in the image should reflect the field structure. Preliminary analysis of the strength and shape of the differential emission measure derived from our spectrum suggests that cooling coronal loops dominate the E region; temperatures as high as $T \approx 10^7$ K are suggested, at which Si-XII emission still occurs, though with a much reduced emissivity per unit emission measure. On the basis of the magnetic topology of the W region and the fact that loops must be rooted in regions of opposite polarity, we interpret the x-ray emission therein as a combination of large-scale loops tracing out the relatively darker, predominantly E-W features, and smaller, lower-lying loops spanning the neutral line in the central part of the region where the brightness appears to peak. This qualitative interpretation is shown in Fig. 3C. Although the finest features in the image indicate an angular resolution of ~5 to 10 arc seconds, there is a diffuse quality to most of the image. Interestingly, the long sausage-like feature stretching from northeast to southwest and then curving back around to the north looks like a hollow tube. One possibility is that the core plasma is either too hot or too cool to emit Si-XII radiation strongly.

As the first astronomical image obtained by a normal incidence x-ray telescope, the image is of some interest for its own sake. The simple optical system introduced primarily two aberrations, coma and astigmatism (spherical aberration is minimal in an *f*/20 system). For a perfectly figured spherical surface optimally focused, the geometry of the optical system would have allowed for ~3 arc seconds resolution within ~12 arc minutes of the center of the field of view. The actual solar image shows linear and curvilinear features whose widths are ~23 arc seconds; the broad, linear features also show transverse brightness gradients over regions as narrow as 5 arc seconds. Despite the aberrations of this simple telescope, and the possible effect of defocusing, our postflight analysis indicates that these details of the observed structures are unlikely to be optical artifacts. Even with all the shortcomings resulting from the low-budget nature of the experiment, the ability to make this kind of photograph from a normal incidence multilayer telescope is an encouraging development for x-ray astronomy.

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# Bat Predation and Its Influence on Calling Behavior in Neotropical Katydids

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**Insectivorous bats have influenced the development of antipredator behavior in moths, green lacewings, crickets, and mantids; until recently, such adaptations were unknown in katydids. Foliage-gleaning bats in Panama can use the female-attracting, airborne calling songs of nocturnal katydids to locate prey. They also feed heavily on these insects. Katydid species sympatric with these bats exhibit markedly reduced calling song duty cycles. Males supplement shortened songs with complex, species-specific tremulations that generate vibrations that are inaudible to bats but reach conspecific females through a shared plant substrate. Female katydids do not call audibly but are also preyed on in large numbers, perhaps as a result of moving toward calling males.**

IN MANY ANIMAL SPECIES, MEMBERS OF one sex use acoustic signals to attract mates (*1*). Mate-attracting calling songs are species-specific, unambiguous, and highly localizable, which helps them function successfully in sexual pair formation. These same characteristics, however, reveal the location of calling animals to predators and parasites (*2, 3*), including bats. In a study in Panama, bats responded to tape recordings of male katydids (Orthoptera: Tettigoniidae) (*4*). This report describes field and flight cage experiments with live insects to show that at least four species of tropical New World foliage-gleaning bats (FGB) (Phyllostomidae: Phyllostominae) exploit katydid songs as prey-finding cues. We show that the song duty cycle in katydids (proportion of time spent singing) is markedly reduced in species occurring in the understory of a mature forest with FGB, but not in species in secondary growth areas without these bats (*5*). We also report the occurrence of tremulation (vibration) signals in forest katydids that offset the information loss of a lowered duty cycle. These male katydids supplement their acoustic cues with complex species-specific body vibrations that are inaudible to bats, but travel through plants to conspecific females. Insectivorous bats and their prey have long coevolutionary histories, and bats have influenced the development of behavioral and morphological antipredator adaptations in moths, green lace-wings, crickets, and mantids (*6*). We present findings of widespread behavioral antibat defenses in katydids, another large group of insects.

