ACOUSTIC AND MATING BEHAVIOR OF A MEXICAN KATYDID, PTEROPHYLLA BELTRANI (ORTHOPTERA:TETTIGONIIDAE)

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ABSTRACT

Males of the Mexican katydid, Pterophylla beltrani, sing day and night and form aggregations at the ends of tree branches. Males of other pterophylline species sing only at night and from singing sites which may be 15 m from nearest singing neighbors. When singing alone (solo calling), P. beltrani males produce mostly 2-pulse (range 1-5) phrases (a pulse is the sound produced during the closing phase of a wingstroke cycle). Phrases are produced at a rate of 78-126/min and the pulse rate of 15-20/sec (25-30°C) is the fastest reported for the Pterophyllina. Acoustic interaction of male pairs (<1 m apart) consists of soloing (singing two or more phrases prior to response of partner), synchronizing (overlapping) phrases, and alternation of single or grouped phrases. During alternation, a katydid's phrase rate is slowed compared to the rate of solo and synchrony, and phrases may be lengthened by one pulse. In contrast, when a katydid solos during acoustic interaction the solo rate is faster than that of solo calling. When antennating, or being antennated by, another male or female, P. beltrani males sing at a rate which is equivalent to that of soloing during acoustic interaction. P. beltrani males and females produce erratic “disturbance” sounds when handled. The nature of acoustic interaction is compared with that of Pterophylla camellifolia males (Shaw 1968) and proximate mechanisms suggested, copulatory behavior is described, and possible mating strategies are discussed.

RESUMEN

Los machos de Pterophylla beltrani (Tettigonidae:Pseudophyllinae) cantan día y noche y forman agregaciones en las terminaciones de las ramas. Los machos de otras especies de Pterophylla cantan solamente de noche y desde sitios que podrían estar a 15 m distantes de los vecinos más cercanos. Cuando un macho de P. beltrani canta individualmente, este produce principalmente frases de dos pulsaciones (rango de 1-5)
(la pulsación es el sonido producido al cerrar las alas durante el ciclo completo de apertura y cierre de las mismas). Las frases se producen con una frecuencia de 75-126/min, siendo la frecuencia de pulsación de 15-20 seg (25-30°C) la más rápida que ha sido reportada para los Pterophyllini. La interacción acústica de pares de machos (distanciados a < 1 m) consiste en el canto solitario (cantado 2 o más frases antes que responda su compañero), el canto de frases sincronizadas (traslapadas) y la alternación de una o varias frases. Durante la alternación, la frecuencia de las frases es lenta comparada a la frecuencia del canto solitario o del canto sincronizado, y las frases se pueden alargar por una pulsación. En contraste, cuando el *P. beltrani* canta solo durante la interacción acústica la frecuencia de estos cantos solos es más rápida que la del canto solitario verdadero. Al tocar o ser tocados por las antenas de otro macho o una hembra, los machos *P. beltrani* cantan a una frecuencia equivalente a la del canto solo durante la interacción acústica. Machos y hembras de *P. beltrani* producen sonidos erráticos cuando son molestados. La naturaleza de la interacción acústica se compara con la del macho de *Pterophylla camellifolia* (Shaw 1968) y se sugieren mecanismos similares, se describe el comportamiento copulatorio y se discuten las posibles estrategias de apareamiento.

*Pterophylla beltrani* (Bolivar and C. Bolivar) was first described in 1942 (Bolivar & Pieltain 1942). The authors suggested morphological similarities with *Pterophylla camellifolia* Fabricius and *Pterophylla robertsi* Hebard but greater affinities with *P. robertsi*. *P. beltrani* adults feed primarily on live oak (*Quercus* spp.) but females preferentially oviposit in the woody parts of “la nacahua” (*Cordia boissieri* A. DC.) and “la hoja ancha” (*Flourensia laurifolia* DC.) (Barrientos & Ortega 1985, Barrientos et al., unpublished). Bolivar & Pieltain (1942) report *P. beltrani* in trees of *Acer* spp. in an oak forest. The exact geographic distribution of *P. beltrani* is unknown; however, it has been reported from the Mexican states of Nuevo Leon and Tamaulipas (Bolivar & Pieltain 1942, Barrientos et al. 1984).

