplet repetition rate (around 80 Hz); the fundamental is slightly elevated (940 Hz).

3.1.2. *Pomponia imperatoria*, calling song. The spectrogram and time structure of the conspicuous *P. imperatoria* song are shown in fig. 3. Songs with an average duration of 18 s (n=8) are repeated irregularly after pauses between 30 s and several minutes. The sound is very similar to a blast of a flourish of trumpets, and the song can be described quite accurately as a sequence of blasts of decreasing duration, becoming clearly separated and fainter towards the end of the song (fig. 3b-d).

Spectrogram and power spectra show a constant fundamental frequency of 730 Hz with higher harmonics throughout all song parts, with a dominant carrier frequency at 3.6 kHz (fig. 3g). As shown by the power spectra (fig. 3g-i), frequency composition remains similar during all phrases. The underlying waveform of chirps (fig. 3e,f) consists of coherent oscillations at the carrier frequency of 3.6 kHz (fig. 3g), with a slight amplitude modulation at the fundamental frequency of 700 Hz. Wave trains are coherent, and amplitude mo-
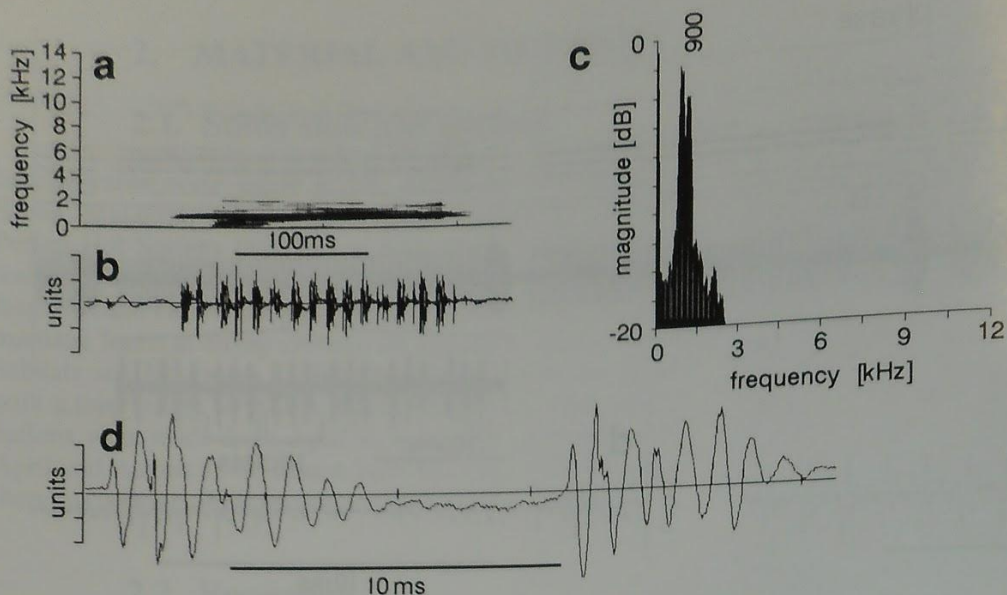
Fig. 2. *Dundubia vaginata*: spectrogram, power spectrum and waveform of disturbance squawk.
a) The spectrogram generated by FFT (1024 pt, Blackman window) reveals a dominant frequency of 900 Hz.
b) The temporal structure of the disturbance squawk reveals chirps corresponding to outward tymbal clicks. Their duration of 8 ms corresponds to the length of B-part chirps. (cf. fig. 1d)
c) Power spectrum of disturbance squawk, showing the dominat 900 Hz frequency and the chirp repetition rate of 88 Hz.
d) Temporal fine structure of chirps. The 7 peaks probably correspond to the 7 sclerotized tymbal ribs stimulated during inward tymbal buckling.

dulation is barely visible in the first phrase, (fig. 3e), but much deeper in the following ones (fig. 3f). This results in sharper frequency bands when comparing power spectra of the first chirp (fig. 3h) with those from following ones (fig. 3i).
The first chirp is characterized by a dramatic crescendo and a duration of 1300±200 ms, while the following chirps are significantly shorter (270±50 ms) and fade out towards the end of the song.

Pomponia imperatoria, **disturbance squawks.** The spectrum and time structure of the disturbance squawk is depicted in fig. 4. It consists of a pure fundamental frequency of 700 Hz (fig. 4c). The fine structure of pulses (fig. 4d) shows that tymbal clicks are not as clearly separated as in *D. vaginata*, probably due to a tonal in- and out movement of the tymbal.