We baited mist nets with singing male katydids to demonstrate that bats respond to song cues (*7*). Members of four FGB species (six *Micronycteris megalotis*, eight *Micronycteris hirsuta*, nine *Tonatia silvicola*, and one *Trachops cirrhosus*) responded to the calls and were caught in nets. These FGB were not attracted to control nets baited with silent females ($\chi^2 = 24$; $P < 0.001$).

Analysis of prey remains (culled, sexually dimorphic whole insect wings) that accumulate in natural FGB roosts (*8*) showed that at least one species fed heavily on katydids; 40.1% of 10,944 insects found in 12 *Micronycteris hirsuta* feeding roosts were katydids. Although they do not call, at least 50% of the katydids consumed were female. How these were located by the bats is not known.

To explore the influence of FGB predation on katydid call design, we recorded and analyzed calling songs (*9*) from 43 forest-dwelling katydid species and compared them to calls from the four dominant species who dwell in clearings. Clearing katydids signal with conspicuous calls; they have

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broadband carrier frequencies, in or near the upper audio range, and relatively high duty cycles (Fig. 1A). Conversely, calls from forest forms have sinusoidal frequencies (purer tones) in the high audio or ultrasonic range and remarkably low duty cycles (Fig. 1B), attributes that make them difficult for mammalian ears to locate (*10*). Only one forest katydid, *Ischnomela pulchripennis* (*11*), has localizable call features. It sings from large (2 m) terrestrial bromeliads (*Aechmea magdalanae*) that are covered with long, sharp spines that could injure a bat's delicate wings. It is not taken as prey. In contrast, the other forest katydids called when they were fully exposed from understory plant leaf surfaces.

To determine the potential selective advantage of inconspicuous katydid calls (*12*), we compared the average response times of *Tonatia silvicola* to katydids producing frequent (60 calls per minute) and infrequent (<1 call per minute) calls (*13*). Bats located frequent callers in 26 ± 11 seconds (mean ± standard error; $n = 35$), and flew directly to the insect producing the sound. The bats took significantly longer to locate infrequent callers (34 ± 11 minutes; $n = 35$; $U = 1225$, $t = 7.20$, $P < 0.0005$; median value, 6 minutes and 35 seconds), because responding bats made repeated short, erratic flights lasting only as long as the insects' calls. The bats did not locate silent insects.