Little has been reported regarding the acoustic and reproductive behavior of *P. beltrani*. According to Barrientos et al. (unpublished), males begin to sing two or three days following eclosion and produce calling and “territorial or defensive” sounds. The same authors also report that mating occurs between 0800 and 1000 h, copulation lasts ca. 35 min, and involves the transfer of an external spermatophore. This paper describes the courtship, copulation and the acoustical repertoire of *P. beltrani* including acoustical interactions between pairs of males.

**Materials and Methods**

Adult male and female specimens of *P. beltrani* were obtained with the aid of Ms. Barrientos, Instituto de Investigaciones Alimentarias, Cd. Victoria, Tamaulipas, Mexico. Males and females of *P. beltrani* were collected by climbing oak trees, shaking katydids-bearing limbs, and plucking individuals from vegetation after they had jumped, spread their tegmina and wings, and glided up to 30 m from their host trees. These adults, collected on August 8, 1984, near the village of Alta Cumbre, Tamaulipas, and some eggs and nymphs from Ms. Barrientos’ laboratory were transported by car to Iowa State University.

Eggs, nymphs and adults were maintained in Percival® environmental chambers on a 12 L:12 D light regime, at temperatures of 29°C L and 27°C D, and 40-60% R.H. Adults and nymphs were provided with oak leaves (*Quercus* spp.) and water (cotton-capped vials). Adults living into late fall were given lettuce and chicken mash. During the summer and fall of 1984, sounds and behavior were recorded, described and analyzed utilizing adults collected in the field and reared from nymphs. In 1985, adults were
reared in the laboratory from eggs brought from Mexico and from eggs laid by pregnant females collected in Alta Cumbre or by females mated in the laboratory. Behavioral observations were recorded from varying numbers of katydids placed in 25 x 30 x 52 cm glass terraria. Sounds were recorded from katydids in the terraria and from katydids maintained in 9 x 10 x 17 cm wire screen cages. All sound recordings and behavioral observations were made in an acoustic isolation chamber (4.0 x 3.3 x 2.4 m) (Industrial Acoustics Company, Inc., Bronx, N.Y.). Sounds were recorded using a Panasonic WM-1150 or a Bruel & Kjær 1.3 cm microphone and a Sony TC-5300 or a Precision Data, Inc. PI-6204 tape recorder. Sounds were analyzed using a Kay 7029A Sonograph (sound spectrograph) and a Tectronix 5110 oscilloscope in conjunction with a Grass Model C4R kymograph camera.

Thirty-nine different males were used to record the various song types. Males to be recorded were moved from the environmental chamber to the acoustic chamber. After a recording session, males were returned to the environmental chamber and placed on a different shelf from those not yet recorded.

In order to compare singing rates (expressed as phrase periods, Fig. 1) of different katydids in different contexts recorded at different temperatures, two types of statistical analyses were utilized. A mixed-effects ANOVA (Snedecor & Cochran 1980) allowed the separation of variance resulting from differences among katydids (inherent and temperature induced) from that resulting from differences among response types. LSD tests (Steel & Torrie 1980) were then used to determine significant differences between phrase periods of paired combinations of response types (Table 1). The second type of analysis, analysis of covariance with temperature as the covariant, utilized regression curves of response type and temperature to create adjusted means which were compared by means of Student's t-test (Tables 2 and 3).

RESULTS

Field Observations

On Aug. 1984, K. Shaw, a graduate student (B. Smith), and L. Barrientos and her co-worker (T. Reyes) visited a population of *P. beltrani* near the village of Alta Cumbre. The katydids were in a montane forest of live oak (*Quercus* spp.). Males and females formed large aggregates at the end of branches at or near the top of ca. 5-6 m high trees. Many males were producing songs consisting of a continuous production of short phrases (Fig. 1) during a hot (27°C shade) afternoon (1300 to 1600 hr). Because of the number of katydids singing, it was difficult to ascertain the nature of acoustic interaction. *P. beltrani* males probably also sing at night. The colony was not visited at night but males have sung at night in the darkened laboratory.

Solo calling

Detailed analyses of song parameters were made from solo calling songs (Fig. 1), i.e., songs of isolated caged males or terrarium males in which only one male was singing and other males were stationary 30 cm or more from the singing male. Sonographic analysis indicated that most of the sound energy of solo calling falls between less than 1 to approximately 10 kH, (two to three phrases analyzed for five *P. beltrani* males). Our analysis showed continuous but decreasing sound energy up to 40 kH, (the upper frequency range of the microphone) but, as in many other tettigoniids, sound energy probably occurs up to at least 100 kH, (Elsner & Popov 1978).