3.2. Morphology

3.2.1. *Dundubia vaginata*. Males of *D. vaginata* are characterized by long opercula, covering the first 5 abdominal segments and two rectangular transparent areas of 5 mm length and 3 mm broad at the 2. and 3. abdominal segment (fig. 5). The thickness of the abdominal cuticula was determined by a dial gauge and lies around 30μm (fig. 5), while the cuticula of the transparent rectangle is much thinner (10μm). This probably

corresponds to a lower acoustic impedance. With the opercula removed, it is possible to observe vigorous vibrations of the transparent areas during disturbance squawks. This means that acoustic energy is mainly radiated via these windows and modulated by the overlying opercula.

3.2.2. *Pomponia imperatoria*. With 6 cm body length, *P. imperatoria* belongs to the largest tropical cicadas. Based on subtle differences in coloration, DISTANT (1905) differentiates *Pomponia merula* Distant 1905 from *P. imperatoria*. Moulton (1923) suspects that *P. merula* replaces *P. imperatoria* in Borneo, but a thorough revision, possibly including song analysis, is necessary to decide their systematic status. Meanwhile, we will use the older name of *P. imperatoria* for the specimens studied here.
The opercula are short, covering only the tymbal, and no transparent areas as in *D. vaginata* are visible.

3.3. Temporal and spatial distribution

3.3.1. *Dundubia vaginata*. *D. vaginata* songs could be heard during all months covered by our investigation, i.e. between February and October. Abundance of adults flying to artificial lights as well as song activity of mature males show a maximum between March and April. Individuals start singing around 11:30. Song ac-
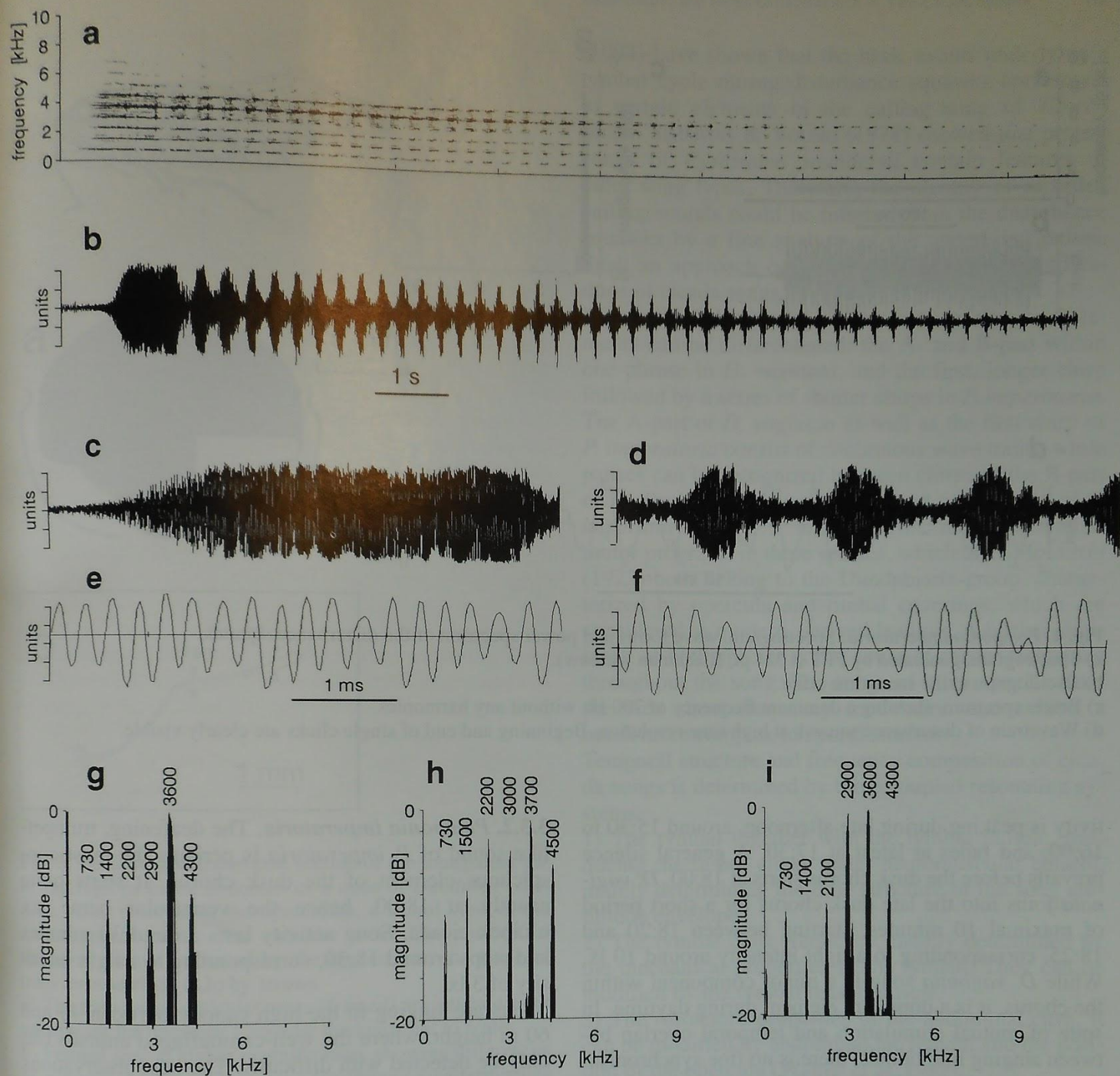
Fig. 3. *Pomponia imperatoria*: Spectrogram, wave forms and power spectrum of the calling song.

