

ACOUSTIC COMMUNICATION AND
BAFFLING BEHAVIORS OF CRICKETS

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In most crickets acoustic communication plays a major role in pair formation. Generally the male produces a species-typical calling song and conspecific females use these signals to locate "suitable" mates. The calling songs of crickets have been used in a variety of studies including investigations of circadian rhythms (Loher 1972, Sokolove 1975), as aids in systematics (Alexander 1962), and more recently, in studies pertaining to reproductive competition and sexual selection (Blum and Blum 1979, Gwynne and Morris 1982). But very little work has been conducted on cricket sound production and propagation.

Almost everyone is familiar with the calling songs of male crickets, but few have actually approached and watched a songster perform under natural conditions. The peculiar behaviors and often unusual postures males assume while calling are surprising. Observations on these have prompted this paper, although its foundation in the physical aspects of bioacoustics comes from a paper by Michelsen and Nocke (1974). I will discuss the adaptive significance of the calling postures of male crickets as related to the physical problems associated with sound production.

THE VIBRATING MEMBRANE, AND A PROBLEM

In crickets sound is produced by the vibration of membranous areas of the forewings (tegmina). These membranes are caused to vibrate during stridulation when the scraper (plectrum) of the left tegmen is drawn across the file (pars stridens) of the right tegmen. These stridulatory structures are closely associated with membranous areas of the wings that vibrate at the tooth-impact frequency of the scraper on the file teeth (see Nocke 1971 and Sismondo 1979). Sound production occurs only on the closing stroke of the wings and each wingstroke delivers a *pulse* of sound.

This vibrating membrane system can be imagined as a piston or disc (Fig. 1a and b). When the disc vibrates (moves back and forth in space) it produces sound waves, that is, compressions and rarefactions. As these radiate away from the source the sound pressure (intensity) decreases due to geometric spreading—the same acoustical energy occupies a larger volume. Ideally, for each doubling of distance from the source the sound pressure decreases by 6 decibels.¹

During vibration as the disc moves in one direction a compression is produced on one side, and simultaneously a vacuum or rarefaction is created on the opposite side of the disc. A single vibrating disc thus acts as a dipole source with two sound outputs produced, one on each side of the disc. The outputs are equal in amplitude and have the same wavelength, but are opposite in phase (Fig. 1a and b).

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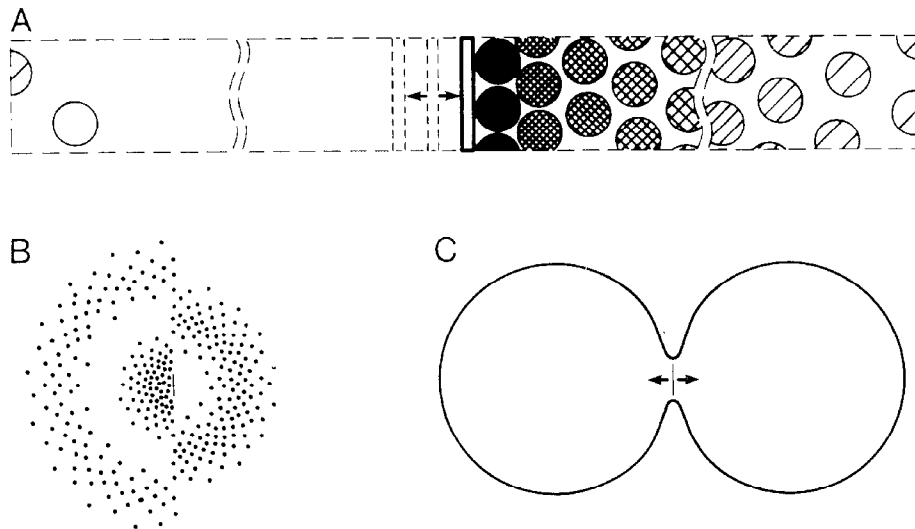


Fig. 1a. Sound produced by vibration of disc or piston. As the disc moves to one side (to right) it produces a compression of air molecules while simultaneously producing a vacuum (rarefaction) on the opposite side of the disc. Shading of circles represents the degree of molecular displacement in sound waves (i.e. black circles represent compression and no circles represent rarefaction). The rate of disc vibration determines the frequency of sound produced.

1b. Phase relationship of output from vibrating disc. Outputs on opposite sides of the disc are out of phase (180°). As sound waves radiate from source the intensity decreases due to the same acoustic energy occupying a larger volume.

1c. Sound field from a dipole source. If the vibrating disc is small, relative to the wavelength of sound produced as in (1b), the two outputs will interfere along the edges of the disc. Since they are opposite in phase, they cancel each other. The result is a dumbbell-shaped sound field.