The calling sound consists of the repetitive production of 1- to 5-pulse phrases (see End Note for definitions) with 2-pulse phrases being, by far, the most common (Fig.
Fig. 1. Songs of *P. beltrani*. o—one or two sounds produced during wing opening; c—sounds or pulses produced during wing closure; pl—phrase length; pi—phrase interval. Phrase length + phrase interval = phrase period.

1). Of 53 males for which pulse number was determined, the distribution of modal phrase pulse numbers was as follows (numbers in parentheses represents production of phrase pulse numbers other than modal): 1-pulse, n=1; 2(1)-pulse, n=2; 2-pulse, n=39; 2(3)-pulse, n=6; 3(2)-pulse, n=2; 3(4)-pulse, n=2; 4(5)-pulse, n=1.

For nine katydids (9-11 phrases per katydid), mean phrase lengths, intervals and periods (parameters indicated in Fig. 1) of 2-pulse phrases ranged from 84-117 (x = 105.8 ± 25.1) msec, 380-682 (x = 492.5 ± 104.6) msec, and 483-796 (x = 594.9 ± 116.2) msec respectively, resulting in phrase rates of 1.3-2.1 per sec (x = 1.7 per sec) (25-30°C).

The mean length of the first pulse of katydids' 2-pulse phrases was significantly longer than that of the second pulse (first pulse: 39-57 (x = 48.0 ± 6.1) msec; second
TABLE 1. COMPARISON OF MEAN PHRASE PERIODS (IN MSEC) OF RESPONSE TYPES OCCURRING DURING ACOUSTIC INTERACTION OF PAIRS OF *P. BELTRANI* MALES.

<table>
<thead>
<tr>
<th>Response type</th>
<th>Mean¹²</th>
</tr>
</thead>
<tbody>
<tr>
<td>solo</td>
<td>346.3 a</td>
</tr>
<tr>
<td>overlap</td>
<td>421.5 b</td>
</tr>
<tr>
<td>alternation</td>
<td>628.4 c</td>
</tr>
<tr>
<td>extended delay</td>
<td>1090.6 d</td>
</tr>
</tbody>
</table>

Two-way mixed effects ANOVA
katydid, $F = 11.06, df = 21,621; P < 0.0001$
response type, $F = 298.05, df = 3,621; P < 0.0001$

¹Means identified by different letters are significantly different (LSD test, $P < 0.05$).
²Temperature range 25-30°C.

TABLE 2. COMPARISON OF MEAN PHRASE PERIODS (IN MSEC) OF SOLOS OCCURRING IN DIFFERENT SONG TYPES OF *P. BELTRANI* MALES.

<table>
<thead>
<tr>
<th>Solo type</th>
<th>Mean¹²</th>
</tr>
</thead>
<tbody>
<tr>
<td>solo calling</td>
<td>573.3 a</td>
</tr>
<tr>
<td>solo after acoustic interaction</td>
<td>419.0 b</td>
</tr>
<tr>
<td>solo during acoustic interaction</td>
<td>345.1 b</td>
</tr>
<tr>
<td>courtship</td>
<td>325.5 b</td>
</tr>
</tbody>
</table>

Analysis of Covariance

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (covariate)¹³</td>
<td>1</td>
<td>22875</td>
<td>22875</td>
<td></td>
</tr>
<tr>
<td>Solo type</td>
<td>3</td>
<td>309658</td>
<td>103220</td>
<td>11.36</td>
</tr>
<tr>
<td>Error</td>
<td>32</td>
<td>290810</td>
<td>9088</td>
<td></td>
</tr>
</tbody>
</table>

36  623343

¹Means adjusted for temperature differences (25-30°C).
²Means identified by different letters are significantly different (Student t-tests, $P < 0.01$).
³The effect of temperature after solo type was entered into the analysis was not quite significant at $P < 0.05$ ($F = 2.08, P = 0.066$).

TABLE 3. COMPARISON OF TEMPERATURE-ADJUSTED MEAN PHRASE PERIODS (IN MSEC) OF SOLO CALLING AND RESPONSE TYPES OF ACOUSTIC INTERACTION FOR *P. BELTRANI* MALES.