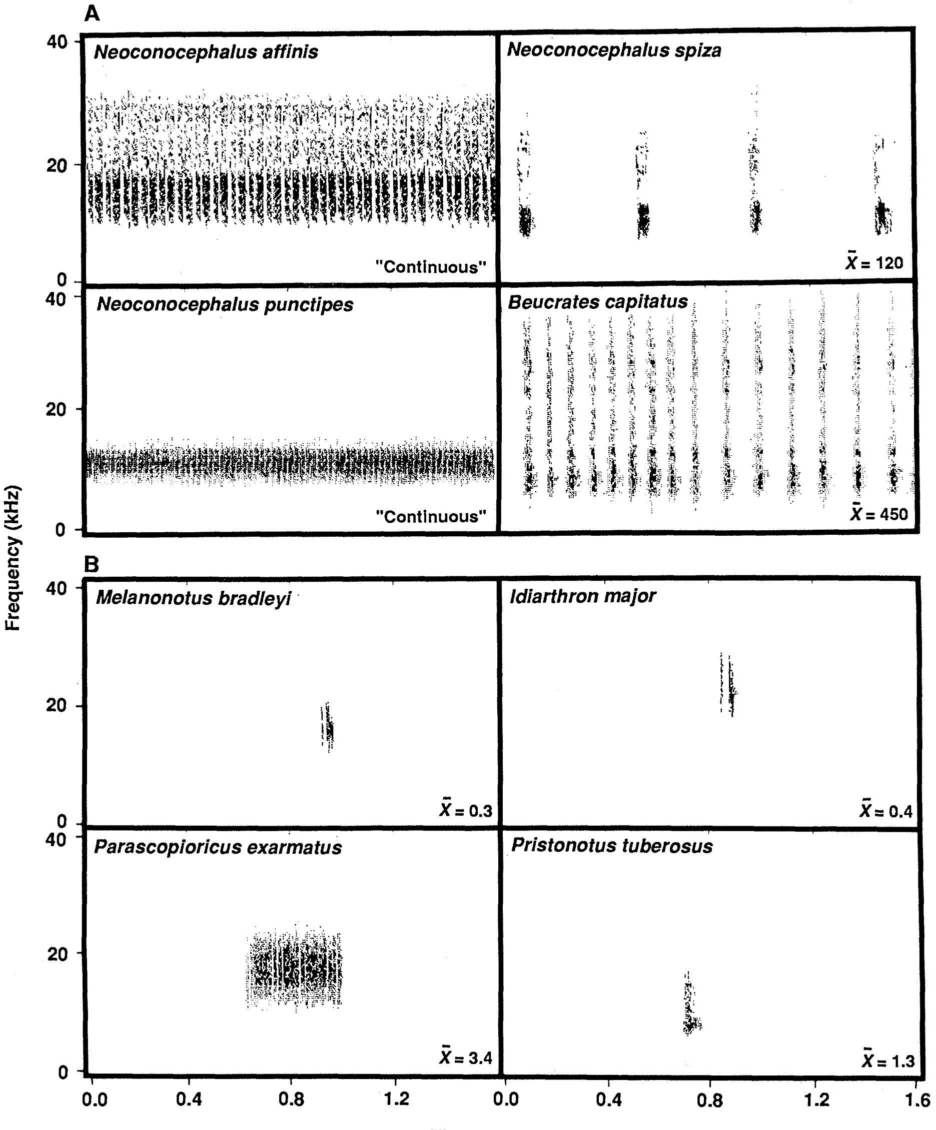

**Fig. 1.** (**A**) Audiospectrograms of airborne calling songs of four dominant clearing katydids (Orthoptera: Tettigoniidae) on BCI. These insects are not preyed on by bats. Their calls emphasize audio frequencies, are broadband, and are produced frequently. (**B**) Airborne calling songs of four forest-inhabiting katydid species on BCI. These calls are short, infrequent, and relatively high and pure in tone, making them difficult for mammalian ears to localize. They typify katydid songs in areas inhabited by tropical New World foliage-gleaning bats (Phyllostomidae: Phyllostominae). $\bar{X}$, average call repetition rate per minute for three to five individuals.

Reduced song production in katydids was unexpected since, worldwide, these animals are considered among the most acoustically active of insects. Moreover, short, inconspicuous calls increase localization difficulties for attracted females. So, it is not surprising that forest katydids supplemented their songs with another type of communication, in the form of complex and vigorous body vibrations that are strong enough to visibly shake plants but are inaudible and travel through plants to other individuals. These tremulations were originally described in a Costa Rican katydid by Morris (*14*), who also suggested their role in reducing bat predation. Tremulations appear more costly energetically to produce than short airborne calls, but they are not perceived by FGB.

Tremulations were observed in 13 species of forest katydids (*15*) and recorded from males of six species (*16*) (Fig. 2). The vibrations are structured, stereotypically amplitude-modulated, species-specific, and produced only at night between (but not during) the short acoustic calls. Isolated males in cages produced tremulations in the absence of females. Females near conspecific males answered with tremulations of their own, leading males to tremulate more often and to cease audible calling (*17*). Males and females in separate opaque cages on the same wooden bench communicated with one another in this fashion for several hours even when separated by distances of 2.5 m.

With the exception of the insects described here, vibrations in katydids, when they occur, are produced only after individuals come together as a result of acoustic signaling (*18*) or, as simultaneous but weak by-products of stridulation (song production) that aid neurologically in species-specific song coding (*19*). Tremulations in the katydids described here are temporally distinct from stridulation and are produced in the absence of females. Katydids appear to have developed this form of communication, at seemingly increased energetic costs, to supplement reduced audible outputs. They are analogous to the cues used by some spiders to attract mates (*20*) and should function at long range through the substrate since katydids have sensitive vibration receptors (subgenual organs) (*21*).