When the size of the disc is small relative to the wavelength of sound produced, as in crickets, the output from one side of the disc (membrane) interferes with the output from the other side *along the edges of the disc*. Since the two outputs are opposite in phase, they exactly cancel each other (destructive interference). As a result, intensity measurements around the disc are maximum perpendicular to the disc surface, but along the disc edges no sound is perceived. The output is highly directional, with a dumbbell-shaped sound field (Fig. 1c). The energetic cost of calling may exceed 10 times that of resting (Prestwich and Walker 1981). Much of this is wasted simply because the size of the disc is small compared to the wavelength of the sound produced (diameter is less than $1/2$ wavelength (λ), Olson 1957). Because crickets are small they have small wing membranes that are inefficient sound producers.

SOLUTIONS

There are two possible means of reducing the loss of acoustical energy caused by the destructive interference of the outputs from the two sides of the disc. One means is to produce higher frequency sounds with wavelengths

that are short compared to disc diameter. But high frequencies attenuate more rapidly than low frequencies, and for a given input of energy are less effective in long-range acoustic communication (Wiley and Richards 1978, Michelsen 1978). To be efficient, crickets would have to produce sounds with ultrasonic frequencies (Michelsen and Nocke 1974); but, to have an appreciable range, these signals would have to be produced at higher intensities and would require greater energy input. There is a conflict. The frequency for efficient sound production (acoustic output/energy expenditure) is not the best one for signal effectiveness (i.e. maximum range of the signal).

Compromises between efficiency and effectiveness seem evident in the mole crickets. In species that call in specialized acoustic burrows (increased efficiency) calling song frequencies are low (increased effectiveness) compared to males of species that call without such burrows (Forrest 1982a).

A second possible mechanism that could increase the efficiency of sound production is a baffle system. Simply stated, a baffle is an acoustical shield or partition. A baffle used in conjunction with a dipole source partitions the two acoustic outputs and prevents interference along the edges of the disc or membrane. One such baffle system places the vibrating disc in a "speaker cabinet" and the walls of the cabinet keep the outputs from the two sides of the disc from interfering with each other (Fig. 2a). If the cabinet is closed such that the distance from the disc to the cabinet's back wall is one quarter of a wavelength of the sound produced, the cabinet ("a closed box") will act as a resonating chamber. Sound produced on the box side of the disc bounces off the cabinet's back wall and returns to the disc (total distance $1/2 \lambda$) in phase with the output of the other side of the disc (Fig. 2c). The acoustic energy of the one output is used as mechanical energy to help drive the oscillator.

In another baffle system the sound radiator is placed in a channel (Fig. 2d). This directs the outputs away from each other, eliminating acoustic interference. The channel walls prevent geometric spreading of the sound waves and, if the waves are perfectly reflected in the channel, no attenuation occurs (Michelsen 1978).

A third system puts the vibrating disc or membrane in a planar surface or wall. The wall extends in all directions from the edges of the disc and separates the two outputs of the dipole source (Fig. 2f).

In general, baffles act to increase the length of the acoustic path between the front and back of the disc. In order to be efficient the distance of the path must be at least one-quarter wavelength of the sound produced. At this distance a "finite baffle" will behave as an "infinite baffle" (Olson 1957; see also, Michelsen and Nocke 1974). However, the sound fields produced by an acoustic radiator in a finite baffle deviate from theoretical fields predicted assuming an infinite baffle. These deviations are minimized if the baffle is irregularly shaped (Nichols 1946). These factors become important when considering baffle systems used by crickets (below).

BAFFLES AND GROUND DWELLING GRYLLOIDS

In crickets the vibrating membrane is located in the dorsal fields of the forewings. Males of ground dwelling species call with the tegmina raised at about a 45° angle to the body axis. A speaker cabinet is formed by the dorsal and lateral fields of the elevated forewings, and the lateral fields form the