<table>
<thead>
<tr>
<th>Differences between temperature-adjusted means</th>
<th>$F$¹</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>solo calling – solo = 219.8</td>
<td>28.38</td>
<td>0.001</td>
</tr>
<tr>
<td>solo calling – overlap = 143.1</td>
<td>10.92</td>
<td>0.0048</td>
</tr>
<tr>
<td>solo calling – alternation = –45.4</td>
<td>0.49</td>
<td>0.4979</td>
</tr>
<tr>
<td>solo calling – extended delay = –559.7</td>
<td>8.90</td>
<td>0.0088</td>
</tr>
</tbody>
</table>

¹$F$-statistic for testing difference between adjusted means in analysis of covariance.
pulse: 23-40 (\(\bar{x} = 32.7 \pm 6.1\) msec; \(t = 3.75-42.1, p < 0.01-0.001\)) and the mean interval between pulses was two to four fold shorter (9-22 (\(\bar{x} = 17.2 \pm 4.2\) msec)) than the length of the initial pulse. Not enough 3-pulse phrases were recorded to compare the magnitude of the second intervals and their pulses, but oscillographs from song selections of three 3-pulse katydids suggested that the second interval is longer than the first and that the third pulse is longer than the second.

Although the relation of the cycle of wing movement to sound production was not analyzed, it is assumed that the most prominent sounds (pulses) are the result of wing closure as occurs in P. camellifolia (Pierce 1948). In P. camellifolia, a short, relatively soft sound may occur during the initial opening of the wings prior to the series of wing movements associated with a multi-pulsed phrase. Although always shorter than pulses assumed produced during wing closure, the sound level of presumed wing-opening sounds was quite variable among males of P. beltrani. For some males, wing-opening sounds were as intense as wing-closing pulses (Fig. 1). In addition, two wing-opening sounds preceding the longer pulses of wing closure were not uncommon (Fig. 1). All measurements of pulse and phrase length reported in this paper omitted the sounds generated by wing opening because their existence and intensity varied among the calling sounds of different katydids and even within the calling sound of an individual (Fig. 1). If included, such sounds would increase phrase length by as much as 37 msec.

Acoustic Interaction

Acoustic interactions between pairs of males were recorded from males 0.15 to 1.0 m apart. From the conditions observed in the field, it is unlikely that acoustic interaction at greater distances is common. To analyze acoustic interactions, varying lengths (12-12 phrases) of 11 paired interactions were taped and oscillographs made at a later date.

Acoustic interactions consisted of a combination of soloing, phrase alternation and phrase overlap or synchrony. Pairs of katydids alternated single phrases (c, Fig. 1) or sequences of two or more phrases (= solos) termed extended delay (d, Fig. 2). Alternation was intermittently interrupted by synchronous (S, Fig. 2) or almost synchronous (0, Fig. 2) production of phrases.

During the 11 paired interactions, seven of the 22 males produced two different phrase lengths. Six males produced 2- and 3-pulse phrases: one male produced 3- and 4 pulse phrases. All but one of the 70 (36%) longer phrases followed alternation or extended delay; shortening of phrase length never occurred following alternation or extended delay.

For purposes of analysis, the temporal relationships of the phrases of two acoustically interacting males were classified into the following response types (Fig. 2): 1) solo: one male sang two successive phrases and the partner was silent or the partner's phrase synchronized with the first male's second phrase (a, Fig. 2); 2) overlap solo: the partner's phrase was synchronized with or overlapped the other katydid's first and sometimes second phrase (b, Fig. 2); 3) alternation: the partner's phrase fell between two successive phrases by the other male (c, Fig. 2); 4) extended delay: two or more partners' phrases fell between two successive phrases by the other male (d, Fig. 2).

The sequence of response types was quite variable within and between katydid pairs. Within paired interactions, one male usually sang more phrases than the other (\(\bar{x} = 61\%\) [range: 51-67%] and \(39\%\) [range: 33-49%]) and, the mean percentage of solos and overlap solos was 61\% (range: 0-100\%) while that of alternations and extended delays was 39\% (range: 0-100\%). Solos averaged 31\% (range: 0-83\%) while synchrony or overlap affected 30\% (range: 0-61\%) of a katydid's phrases. Alternation averaged 17\% (range: 0-72\%) and extended delay averaged 22\% (range: 0-58\%) of response types.
PTEROPHYLLA BELTRANI

ACOUSTIC INTERACTION

Fig. 2. Types of acoustic interaction between pairs of P. beltrani males. A. two males alternating phrases. B. two males alternating groups of solos. 1 and 2 indicate phrases of two different katydids; S = synchronous overlap of phrases of two katydids; zero = non-synchronous phrase overlaps. Small letters identify bracketed response types: a—solo, b—overlap solo, c—alternation, d—extended delay.