Predation on sexually signaling males is an important mortality factor, and bat predation has influenced the evolution of calling in animals such as neotropical frogs (*3*). Because FGB eat large numbers of katydids, respond to their airborne calling songs, and have considerable difficulty in locating sporadic callers, it is reasonable to suggest that they have also influenced calling song design in these insects. Selection for signals that are transmitted through substrate, and as such

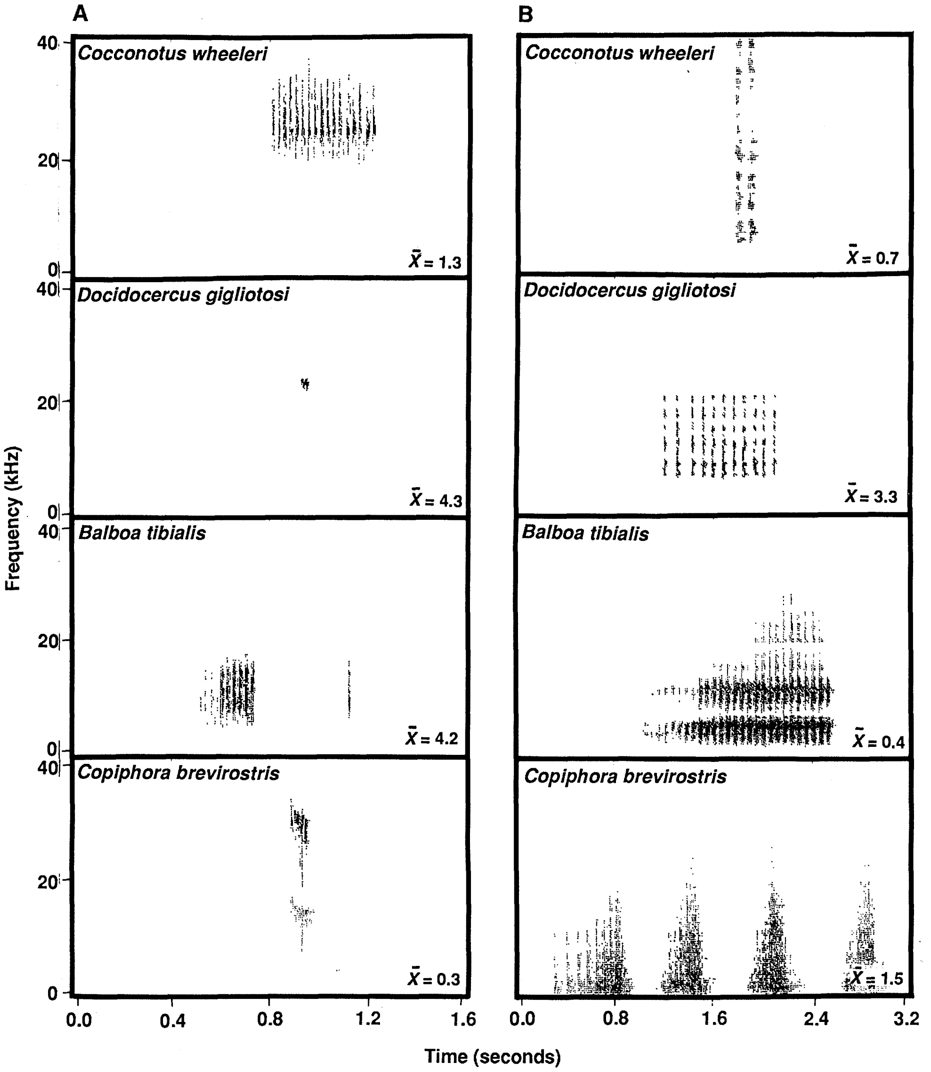

**Fig. 2.** Patterned, species-specific, male-produced, airborne- (**A**) and substrate-transmitted (**B**) calling songs of four forest katydid species on BCI. Tremulations were also recorded from *Acanthodis curvidens* and *Eucocconotus camerani*. Individual tremulation pulses in the last three pulse sequences of *Copiphora brevirostris* occur too rapidly to be differentiated by the recording method used (*16*). However, they can be seen in the first pulse sequence. Tremulations are not audible; the spectral component of the patterns is an artifact of the atypical substrate used to record the signals. Also, the time scales differ for the two types of signals. $\bar{X}$, Average call repetition rate per minute for three to five individuals.

do not compromise the vital process of mating, is an adaptive response in the presence of acoustically orienting predators. This finding will revise the notion of the exclusive role of acoustic song in katydid pair formation.