a) Spectrogram of a calling song, generated by FFT (1024 pt, Blackman window).
b) Oscillogram at the same time scale. The first chirp is longer and louder than the following chirps, which fade towards the end of the song.
c) Oscillogram of the first phrase at higher time resolution.
d) Oscillogram of the following, shorter phrases at higher time resolution.
e) Wavetrains from the first chirp show only slight modulation.
f) Wavetrains making up successive chirps show much deeper modulation, but are coherent without interrruption.
g) Power spectrum of entire calling song, showing the prominent carrier frequency of 3600 Hz.
h) Power spectrum of 1 s from the first chirp, showing sharp frequency bands.
i) Power spectrum from 1 s of successive chirps, showing broader frequency bands.
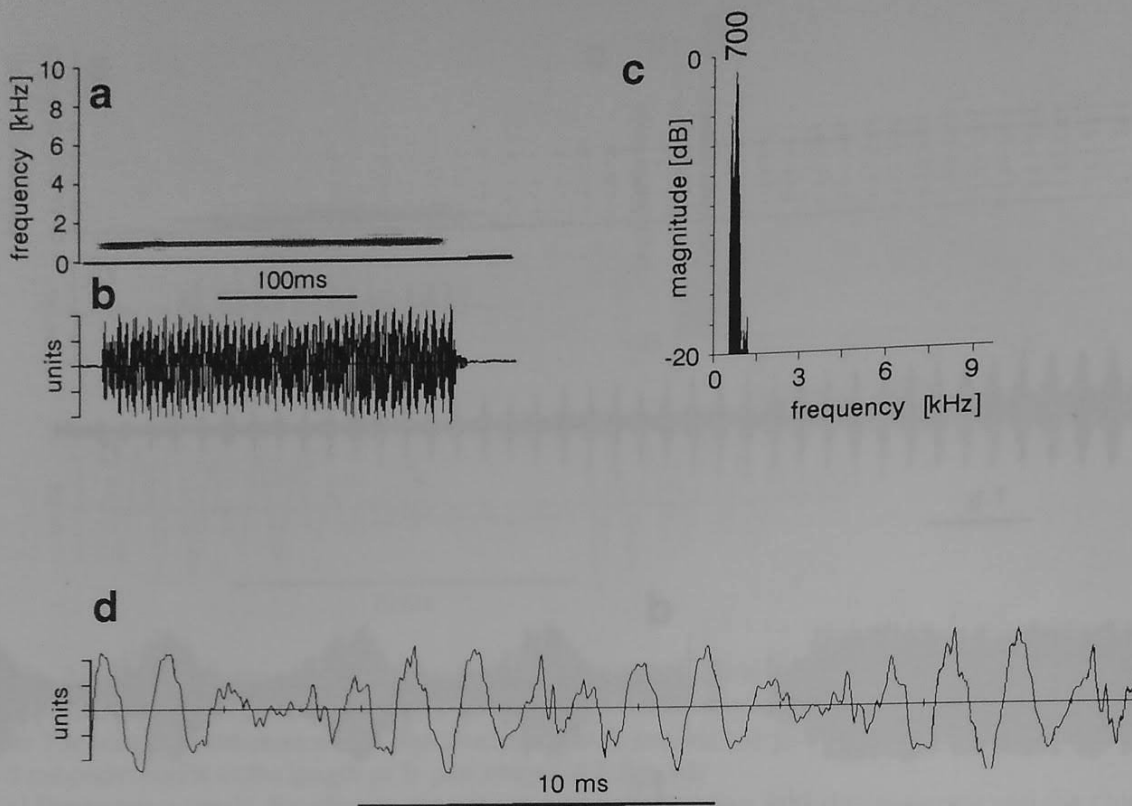
Fig. 4. *Pomponia imperatoria*: Spectrogram, wave forms and power spectrum of the disturbance squawk.
a) Spectrogram, generated by FFT (1024 pt, Blackman window).
b) Oscillogram at the same time scale.
c) Power spectrum, showing a dominant frequency of 700 Hz without any harmonics.
d) Wavetrain of disturbance squawk at high time resolution. Beginning and end of single clicks are clearly visible.