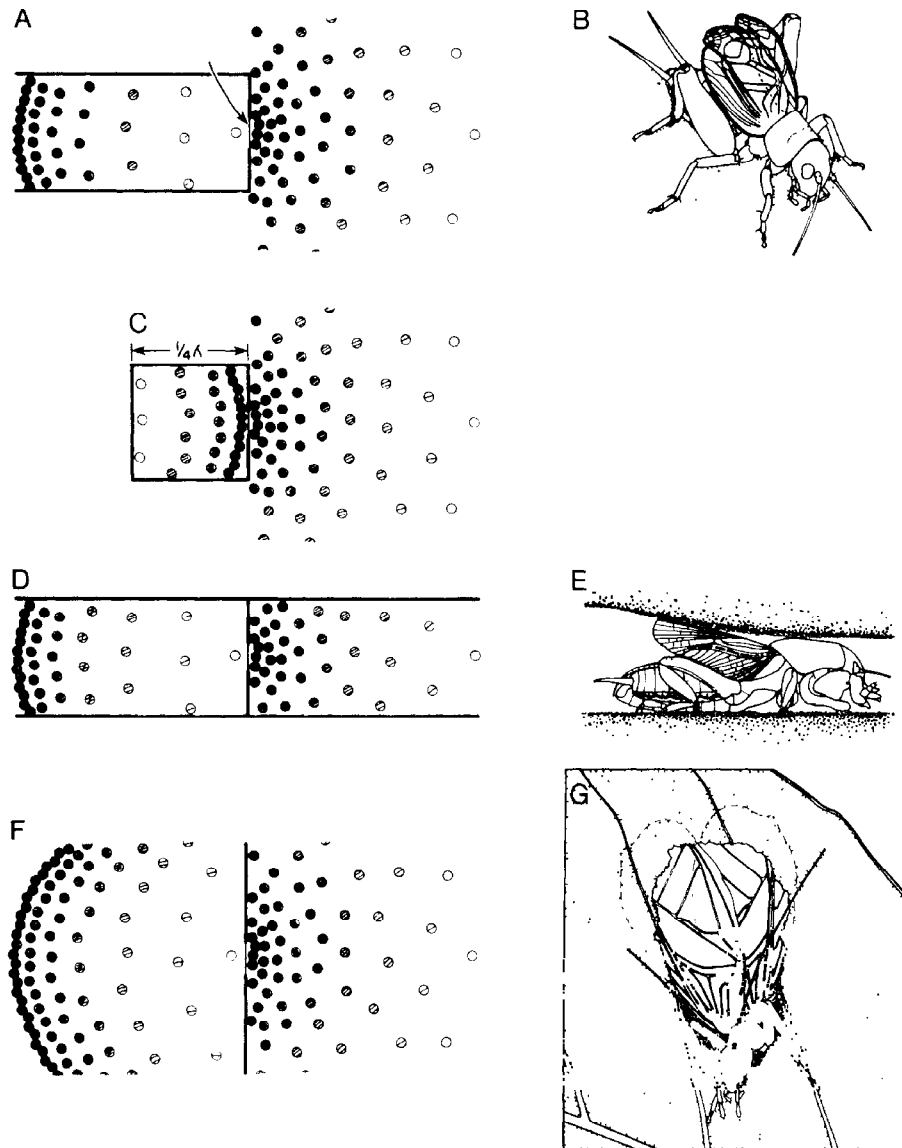


Fig. 2. Baffle Systems.

a. "Speaker cabinet" type baffle system prevents interference along edges of disc or membrane (arrow). The walls of the cabinet direct the output from one side of the disc back and away from the other output. Shading of circles shows amplitude of displacement of molecules where dark circles represent compressions.

b. Calling posture of a ground dwelling gryllid, *Anurogryllus arboreus*, shows "speaker cabinet" baffle system. Vibrating membranes are located in dorsal fields of raised forewings. Cabinet "walls" are formed by lateral fields and large hind femurs.

c. "Closed box" baffle system. The box acts as a resonating chamber. Sound waves produced on the box side of the membrane bounce off the back wall of the box and return to the membrane (total distance $1/2\lambda$) in phase

walls of the cabinet (Fig. 2b). Nocke (1971 cf. fig. 8) has shown that there is a reduction of acoustic interference at the sides of the membranes of calling *Gryllus campestris*, but that interference occurs at the posterior ends of the raised tegmina where no baffle exists. In another ground dwelling species, *Anurogryllus arboreus*, Paul and Walker (1979) showed that some interference exists both above and to the sides of calling males even though lateral fields are also present in this species.

I have observed the postures of calling males of several species of crickets and have noticed that the (broad) femurs of the hind legs are positioned just below the lateral fields of the forewings (Fig. 2b). The femurs may extend the walls of the cabinet and increase the distance between the front and back of the raised forewings. Sound fields of calling males with hind legs and/or lateral fields removed may reveal the functions of these structures in the baffle system. Comparative studies of species that have different frequency signals but similarly sized membranes, lateral fields, and hind femurs may also be revealing.

BAFFLES OF BURROWING CRICKETS

Numerous species of crickets are subterranean and live in extensive burrow systems. In many of these, males often call at the entrance of their burrow (e.g. *Anurogryllus* spp. Walker 1980, Walker and Whitesell 1981; *Gryllus* spp. Alexander 1961). A male that positions himself at the burrow entrance so that his raised tegmina fill the entrance, could be using the soil surrounding the burrow as a baffle and the burrow system as a "speaker cabinet" or "closed box" (see Fig. 2a and c). *Gryllus rubens* males sometimes call from such a position. While calling, male *Anurogryllus muticus* construct and situate themselves in depressions in the soil. Raised forewings are held parallel to and $1/4 \lambda$ away from the bottom of the depression. This system acts as a closed box (in preparation). Males of *Valerifictorus micado*, the Japanese burrowing cricket, are known to construct and call within a hood at the entrance to their burrow (Alexander 1961). This structure must have some effect on sound production, and perhaps that is its raison d'etre.