The phrase periods of the four response types were significantly different from one another such that solo < overlap solo < alternation < extended delay (Fig. 3, Table 1). Thus, during acoustic interaction, anytime one katydid produced one or more phrases during the period of two successive phrases of the other katydid, the other katydid's phrase rate usually was slowed.

Comparison of the phrase periods of solos before, during and after acoustic interaction indicated that males increase solo rate during acoustic interaction and maintain it for some period following termination of the singing of an interacting partner (Table 2). When compared to the slower rate of soloing during solo calling, the only response type of acoustic interaction that is significantly slower is extended delay (Table 3).

Courtship and Copulation

Courtship was identified when a male lowered its abdomen and raised its tegmina. A silent or singing male could be induced to court by alternating or being antennated by a female or another male. Courtship soloing was significantly faster than solo calling, but the mean phrase periods of courtship and soloing during and after acoustical interaction were not significantly different (Fig. 3, Table 2). When courting, males showed very rapid abdominal pumping which appeared to be an increase in respiratory rate; however, the movements could have been associated with spermatophore formation (T. Walker, personal communication).

Receptive females climbed onto the back of courting males. Although females became active and began to move toward a calling male, they did not hesitate to attempt to mate with a silent male that they contacted during movement. Some silent and all singing males assumed the courtship posture immediately after being antennated by a female. Non-receptive males rejected females by kicking them with their hind legs and moving away. Some females induced unreceptive males to kick and retreat by biting them on their hind legs.
Fig. 3. Range of mean phrase periods (n = 7-19 katydids) for solo calling, the response types of acoustic interaction, soloing after acoustic interaction and courting. 0—solo calling, 1—solo, 2—overlap solo, 3—alternation, 4—extended delay, 5—solo after acoustic interaction, 6—courting.

After a female climbed onto the back of a courting male, successful copulation was initiated by the male slipping the female's ovipositer into the terminal slit of his subgenital plate (Fig. 4) while simultaneously grasping the base of the female's ovipositor with the proximal hooks on the dorsal arms of his cerci (Fig. 4). Apparently, the pushing of the female's abdomen dorsally with his subgenital plate aids in exposing the female's
genital opening. The very prominent ventral curved arms of the male's cerci (Fig. 4) hooked around the female's abdomen. After engagement of the genitalia, the male loosened his tarsal hold on the substrate and hung head down from the female. The male appeared to be supported by his hind legs grasping the female's, the cercal hold on the base of the female's ovipositer, and genital attachment. In the copulation described here in detail, the male intermittently grasped the branch below with his forelegs, however, the front legs usually were held at an angle of approximately 90° to the body.

Copulation consisted of accordion-like movements of the abdomen which resulted in the male rocking to and fro. During copulation, the male continued the rapid abdominal pumping initiated during courtship. The tip of the spermatophore was visible after ca. 1 min of copulation. For ca. 10 min, the strong, pumping movements of the male's abdomen occurred at a rate of ca. 10/min; then, they increased dramatically to ca. 120/min. During these very rapid abdominal contractions, the male's body and legs flailed back-and-forth. The male ceased the contractions every 10-15 sec and tightly tensed its whole body before resuming the contractions within a few sec. After 2-3 min, the male alternated 2-3 sec of rapid abdominal pumping with equivalent lengths of cessation of pumping while tensing his body.

After 3 to 4 minutes, abdominal pumping assumed a low intensity, very rapid vibration and the female began to crawl across the branch dragging the male with her. After ca. 7 min of this, during which the female appeared to be attempting to disengage from the male, the couple separated terminating a 25 min copulation period. Of five copulations observed, copulation time ranged from 25 to 38 min.

The external spermatophore was relatively small (estimated to be considerably less than 10% of wet body weight; see Gwynne 1983), and consisted of a narrow throat and
two sperm sacs. After separation, the male continued abdominal contractions at a rate considerably faster than the female (male: ca. 375/min; female: 60-80/min). Within 2 min following separation, the male groomed his tarsi by drawing them through his mouthparts, and in another 3 min bent his head ventrally and posteriorly to groom his genital area.

After ca. 6 min from separation, the female bent her head ventrally and posteriorly and began to eat the spermatophore; she continued to eat the spermatophore until it was completely consumed after 6.5 min. After this, the female groomed the ovipositor with her mouthparts.

Disturbance sound.

