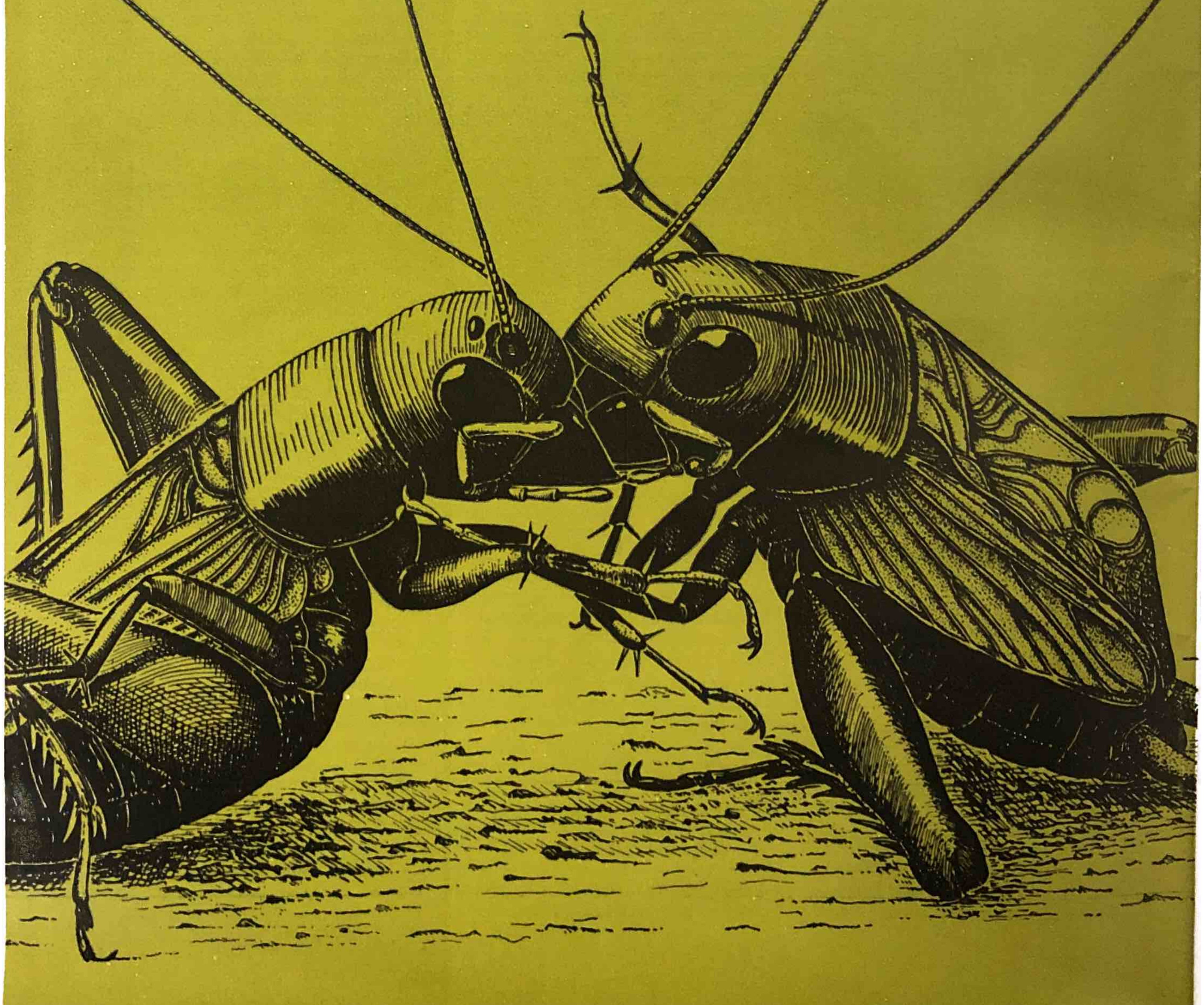
The Evolution of Cricket Chirps

by RICHARD D. ALEXANDER



O cricket, who cheats me of my regrets, the soother of slumber,
Muse of ploughed fields and self-formed imitation of the lyre,
Chirrup me something pleasant. . . .
How I wish, O cricket, that you would deliver me
from the troubles of much sleepless care,
Weaving the thread of a voice that causes love to wander away.
And I will give you for morning gifts drops of dew,
And a leek, ever fresh, cut up small for your mouth.