The most specialized burrowing crickets are mole crickets. In these species the entire life of the animal may be spent underground, and males call from within their burrows (Bennet-Clark 1970, Nickerson et al. 1979, Forrest 1982a). This calling habit is probably like placing a sound radiator in a

with output produced on the other side of the membrane. The acoustic energy is used to help drive the membrane. Shading of circles are the same as in (a).

d. Sound waves in a channel. The walls of the channel direct sound outputs away from each other and prevent destructive interference of the two sources. If the walls are perfectly reflective to sound waves no attenuation occurs in the channel or tunnel.

e. Calling mole cricket in subsurface tunnel. Illustration shows similarity to baffle system in (d).

f. Vibrating disc in planar baffle. The wall partitions two outputs and prevents interference. Baffle systems need only be $1/4\lambda$ of sound produced to produce maximum efficiency.

g. *Oecanthus burmeisteri* looking up through and calling in a hole it has made in sunflower leaf. The leaf acts like the partition, or wall, shown in (f). (Redrawn from Prozesky-Schulze et al. 1975. *Nature* 255: 142-143).

channel: With the tegmina raised within the tunnel the surrounding soil acts as an infinite baffle, and the tunnel as a channel or sound guide (Fig. 2e). Sound should travel great distances and remain at high intensity in the burrow system because there is minimal attenuation and spreading loss in a channel.

Males of four mole crickets (*Gryllotalpa gryllotalpa*, *G. vineae*, *Scapteriscus acletus*, and *S. vicinus*) construct specialized acoustic burrows that open at the soil surface through an exponentially expanding horn (like the bell on a musical instrument, such as a tuba). Bennet-Clark (1970) showed that the horn increases the efficiency of sound production in *Gryllotalpa gryllotalpa* and *Gryllotalpa vineae*. The bulb, an enlarged portion of the tunnel approximately $1/4 \lambda$ in length, is located anterior to the calling male and is used to tune the horn. In *G. vineae* the horn also directs the output. This directed output is believed to increase the probability that flying females will be "captured" by a male's sound field. No work has been conducted on the efficiency of sound production in other species. It is known that flying females of *S. acletus* and *S. vicinus* preferentially land at louder calling males (Forrest 1982b) and this would escalate selection for increased efficiency and power output.

BAFFLES AND VEGETATION INHABITING CRICKETS

Unlike ground dwelling and burrowing species, the males of most vegetation inhabiting species (*Neoxabea*, *Oecanthus*, *Anaxipha*, and *Cyrtoxipha* spp.) hold their forewings at right angles to the body axis while calling. The loss of acoustical energy to the sides of the crickets is so marked that Williams (1945), a violinist, on casual walks in the California countryside noticed the directional output of a tree cricket, *Oecanthus argentinus*. I have noticed that calling males of three *Oecanthus* spp. in Florida often perch precariously on the edges of leaves and that males actually twist their bodies to one side so that the lateral edge of the raised tegmen is adjacent to the leaf edge (Fig. 3). This may increase the efficiency of sound production because the leaf acts as a partial baffle (i.e. a "wall" partially surrounding the vibrating membranes). I have also observed many individuals of *Orocharis luteolira* and two *Anaxipha* spp. calling in this way. Perhaps this is common in leaf inhabiting species.

Oecanthus males can also be found calling with their raised tegmina in the notch of a leaf (Fig. 4). The leaf surrounds most of the vibrating wing membranes and may increase the baffle effect of the leaf. I even observed a male *Oecanthus niveus* calling with his raised tegmina between two leaves; he had pulled one leaf closer to the other with a mesothoracic leg so that the two leaf edges were adjacent to the lateral edges of both wings (Fig. 5)! I have also seen *Oecanthus* males calling with raised tegmina in leaf holes. Here the leaf surface completely surrounded the raised wings. These holes were made not by the cricket but by the feeding of other insects. These different calling postures may represent the evolutionary sequence to the leaf baffle used by male *Oecanthus burmeisteri* (Prozesky-Schulze et al. 1975). These males gnaw a pear-shaped hole in a leaf and situate themselves in it so that the vibrating wing surfaces occupy the hole and are surrounded by the leaf (Fig. 2g). The leaf baffle increases the amplitude of a male's calling