Males and females of *P. beltrani* may produce very erratic disturbance sounds (Fig. 1) when grasped. It is assumed that such sounds would be produced when the insects are grasped by predators. Sound components and intervals were very variable (Fig. 1).

There was considerable variation in ease of elicitation of the disturbance sound. Males did not always produce these sounds and females were even less likely to do so. During one afternoon’s attempt to record the disturbance sound, two of five males and none of eight females produced sounds when grasped and manipulated for a few seconds. On another afternoon, 15 females were handled before the last one emitted the sound.

**Discussion**

Bolivar & Pieltaint (1942) suggested morphological similarities between *P. beltrani* and *P. camellifolia*. Since we have described the songs of *P. beltrani* and since songs of *P. camellifolia* have been described and analyzed in some detail (Shaw 1968), how do they compare?

Three populations of *P. camellifolia* have been differentiated based upon differences in morphology and calling song (Alexander 1968, Shaw 1968, Shaw & Carlson 1969, North & Shaw 1979). These populations have been termed northern (occurs from New England to the northern edge of the Appalachians and west to at least midway between the Mississippi and Missouri rivers), southeastern (occurs south and east of the Appalachians into northern Florida) and western (currently only reported from central and southeastern Iowa but males have been heard in northwestern Missouri (unpublished)). Alexander (1968) and Shaw & Carlson (1969) suggest the possibility of a fourth population in Georgia, Alabama and Louisiana.

The range and mode of phrase pulse numbers of *P. beltrani* and northern *P. camellifolia* are the same whereas those of the southeastern and western *P. camellifolia* populations are greater (Table 4). *P. beltrani* songs exhibit the fastest pulse rate, the shortest phrases and the fastest phrase rate (Table 4). *P. beltrani* songs are unusual in the loud but shorter sounds produced during wing opening (Fig. 1). A short, usually softer sound, may be produced by *P. camellifolia* males preceding only the initial pulse of a phrase.

Bolivar & Pieltaint (1942) indicated that morphologically *P. beltrani* was more similar to *P. robertsi* than *P. camellifolia*. The only description of the song of *P. robertsi* was Hebard’s (1941) statement that ‘the song was noted to be four or five rather rapid notes, ‘cha-cha-cha-cha-cha’.” If these are phrases, *P. robertsi* produces a very unique song consisting of groupings (sentences) of five phrases. If these are pulses, then Hebard is describing a 5-pulse phrase. Hebard reports *P. robertsi* males calling day and night and he describes a nocturnal song produced when temperatures might be cool enough for humans to differentiate individual pulses within a 4- or 5-pulse phrase. Barrientos
TABLE 4. COMPARISON OF PTEROPHYLLA CALLING SONGS.

<table>
<thead>
<tr>
<th>Species or Population</th>
<th>Pulse No.</th>
<th>Pulses/sec</th>
<th>Phrase Length (msec)</th>
<th>Phrases/min</th>
<th>Temp °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. beltrani</td>
<td>Range 1-5</td>
<td>Mode 2</td>
<td>15-20</td>
<td>106</td>
<td>78-126</td>
</tr>
<tr>
<td>P. camellifolia¹ (northern)</td>
<td>1-5</td>
<td>2</td>
<td>6-8</td>
<td>250</td>
<td>60</td>
</tr>
<tr>
<td>P. camellifolia² (western)</td>
<td>5-22</td>
<td>8</td>
<td>6-8</td>
<td>1150</td>
<td>30</td>
</tr>
<tr>
<td>P. camellifolia³ (southeastern)</td>
<td>3-8</td>
<td>4</td>
<td>10-11</td>
<td>300</td>
<td>58</td>
</tr>
</tbody>
</table>

¹Shaw 1968  
²North and Shaw 1979  
³Alexander 1966, Shaw 1968

(personal communication) has collected specimens in the same area (near Ciudad Victoria, Tamaulipas, Mexico) at different times and these have been identified by D. Nickle of the U.S.D.A. Systematic Entomology Laboratory as P. beltrani on one occasion and P. robertsi on another. Barrientos is currently attempting to clarify the distribution and taxonomy of P. beltrani and P. robertsi.