tivity is peaking during late afternoon, around 15:30 to 16:00, and fades at latest at 17:30. A general silence prevails before the dusk chorus starts at 18:00. *D. vaginata* joins into the late dusk chorus for a short period of maximal 10 minutes, starting between 18:20 and 18:25, corresponding to a light intensity around 10 lx. While *D. vaginata* song is a minor component within the chorus, it is a dominant element during daytime. In spite of mutual stimulation and temporal overlap between singing individuals, there is no fine synchronisation of songs. At brightly lit full-moon nights, some singing individuals could be heard.

In mature mixed dipterocarp forests, individuals sing at the lower strata, sitting on stems at a height between one and several meters. *D. vaginata* is among the few species to be heard in severely degraded forests, but it is not clear if populations reproduce at these sites, or immigrate from undisturbed habitats.

Interestingly, *D. vaginata* individuals where caught but not heard at Headquarters (1500 m) and Sayap (900 m), but singing males are restricted to lowland and lower montane mixed dipterocarp forest. *D. vaginata* is widely distributed in the Greater Sunda Islands, the Philippines, and the mainland of South East Asia (J. P. DUFFELS, in litt. 1992).

3.3.2. *Pomponia imperatoria*.

The deafening, trun like sound of *P. imperatoria* is perhaps the most spicuous element of the dusk chorus. It starts exactly at 18:00, hence the vernacular name o'clock cicada. Song activity lasts around 30 min and stops around 18:30, corresponding to a light in sity of 3 lx.

Males are singing in the high canopy between 40 60 m height, where the well-camouflaged animals only be detected with difficulty. The best observat and recordings were made from the canopy walk system at Poring. Males change positions between not during their songs. The species is associated lowland and lower montane mixed dipterocarp fo At Poring, it could be heard from March until Nov ber. In warm nights, males and females approach ar cial lights, but never in great numbers.