Modified from translation of Meleager (*ca.* 100 B.C.).
LAFCADIO HEARN. *Insects and Greek Poetry.*

Crickets must have been a particular source of curiosity for as long as there have been humans to be curious. Poets, philosophers, scientists, and primitive peoples—all have left some special indications of their interest in one kind of cricket or another. In addition to verses about crickets, written in many languages, one could cite the antiquity of cricket fighting as a sport in the Orient; the almost universal fame of Milton's "cricket on the hearth"; and the practice, developed independently in several parts of the world, of keeping crickets for food, for their songs, and for driving away "evil spirits." Even today, with so many millions of the world's population concentrated inside cities of macadam, steel, and concrete, the producer of a television show or motion picture can make his scenes nocturnal with only a token drop in light intensity if he simultaneously adds the chirp of a cricket in the background.

The source of the cricket's charm is obvious. To eliminate it we would need only to silence him, to take the acoustical dimension out of his life. But this would not be a simple exorcism. As the jigsaw puzzle of cricket life slowly assumes shape through a continuing series of investigations on behavior, classification, structure, and physiology, it is increasingly evident that a certain well-known American biologist could not have been more wrong when he wrote that, like the clanking of a knight's armor, cricket chirps were little more than the frictional creakings of an animal with an external skeleton. Indeed, those cricket groups that have lost their ability to stridulate, and along with it their hearing organs, have changed their lives and their body forms so drastically that they are excluded by some insect taxonomists from the elite body of "true" crickets.

Fossil evidence indicates that the crickets (family Gryllidae) became a separate evolutionary line some 150 to 200 million years ago, probably during the Jurassic Period, coincident with the heyday of the dinosaurs. Their acoustical system is even older than that, since their nearest relatives, the katydids and long-horned grasshoppers (family Tettigoniidae), have the same tympanal auditory organs on their front legs and the same stridulatory device on their front wings. It is possible that this is the oldest acoustical communicative system still in existence, and certainly crickets and their relatives were among the first animals to be heavily involved in transforming the previously silent terrestrial environment into the bedlam of noise it had become long before the first humans appeared on the scene.

Crickets are the master musicians of the insect world. They have, within a single species, at least as many different kinds of acoustical signals as any other kind of insect; they produce some of the loudest of all animal signals (over 100 decibels at distances of a few inches); and they are the only animals known to be capable of producing a "pure" frequency with a stridulatory, or rubbing, device. (Pure frequency means that a single frequency so dominates the sound that all others are inaudible and, for practical purposes, insignificant. Such a sound is difficult to achieve. Not even an electronic audio-oscillator, for example, has been able to produce an absolutely pure frequency.)

The cricket stridulatory and auditory organs (*page 29*) are complex devices that have evolved together as a functional unit for a long time; they could not have appeared through a single change, or even a few mutations, but had to develop through a long sequence of small, step-by-step alterations. There are no fossils of rudimentary versions of these devices, but there is evidence of their precursors among the living relatives of crickets. Non-acoustical relatives of crickets have a large clump of sensory cells, called the subgenual organ, in the same general location on the forelegs as the crickets' auditory organ. The cells apparently function as proprioceptors, supplying information to the insect's central nervous system about the position of the leg. These proprioceptive cells are believed to be the forerunners of the tibial auditory organ, and we can speculate that the device may have passed through a vibration-perceiving stage, during which it was sensitive only to transverse waves that were transmitted through the substrate. Subsequently, at one spot the cuticle thinned and special membranes appeared, making the spot gradually more sensitive to the air-transmitted, longitudinal waves that we call sound.