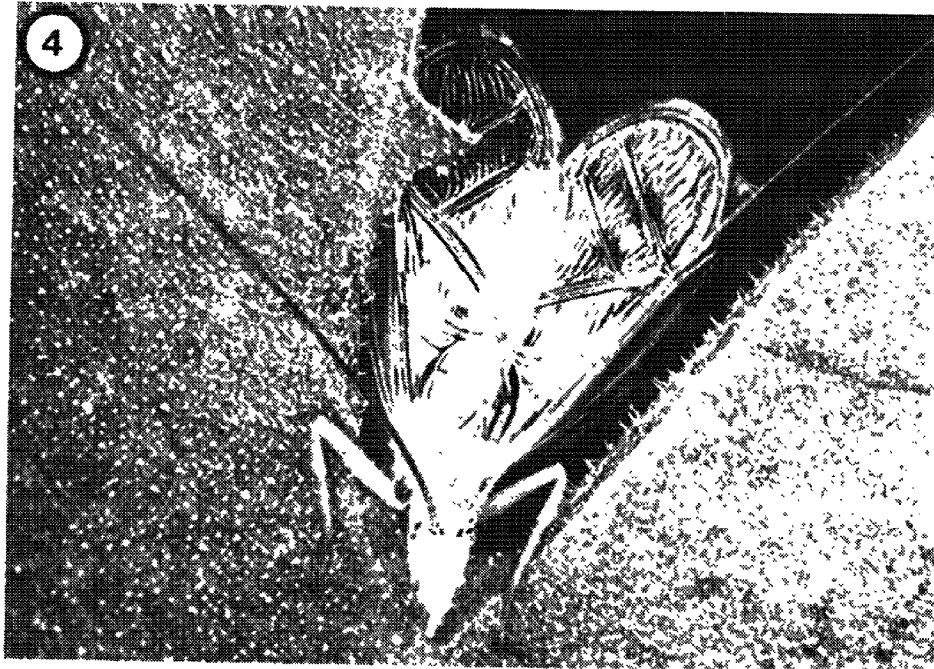


Fig. 3-4. (3) *Oecanthus* male calling on leaf edge. The body axis of the cricket is twisted so that the edge of one raised forewing is adjacent to the leaf edge. The leaf acts as a partial baffle surrounding a portion of the vibrating wing membranes. (4) *Oecanthus* male calling in leaf notch. Leaf surfaces surround a large portion of wing membranes, increasing the effectiveness of the baffle.

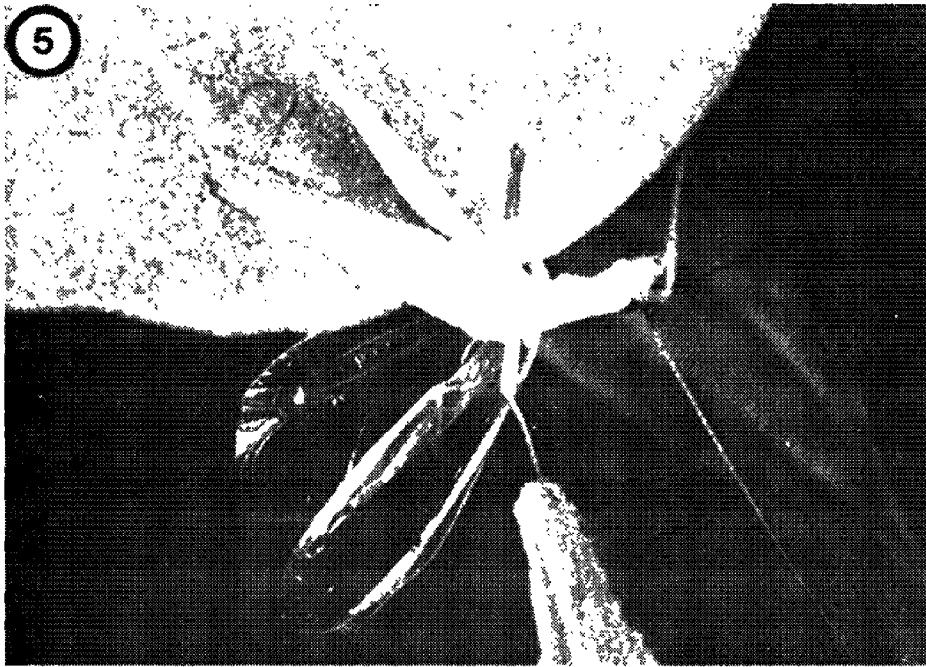


Fig. 5. *Oecanthus niveus* male calling between two leaves. The male is using a mesothoracic leg to pull one leaf nearer to wing membranes. Note the positions of the hind legs showing extreme twist of cricket's body.

song 2.5-3.5 times that of the same male calling without the baffle (Prozesky-Schulze et al. 1975).