The field acoustical behavior of P. beltrani is very different from that of any of the P. camellifolia populations. P. camellifolia sings at night and adjacent males alternate phrases at nearest neighbor distances (NNDs) of 8-15 m (Shaw 1968). In contrast, P. beltrani males sing day and night and, when observed, formed dense aggregations (tens to hundreds of males and females in contact or within antennal contact of one or more neighbors) at the end of tree top branches. When P. camellifolia males are less than 1 m apart, they produce aggressive sounds which typically involve alternation of longer phrases (typically 1-4 pulses longer than the phrase of solo calling although up to 30 additional pulses have been reported (Alexander 1960)). Some males may not lengthen their phrases but produce two or more solos at increased phrase rates (phrase intervals decrease by as much as 50% (Shaw 1968)); these bursts of solos are usually alternated with a long phrase of another male.

All of our recordings of P. beltrani males were at NNDs of 1 m or less. Some males increased phrase length but never by more than one pulse. This is similar to phrase length changes by some P. camellifolia males at 8-15 m. Although phrase length differences were great between and within species (e.g., 2-pulse P. beltrani phrase—106 msec; 2-pulse P. camellifolia phrase—250 msec; 6-pulse P. camellifolia aggressive phrase—890 msec), phrase intervals of solo calling of both species were similar (Table 5). The degree of shortening of solo phase intervals elicited by close range acoustic interaction also was similar (Table 5). These similarities in phrase intervals probably represent similarities in recovery times of the two species' "acoustic pacemakers" (Shaw 1968).

The proximate mechanisms of acoustic interaction in P. beltrani appear to similar to those of P. camellifolia (Shaw 1968) as well as several other species of katydids (Busnel et al. 1956, Jones 1966a, 1966b). Alternation and extended delay are probably the result of one katydid being inhibited from singing while its partner is singing. The shortening of solo phrase interval could be the result of a post-inhibitory excitatory phenomenon and/or excitatory effects of non-acoustic stimuli. With P. camellifolia
TABLE 5. COMPARISON OF MEAN SOLO PHRASE INTERVALS (IN MSEC) OF *P. beltrani* AND *P. camellifolia* MALE.

<table>
<thead>
<tr>
<th>Solo type</th>
<th><em>P. camellifolia</em> (27-28.3°C)</th>
<th><em>P. beltrani</em> (25-30°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Range</td>
</tr>
<tr>
<td>solo calling song</td>
<td>6</td>
<td>474-651</td>
</tr>
<tr>
<td>solo during alternation</td>
<td>9</td>
<td>372-603</td>
</tr>
<tr>
<td>solo during aggressive</td>
<td>4</td>
<td>200-240</td>
</tr>
</tbody>
</table>

*S* Shaw 1968  
*N* = no. of katydids; 10-20 phrases/katydid

males, Shaw (1968) could elicit an increase in solo rate and, for a few males, a 1-pulse increase in phrase length in response to electronically-produced sound phrases; however, increasing the length and sound level of the electronically-produced phrases failed to elicit the magnitude of increase in solo rate and phrase length characteristic of acoustic interaction when males are <1 m from one another. These results suggested that non-auditory stimuli emanating from a nearby male were responsible for the enhanced excitatory effect. The rapid solo rate of *P. beltrani's* courtship song, which can be produced when no other males are singing, reinforces the probable role of non-auditory stimuli.

That the phrase periods following phrase overlap were longer than solo phrase periods suggests some inhibition or delay. See Shaw (1968) for a discussion of an increasing inhibitory effect as the interval between the initiation of a katydid's phrase and a "stimulus" phrase are increased.

Because of the probable high energy cost of singing (over 50% of a tree cricket's daily respiratory budget is devoted to calling (Prestwich & Walker 1981)), Alexander (1975) has suggested that an increase in population density of a singing orthopteran species should result in a decrease in time of male calling and an increase in time of male searching. A corollary to this would be an expected decline in the energy utilized in high intensity aggressive acoustic interactions. It is possible that the failure to produce long phrases when in close proximity to other males represents some energy savings for *P. beltrani* males when compared to *P. camellifolia* males; but, a similarity in production of solo bursts at a similarly reduced chirp interval during acoustic interaction and during courting, the latter not occurring in *P. camellifolia*, suggests little if any energy savings. Since *P. beltrani* males are heard singing day and night and because of their tendency to aggregate, it would appear that males of this species would be continually bombarded with potential stimuli for eliciting calling and courting. However, it is unlikely that males sing continuously. In our laboratory, calling was sporadic and not all males called when one male did initiate calling. With 5 or 6 males in the terrarium and an equivalent number in screen cages within 1 m of the terrarium, there would be hours during which no male called and this included times when there were one to two virgin females in the terrarium. When a male did begin to call, he frequently was joined by one to three other males but rarely did all the males sing.