4. DISCUSSION

Bioacoustic monitoring is a powerful tool for stud life history, phenology, diel periodicity and regi distribution of species-rich tropical cicada commu ties. However, identification of songsters is diffi
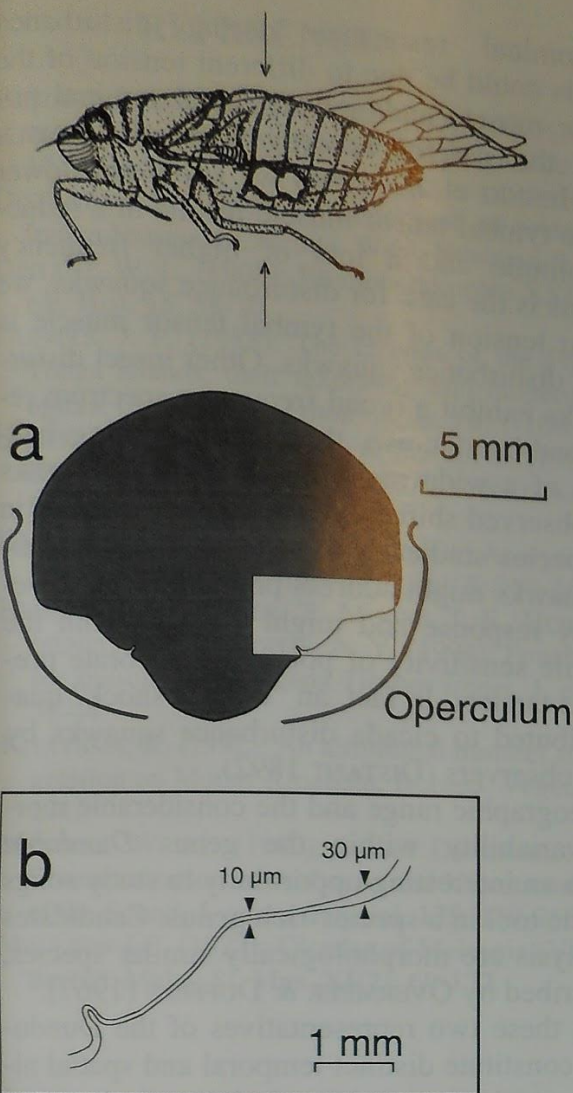
Fig. 5. Location and transverse section of the transparent cuticular regions in the abdomen of a male of *Dundubia vaginata*. After removal of the operculum, a lateral view of the animal reveals transparent cuticular areas. The position of the operculum is indicated by the broken line, the plane of transverse sections (a,b) by arrows.
a) The transparent cuticular areas (framed) are situated right underneath the opercula. Cuticular thickness not to scale.
b) Framed area at higher magnification, showing differences of cuticular thickness. Ventrally, the thinner area terminates at the tergit, with an abrupt change in thickness, while the dorsal area is gradually tapering from 30 μm down to 10 μm. For sake of clarity, cuticular thickness is drawn at an exaggerated scale, indicated by arrows.

within tropical forests. Only few species could be observed directly during calling song production, while disturbance squawks could be recorded from a far greater number of identified species. Though calling and disturbance squawks differ completely with respect to higher frequency composition, the present study shows that fundamental frequency and pulse length are similar, especially when compared with B-parts of the calling songs. Similarly, HENNIG et al.

(1994) have shown that the basic events underlying a tymbal cycle during disturbance squawks correspond to certain elements in the calling song of *Tibicen linnei*. SIMMONS & YOUNG (1978) showed that protest songs of *Cystosoma saundersii* contain features of other song types. Therefore, the identity of recorded calling sounds could be inferred from the disturbance squawks by a fine analysis of the underlying pulses. Such an approach could accelerate further identifications of cicada songs.

Within the calling songs from each species, two elements can be differentiated: the A- and B-part within one phrase in *D. vaginata*, and the first, longer chirp followed by a series of shorter chirps in *P. imperatoria*. The A-part of *D. vaginata* as well as the first chirp of *P. imperatoria* consist of continuous wave trains, while pauses can be recognized between chirps of the B-part of *D. vaginata* and towards the end of the song of *P. imperatoria* (figs. 1 and 3). This indicates similar motor programs in these species, which after MOULTON (1923) both belong to the Dundubiaria-group, characterized by opercula and timbal coverings, which are considered as modern, derived features. A further similarity of both species is the constant carrier frequency throughout the song. The songs of other species from the area show frequency modulation and exhibit a much more complex temporal structure.

Temporal structure and frequency composition of cicada songs is determined by three coupled resonating systems:

1) The tymbal together with the tymbal muscle, producing the in-out clicks under neuromuscular control, mainly determining the time structure of the song amplitude envelope.
2) The tymbal click frequency, mainly determined by the mechanical properties of the tymbal. They can be modified by the tymbal tensor muscle.
3) The resonance properties of the abdominal cave. It can be modified by abdominal movement and the position of the opercula (WEBER et al. 1987).

Tymbal and abdominal cavity act as coupled resonators. The tymbal click frequency produces a forced oscillation of the resonator, resulting in a more or less complex wave form of a carrier frequency determined by the resonator and modulated by the tymbal click frequency. In the species described here, the pure fundamental frequencies produced by tymbal clicks of 900 Hz (*Dundubia vaginata*) and 700 Hz (*Pomponia imperatoria*) are clearly visible within the disturbance squawks (figs. 2 and 4). The seven peaks of one pulse train could correspond to the 7 sclerotized ribs at the tymbal, successively stimulated during inward tymbal buckling, while the outward movement might be toneless. The same frequencies and pulse structure are contained within the calling song, but here each tymbal