The leaves used as baffles are irregularly shaped with diameters greater than $1/2$ wavelength of the sound produced. This makes them effective in increasing efficiency as well as reducing any deviations in sound fields (Olson 1957, Nichols 1946). That *Oecanthus burmeisteri* males have comparatively low frequency calling songs (2000 Hz, Prozesky-Schulze et al. 1975) suggests that increased efficiency may result in the evolution of a more effective long range signal. A similar compromise between efficiency and effectiveness was found in a comparative study of mole cricket calling songs (Forrest 1982a).

OTHER SYSTEMS

Walker (1969) observed another tree cricket, *Oecanthus jamaicensis*, calling with its head and pronotum protruding through a small (5 mm) hole in a leaf. While calling, the forewings were raised parallel and adjacent to the leaf surface. Similar systems occur as morphological structures of male crickets and katydids. In the scaly crickets (Mogoplistinae) and shield-back katydids (Decticinae) a pronotal shield covers the male tegmina. Thiele and Bailey (1980) have shown that in a coneheaded katydid, *Mygalopsis marki*, males with a similar pronotal shield have a sound field characteristic of a mono-pole sound radiator. Apparently the shield completely dampens the output from the dorsal side of the membrane and the result is a less directional, cardioid-shaped sound field, as compared to the

dumbbell-shaped field of a dipole source. How this system affects the efficiency of sound production is unknown. Comparisons of sound fields and energy expenditures of calling males before and after the removal of the pronotum would answer this question.

The "closed box" system may occur in a number of Tettigoniidae (e.g. *Neoconocephalus* spp.) that use very high frequency signals. The lateral fields of the forewings are wide enough to act as efficient baffles and, because of the high frequencies (short wavelengths) used, the distance between the wing membranes and thoracic tergites (the back wall of the box) approximates $1/4$ wavelength. This may add to the power output and decrease energy needed to drive the oscillator. Bailey (1976) noticed that males of *Ruspolia* spp. (Copiphorinae) adjust their position along stems or dried leaves that have a "reflective property not fully understood" and increases the output intensity. These katydids produce a mono-tonal calling song that would be needed for such systems to be effective.

SIGNALING AND DIRECTIONALITY

The directional output of a cricket is a consequence of a dipole sound radiator and the loss of acoustical energy due to destructive interference along the edges of the radiator. Baffles used to increase efficiency will at the same time reduce the directionality of the output. Directional signals, however, may be put to use if males "know" from which direction females will approach. Males could direct signals toward incoming mates and at the same time reduce some of the risk of attracting predators and parasitoids (Burk, this symposium). If females are likely to approach from any direction, males with directional signals can be expected to change positions periodically to advertise in areas to their sides not covered by their sound fields. The calling burrow of *Gryllotalpa vineae* is constructed so that it directs a male's output upward toward flying females, and in such a way as to increase the likelihood that a female will intercept the signal (Bennet-Clark 1970). *Anurogryllus arboreus* is a flightless, burrowing cricket and females approach males by walking. Males often climb tree trunks, and they call at a modal height of 1 m. The broadcast area covered by a male's sound field is more than 10 times that of a male calling on the ground (Paul and Walker 1979). The diameter of the tree trunk, as well as height from which males call, may influence the broadcast area and directionality of a male's sound field. Walker (1982) has shown that females actually prefer mates that call at the modal height over males calling higher on the same trunk. Males of a number of *Gryllus* spp. sometimes call on elevated perches, but factors that influence these behaviors are unknown (Paul and Walker 1979).

Bailey and Thiele (1982) suggest that males might use directional signals for spacing. In the katydid *Mygalopsis marki*, the spacing of males is determined by the perceived intensity of neighboring males' calling songs. To increase the distance of a competitor, a calling male might direct the most intense part of his output toward the rival (Bailey and Thiele 1982). *Gryllus campestris* males have a directional sound field and neighboring, calling males are oriented at right angles to each other (Popov et al. 1975). Such spacing would enable males to signal in areas near neighbors and keep the individuality of a male's calling song intact (see Lloyd 1981).

CONCLUSIONS

The energetic cost of calling by male crickets may exceed 10 times that of resting (Prestwich and Walker 1981). Much of this energy input may be wasted because of the small size of their vibrating membranes and the physical properties of the sound generated by this dipole source. Since these mating signals are fundamental to a male's reproductive success, selection will act on males to reduce costs and increase transmission efficiency and effectiveness. It appears that crickets have solved the physical problems of acoustical efficiency through behavioral and structural adaptations, and crickets in similar ecological situations seem to use similar baffle systems.