How the FGB located the large number of female katydids they consumed is not known. These bats appear to use passive sound rather than echolocation to locate prey (*22*). Most female Orthoptera search for and locate singing males and thus spend more time moving in the open, thereby exposed to bats. They may risk potential predation merely as a result of responding to calling males (*23*). The implications of this selection pressure for the evolution of female katydid behavior are great both in terms of antipredator defenses and in the choice of calling males, but the effects of this pressure are unknown.

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13. Five unfed *Tonatia silvicola* were tested in a red-lit screen flight cage (4.5 by 4.5 by 2.3 m). A bat perched in one corner of the cage and was observed from the opposite corner. A male katydid (*Scorpiorinus fragilis*, about 60 calls per minute, carrier frequency 25.2 kHz; or *Acanthodis curvidens*, <1 call per minute, carrier frequency 13 to 16.8 kHz) in a screen cage (30 by 18 cm) and a control cage containing an equal size female were placed on the floor in the remaining corners, 4 m from the bat. Trials began when the male began to sing and ended when the bat landed on, or within 10 cm of, a cage. Correct choices were not rewarded. Position of the singing insect was changed randomly after each trial. Trials were repeated every 15 to 30 minutes, when the insect resumed singing. The same bats were tested for seven trials each with frequent and infrequently calling katydids. Only one category of insect was tested each night. Female katydids were never approached. *Scopiorinus fragilis* and *Acanthodis curvidens* calls differ in carrier frequency. Therefore, response times to different repetition rates are not really comparable. Both calls, however, elicited immediate flight, indicating that they were perceived by the bats. In a previous study (*4*), *Tonatia silvicola* consistently responded to recordings of a frequent, 12-kHz katydid call in less than 1 minute.
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16. Tremulations were recorded from katydids in wooden cages (40 by 40 by 30 cm) in which one side was a loose glass panel. Each tremulation rattled the glass once, producing an audible sound that was recorded with a Sony Walkman recorder whose microphone was placed on the glass. Tremulation patterns were analyzed with a Uniscan II audiospectrograph (Multigon Industries). Female tremulations were fainter than those of males and could not be recorded in this manner.
17. Alone, two individual *Balboa tibialis* males produced 1.86 ± 2.18 tremulations per 5-minute period

($n = 24$). An answering female, in a separate opaque cage 1 m from the male on the same wooden bench, increased male tremulation production to 12.25 ± 3.09 per 5-minute period ($n = 24$; $U = 569$, $t = 5.83$, $P < 0.0005$; median value, 5.5 tremulations). Males also produced 21.42 ± 13.34 airborne calls per 5-minute period without an answering female ($n = 24$), and no airborne calls when a tremulating female answered.

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# Glycolysis Preferentially Inhibits ATP-Sensitive $K^+$ Channels in Isolated Guinea Pig Cardiac Myocytes

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**In heart, glycolysis may be a preferential source of adenosine triphosphate (ATP) for membrane functions. In this study the patch-clamp technique was used to study potassium channels sensitive to intracellular ATP levels in permeabilized ventricular myocytes. Activation of these $K^+$ channels has been implicated in marked cellular $K^+$ loss leading to electrophysiological abnormalities and arrhythmias during myocardial ischemia. The results showed that glycolysis was more effective than oxidative phosphorylation in preventing ATP-sensitive $K^+$ channels from opening. Experiments in excised inside-out patches suggested that key glycolytic enzymes located in the membrane or adjacent cytoskeleton near the channels may account for their preference for glycolytic ATP.**