click contains higher harmonics, so that the abdominal resonator "rings" at a carrier frequency determined by the abdominal resonator. Additional side bands and impurities are observed within song parts characterized by a fast chirp repetition rate such as the B-part of *D. vaginata*, where a chirp frequency of 80 Hz produces further harmonics and impurities (fig. 1i), as a modulation at frequency m of a given frequency f generates side bands f±m (RANDALL 1977). It is unclear how the more or less continuous wave trains of part A from *D. vaginata* and the first phrase of *P. imperatoria* are generated. They have the same fundamental frequency, but chirp structures are no longer visible. This could be achieved by a noisy out-click or by a 180 degree phase shift between right and left tymbal, thereby complementing each other. However, the latter possibility is highly improbable, as PRINGLE (1955) has shown close coupling between both tymbals. The same author has observed a higher acoustic output of tymbal clicks, together with an increased proportion of higher frequency components, during increased tension of the tymbal tensor muscle. Recent electrophysiological studies by HENNIG et al. (1994) confirm these observations in *Tibicen linnei*. Therefore, modulation of tensor muscle activity might explain the different oscillation modes. In addition, the higher amplitude of the first parts in both species suggests increased "ringing" of the abdominal resonator during this excitation mode. It would be interesting if coherent starting sequences are a consistent feature within songs of species belonging to the Dundubiaria-group.

BENNET-CLARK & YOUNG (1992) suggested that the cicada abdominal cavity can be considered as a Helmholtz resonator radiating through two openings, the tymbals, and suggest a simple formula to calculate the carrier frequency from the dimensions of the abdomen. In our case, however, the abdominal resonator evidently is not ringing during disturbance squawks, suggesting that resonance requires a certain abdominal position of the unrestrained animal. Evidently, the resonator has to be tuned to the tymbal pulse carrier frequency to ring, which is only the case in the intact, undisturbed calling male. Therefore, a calculation of resonance frequencies from the dimensions of the abdomen in dead specimens is impossible for the species studied here. Further complications arise from the thin transparent cuticular areas at the abdomen of *D. vaginata* (fig. 5). These have to be considered as additional acoustic openings, severely affecting the resonance frequency of a Helmholtz resonator (cf. BENNETT-CLARK & YOUNG 1992). Additional modification of resonance properties is possible by the overlying opercula.

The differences in frequency composition of disturbance and calling songs in both species suggest that there is no abdominal resonance during disturbance squawks. This could be due to different tension of the tymbal tensor muscle and/or different abdominal posture. From the careful investigations of PRINGLE (1955) and HENNIG et al. (1994) we know that lower tension of the tymbal tensor muscle results in a reduction of amplitude and a loss of higher frequency modes. As this is the case for disturbance squawks, we can infer that tension of the tymbal tensor muscle is lower during disturbance squawks. Other insect disturbance squawks exhibit a broad frequency spectrum resembling broad-band noise, thereby stimulating hearing systems of a wide range of predators (MASTERS 1980). The observed shift to lower frequency bands in the cicada species studied here suggests that their disturbance squawks might address predators with lowered frequency response and might extend within the range of tactile sensitivity of potential vertebrate predators such as tarsiers. In fact, an "electric shock" quality was attributed to cicada disturbance squawks by early human observers (DISTANT 1892).

The broad geographic range and the considerable morphological variability within the genus *Dundubia* could provide an interesting opportunity to study songs as a systematic tool in a species-rich genus. Candidates for song analysis are morphologically similar species, recently described by OVERMEER & DUFFELS (1967). Ecologically, these two representatives of the Dundubiaria-group constitute distinct temporal and spatial niches. *P. imperatoria* sings only at dusk, precisely timed between 18:00 and 18:30, while *D. vaginata* calls during the day, with a short activity bout of only 10 minutes at the end of the dusk chorus. The species sing at different forest strata, with *P. imperatoria* singing at the highest and *D. vaginata* at the lowest forest stratum.

The exact timing of song activity in the range of minutes suggests that a precise trigger such as fading light is used. Candidates for triggering are thresholds of total light intensity (integral over some spectral sensitivity), the velocity of light intensity change, i.e., the first derivative of the light intensity vs. time curve, or a measuring of the characteristic red shift at dusk.