These results and studies indicating the high energy cost of singing (MacNally & Young 1981, Prestwich & Walker 1981) suggest that males must limit their calling time.
Therefore, each male should distribute his calling time to maximize his opportunities for achieving a mating. If receptive females are available equally throughout a 24 hour period, then male calling should be equally distributed over this period (at least over the periods in which calling would not be affected by such factors as temperature change, predator activity, etc.) (Walker 1983). Barrientos et al. (unpublished) report that most matings occur between 0800 and 1000 hrs. This suggests that calling may peak at some time prior to 0800 with the probability of a male calling at other times dependent upon the factors mentioned above, plus any other factors that might affect female receptivity at other periods. A need for field work is obvious.

No courtship song has been reported for *P. camellifolia*. However, the senior author has observed courtship and copulation in *P. camellifolia* on two occasions. There is no recollection of males calling during courtship; males stopped calling and lowered their abdomens as soon as they were antennated by a male or female. In the case of *P. camellifolia*, it is unlikely that another male would be nearby. For *P. beltrani*, it is likely that many nearby males would be calling and in order to compete, it may be important that a male continues to call while courting. The data presented here show that not only does the male call, but he calls at the fastest solo rate possible.

The disturbance sounds of both species are similar in consisting of sound pulses produced at irregular rates. So-called disturbance, alarm or defense signals which are produced “by arthropods held in the hand, or disturbed in various manners such as pinching, probing or restraining are known in almost every order of insect” (Alexander 1967). Such signals are commonly noisilike (i.e., possess a very wide frequency spectrum) and, if they consist of a sequence of pulses, are usually presented at an irregular or erratic rate.

Disturbance sounds may aid insects by startling the would-be-predator, by acting as an aposmatic signal or by mimicking an aposmatic signal (Haskell 1961, Masters 1979). There is some experimental evidence that disturbance sounds do deter predators (reviewed by Masters 1979).

If disturbance sounds are an effective anti-predator device, why don’t all *P. beltrani* males and females produce them every time they are handled, or at least the first time they are handled? Why are females less likely to produce disturbance sounds than males?

**End Note**

Pulse—“...any sound that seems unitary by the methods being used to analyze it” (Alexander 1967). In this paper, pulse refers to the sound presumably made during the closing stroke of a wing movement cycle. However, the songs of some *P. beltrani* males include one or two prominent shorter sounds apparently made during the opening portion of a wing movement cycle. This combination of sounds produced during both opening and closing phrases of a wing movement cycle has been termed a phonatome (Walker and Dew 1972).

Phrase—a sound consisting of one or more pulses or phonatomes.

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A DESCRIPTION OF THE LARVA AND PUPA OF *RUPELA ALBINELLA*, A PEST OF RICE IN LATIN AMERICA (LEPIDOPTERA: PYRALIDAE: SCOENOBIINAE)

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ABSTRACT

The larva and pupa of *Rupeola albinella* (Cramer) (Lepidoptera; Pyralidae: Schoenobiinae) are described. Differences between larvae and pupae of this rice pest and other known Schoenobiinae species are discussed.

RESUMEN

Se describe la larva y la pupa de *Rupeola albinella* (Cramer) (Lepidoptera; Pyralidae: Schoenobiinae). Se discuten las diferencias entre las larvas y las pupas de esta plaga del arroz y de otras conocidas especies de Schoenobiinae.

The subfamily Schoenobiinae (Pyralidae) contains many pests of rice throughout the world (Kranz et al. 1977, Yano 1968). The most common member of this complex in Latin America is *Rupeola albinella* (Cramer), which occurs from Mexico to Brazil (Heinrich 1937). Its usual Spanish common name, at least in Honduras, is *novia del arroz* (= rice sweetheart) (Paseo 1983, Koos & Banegas 1958) although Hummelen (1974) called it the white rice borer. Outbreaks have been reported from the Caribbean (Gooding 1980); Central America (King & Saunders 1984) and the northern portions of South America, including Peru and Colombia (Torre 1961, Cheaney & Jennings 1975).

A morphological description of the larva and pupa of *R. albinella* is presented here to facilitate identification of the immature stages. King and Saunders (1984) illustrated the superficial appearance of the egg, larva and adult in color. Cheaney & Jennings (1975) presented photographs of the larval damage.

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