STUDIES IN INTACT ISOLATED HEART and cultured myocytes have suggested that glycolysis has a special role in maintaining membrane function during myocardial ischemia and metabolic inhibition (*1–5*). In the isolated rabbit ventricle, selective inhibition of glycolysis resulted in much greater extracellular $K^+$ accumulation than selective inhibition of oxidative (mitochondrial) metabolism despite similar total cellular levels of high-energy phosphates (*5*). Extracellular $K^+$ accumulation during early myocardial ischemia results from increased $K^+$ efflux (*6, 7*) and activation of adenosine triphosphate (ATP)–sensitive $K^+$ channels has been implicated as a possible cause of this efflux (*8–10*). These channels open only when the concentration of ATP falls below a critical level. However, the critical level of ATP that completely suppresses ATP-sensitive $K^+$ channels in excised membrane patches from heart is much lower (approximately 0.2 m*M*) than the concentration of ATP during ischemia except at very late stages (*8*). Unless either the sensitivity of ATP-sensitive $K^+$ channels to ATP concentration is markedly altered by other sequelae of metabolic inhibition or ATP stores are compartmentalized in the cardiac cell, it seems unlikely that activation of ATP-sensitive $K^+$ channels could cause marked $K^+$ loss beginning after 30 seconds of ischemia (*6, 7*). The results of this study show that under conditions in which cellular ATP consumption is intrinsically high, glycolytic (anaerobic) metabolism is more effective than oxidative (aerobic) metabolism in suppressing ATP-sensitive $K^+$ channels in patch-clamped single ventricular myocytes. The preference of ATP-sensitive $K^+$ channels for glycolytically generated ATP may be due to the presence of key glycolytic enzymes strategically located near $K^+$ channels.

Single ventricular myocytes were isolated enzymatically from hearts of guinea pigs (300 to 400 g) (*11*) and studied at room temperature by means of the gigaseal patch-clamp technique (*12*). Single-channel recordings were made with fire-polished patch electrodes (tip diameter 1 to 4 μm, resistance 1 to 3 megohms) mounted to the headstage of List EPC-7 patch-clamp amplifier. Data were recorded on a modified videocassette recorder and chart recorder and analyzed on a PDP 11-23 computer. The experimental chamber (0.5 ml) was mounted on the stage of an inverted microscope and was continuously perfused (1 to 4 ml/min) throughout the experiment. The standard filling solution of the patch electrode contained (millimolar concentration): KCl, 150; Hepes, 5; and KOH to bring the *p*H to 7.3. The standard bath solution contained: KCl, 138 to 147 (total $K^+$ concentration 150); Hepes, 5; EGTA, 2; $CaCl_2$, 0.5; $MgCl_2$, 2; and KOH to bring the *p*H to 7.1. Various substrates were added as described later. The free $Ca^{2+}$ concentrations of the patch electrode and bath solutions were 4 to 6 μ*M* and <0.1 μ*M*, respectively. For single-channel recordings during multiple interventions the patch electrode was arbitrarily held at +40 mV relative to the bath. Results are expressed as mean ± standard deviation.

Most single-channel recordings were made from "open" cell-attached membrane patches (*10*) in which first a gigaseal was formed at one end of a cell with the patch electrode. The other end of the cell was then exposed for 10 to 30 seconds to a stream of bath solution containing 0.1% saponin delivered by positive pressure through a second electrode positioned just over the surface membrane. As soon as the membrane in this region was locally disrupted (detected by a slight swelling of the cell easily visible at ×800 magnification), the saponin-containing electrode was quickly withdrawn. Under these conditions, openings of inwardly rectifying $K^+$ channels were commonly observed as long as 2 m*M* ATP was present in the bath solution. The single-channel conductance of these channels determined from the linear portion of the current-voltage (*I-V*) curve was 39 ± 4 picosiemens (pS). Removal of ATP from the bath solution that perfused the cell reversibly activated ATP-sensitive $K^+$ channels in the membrane patch distinguishable from inwardly rectifying $K^+$ channels by their larger single-channel conductance (76 ± 5 pS). Permeabilized cells were capable of generating ATP endogenously by a variety of metabolic pathways when provided with the appropriate substrates (Fig. 1). Washout of 2 m*M* ATP from the bath caused multiple ATP-sensitive

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