Many more adaptations probably exist that increase pair forming efficiency because selective forces have acted in the past and will continue to act on this acoustic signaling system. But such forces are not restricted to crickets or acoustic signals. One needs only *watch* and *ask why* such behaviors are adaptive.

SUMMARY

Male crickets sing and females respond. Because of the small size of their sound radiator (wing membranes) male crickets are faced with a problem. To be efficient sound producers males must transmit high frequency signals. But such signals are less effective over long distances than are those of lower frequencies.

Many species of crickets have various adaptations that increase efficiency and effectiveness. These adaptations are analogous to baffle systems used by acoustic engineers. Cricket species with similar habits use similar baffle systems. In ground dwelling crickets body parts function as "speaker cabinets." Burrowing crickets use their subsurface homes as sound guides and acoustic amplifiers, and vegetation inhabiting species use leaves as baffles.

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APPENDIX

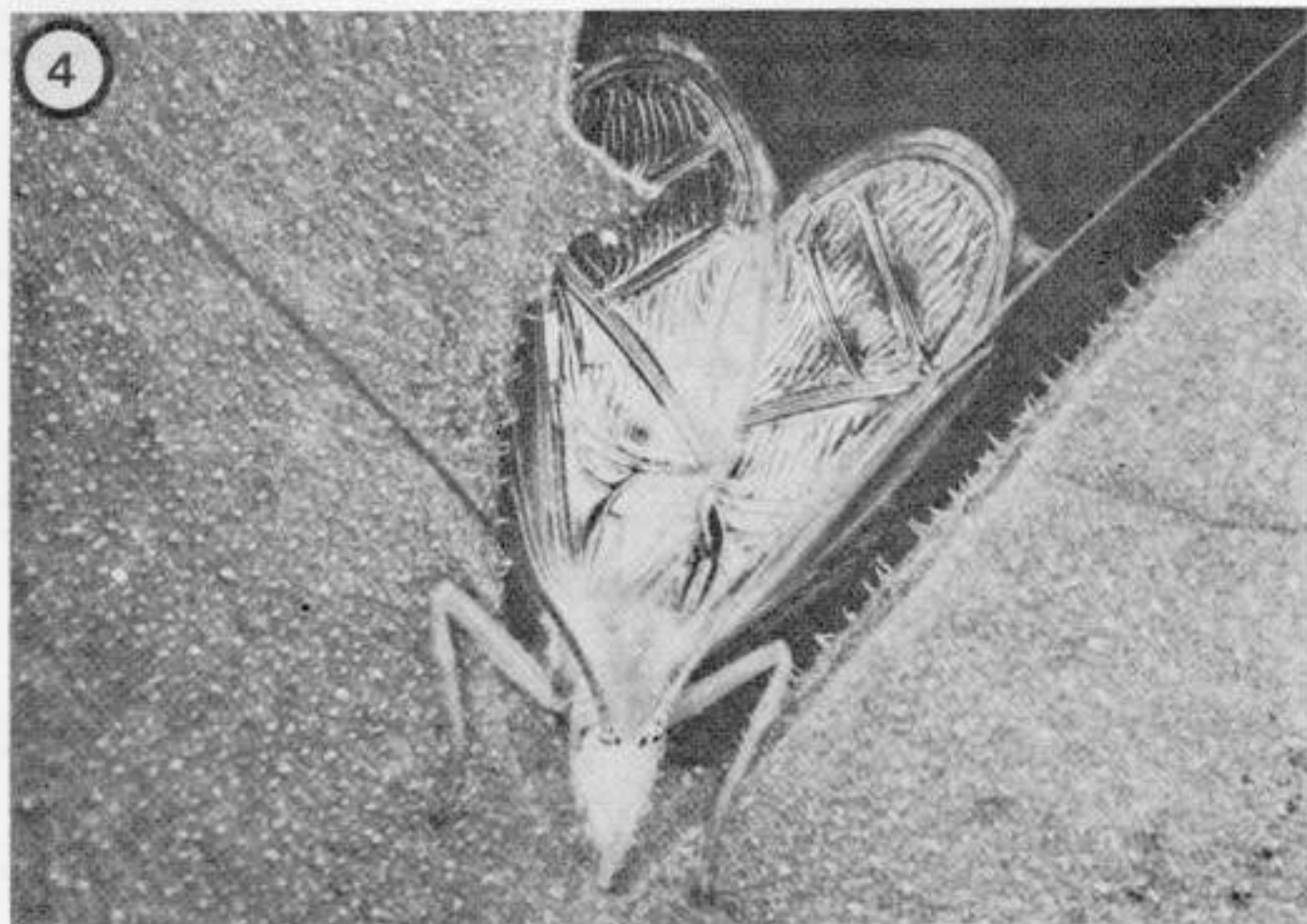
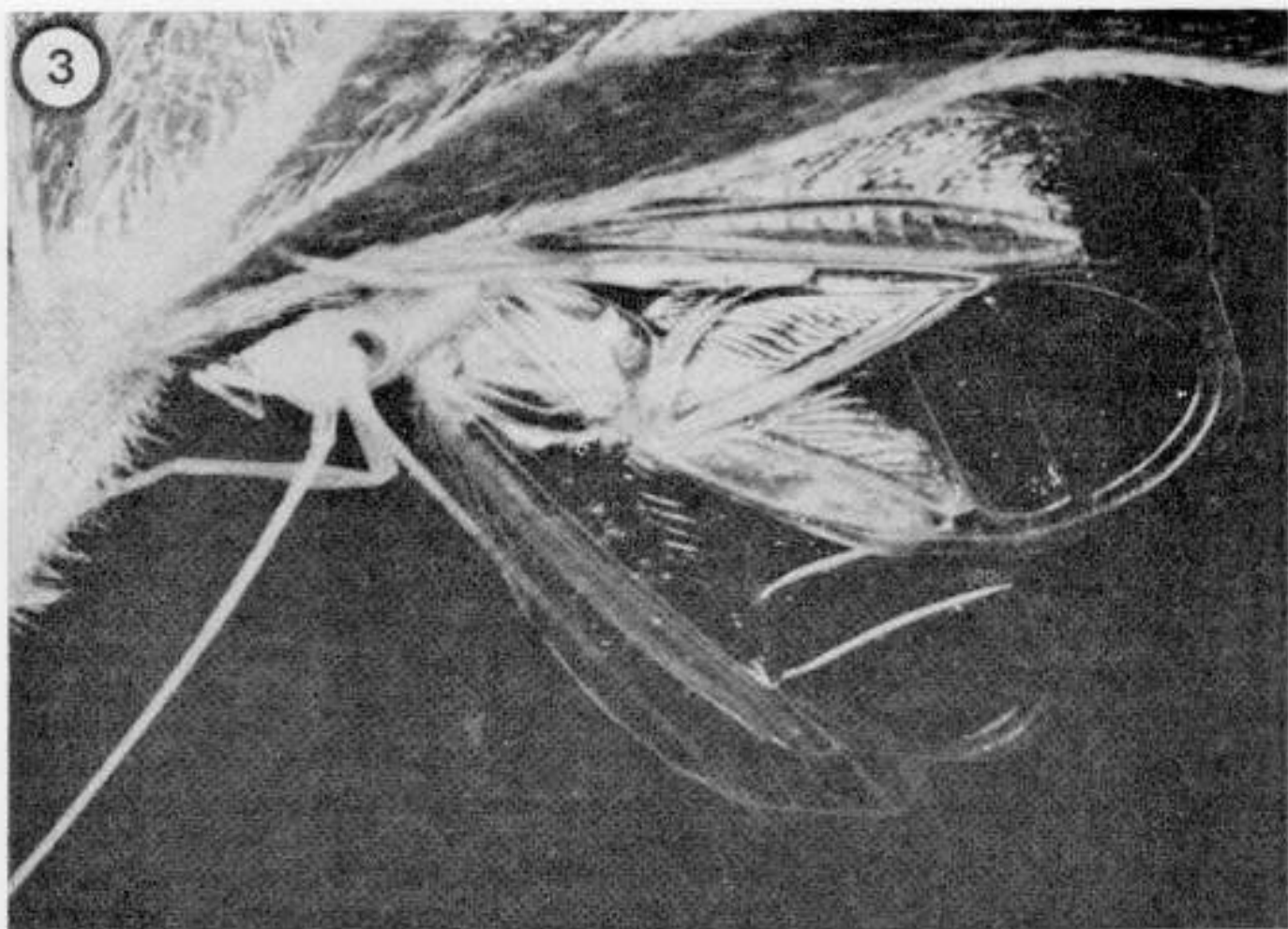
¹A decibel (dB) is a logarithmic unit that expresses the ratio of any two (sound) powers or pressures. Power and pressure levels are usually expressed with respect to a reference level (e.g. power reference $[W_r] = 10^{-12}$ Watts; pressure reference $[P_r] = .0002$ dynes/cm²). Power level in dB can be defined by the equation $PWL = 10 \log W/W_r$ where W is the power and W_r the power reference. Sound pressure level is defined by $SPL = 20 \log P/P_r$ where P is the pressure and P_r the pressure reference.

Note that for a given number of decibels the sound pressure ratio (P/P_r) is equal to the square root of the corresponding power ratio (W/W_r).

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