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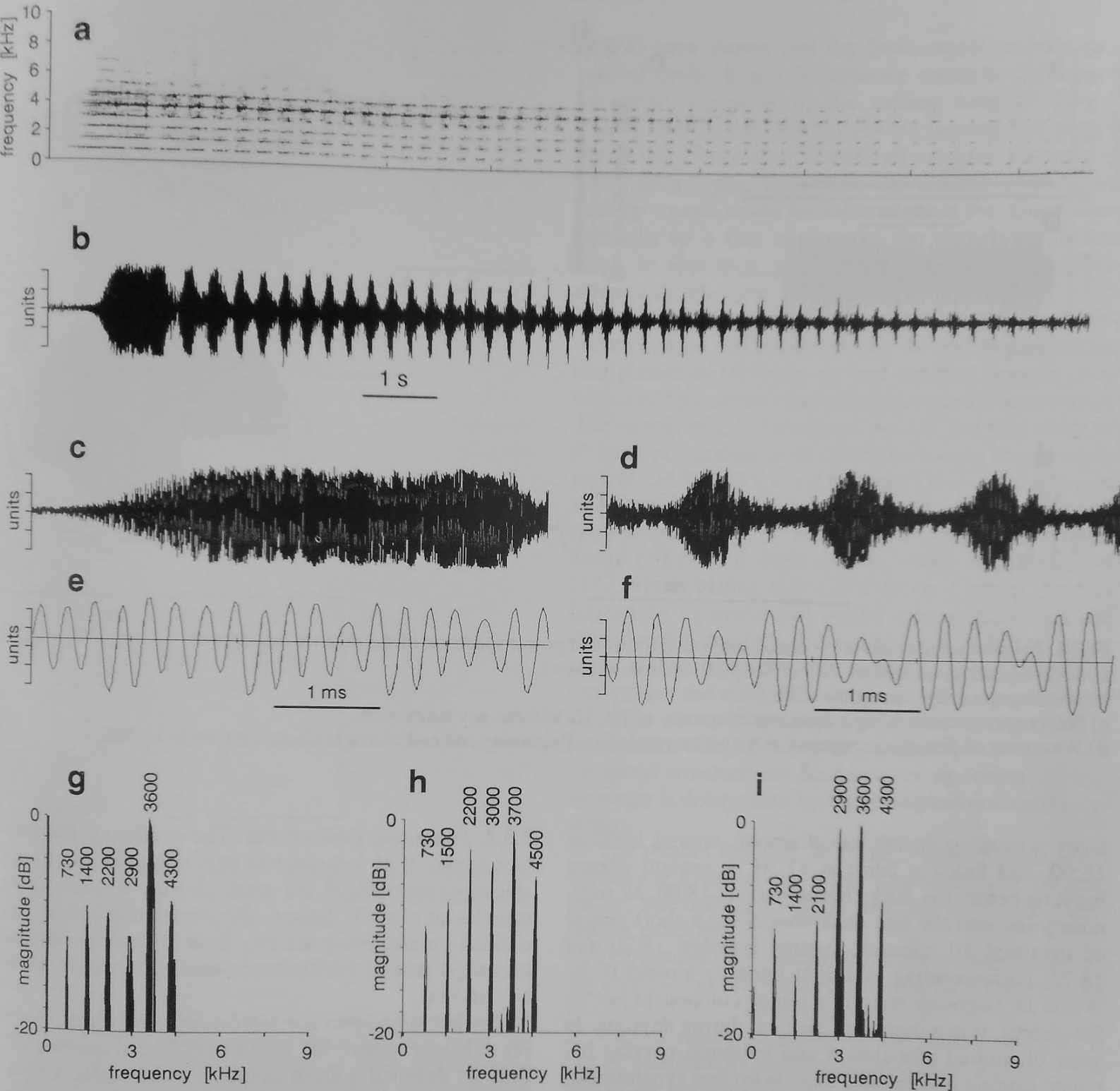
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b) Oscillogram at the same time scale. The first chirp is longer and louder than the following chirps, which fade towards the end of the song.

c) Oscillogram of the first phrase at higher time resolution.

d) Oscillogram of the following, shorter phrases at higher time resolution.

e) Wavetrains from the first chirp show only slight modulation.

f) Wavetrains making up successive chirps show much deeper modulation, but are coherent without interrruption.

g) Power spectrum of entire calling song, showing the prominent carrier frequency of 3600 Hz.

h) Power spectrum of 1 s from the first chirp, showing sharp frequency bands.

i) Power spectrum from 1 s of successive chirps, showing broader frequency bands.