The origin of the stridulatory device on the male cricket's forewings can also be reconstructed, in the absence of fossil evidence, through comparison of living crickets and their relatives. Most of the modern groups of winged insects that have left the oldest fossil records mate with the female climbing on the male's back. Nearly all modern crickets still mate this way, and comparative study correlating structure and behavior suggests that all their ancestors, back to the cockroach line from which they diverged during Paleozoic times, mated in the same fashion. Most cockroaches still start copulation this way (although, like some crickets, they finish the act end to end), and like the male crickets, male cockroaches raise their forewings during courtship, exposing chemical areas on their backs that attract the female into the mating position. But cockroaches never developed prominent stridulatory devices, even though some of them rustle their wings audibly during courtship, and they never developed auditory organs on their forelegs. While crickets and katydids were becoming acoustical, the cockroaches were elaborating chemical and tactual stimuli, and so they remained cockroaches.

It seems beyond question that cricket stridulation originated from the wing lifting and vibrations of courtship. If the auditory organ also evolved in this context, and it seems probable that it did, we may wonder if, during the vibration-perceiving stage postulated above, the source of vibration might not have been the shaking and wiggling body of the male as he vibrated his lifted wings. The advantage of thus providing a vibratory stimulus to the advancing and mounting female could have resulted in a stridulatory ability that would add to the vibrations (and incidentally produce acoustical effects), even before the appearance of auditory ability. This, in turn, could have set the stage for elaboration of the auditory organs and completion of the transition to acoustical living for the ancestor of crickets and katydids.

Although this hypothetical sequence involves a great deal of circumstantial evidence and speculation, the facts fit together so beautifully that, in the absence of any evidence to the contrary, the whole idea seems quite reasonable.

But to account for the appearance of the auditory and stridulatory apparatus is only the beginning of the story. These devices have been around for 150 million years, and during that time their actual structure has changed in only relatively minor ways. Crickets and katydids diverged very early and developed quite different sorts of sounds: crickets, their clear, whistle-like notes; and katydids, their lisps and clicks that are often almost of the nature of white noise (containing an extremely wide spectrum of frequencies). The auditory and stridulatory devices of the two families are correspondingly different. But there are some 2,500 known species of crickets and even more katydids. Hardly any two species have the same sounds in their repertoires. Here, in the analysis of signal diversity, are found the interesting and most difficult questions regarding evolutionary change. In many cases there are no differences at all between the auditory or stridulatory devices of species: song differences depend instead on some unknown variation in their central nervous systems or possibly in their muscles.

You may ask why species differences in cricket stridulations should always be attributed to evolutionary change. After all, humans make different sounds in, say, China and England, but a Chinese baby reared in London would speak perfect English, and a British baby reared in China would speak perfect Chinese. Not so with crickets. So far all of the environmental manipulations that entomologists have been able to dream up, short of actual mutilation, have had no effect on the kind of chirp a cricket makes, or the various chirps to which it can respond. If it does chirp, it gives the right chirp for its species, and it does so the first time it tries, after only a few raspy starts. This is really no surprise, for unlike birds and mammals, or even frogs and toads, most young crickets do not hatch from the egg until long after all individuals of the previous generation have died. This means that there can be no "culture" at all in cricket chirping. Differences among species and differences within species, in both signals and responses, have—in every case tested—been shown to be the result of genetic differences. The only exceptions are song variations such as those brought on by temperature (crickets are cold-blooded animals), and even here, the ability to respond also changes with temperature. Thus, a female cricket can recognize a singing male of her own species only if he is approximately as warm or as cold as she is.

This rigidity in the acoustical behavior of crickets typifies much of the behavior of arthropods. It is not merely a failure to evolve learning; it is another *direction* of natural selection. Selection has been minimizing the chances that the kinds of sounds a cricket makes will be influenced by sounds it hears; there are too many alien sounds in a newly adult cricket's environment, and too few chances of hearing another cricket at just the right moment. This does not make the cricket's chirp any less a product of both hereditary and environmental factors: every characteristic of an organism, after all, depends upon both factors. But the particular environmental factors involved in the development of a cricket's chirp are much more difficult to identify than some of those influencing, for example, bird songs or human vocalizations, and they are evidently less variable among the environments of different individuals of the same species.

The evolutionary elaboration of diversity in cricket signals has taken place in two contexts. On the one hand, species have begun to produce acoustical signals in new situations, and by evolving the ability to make use of such innovations, they have increased the number of effective signals in their repertoires. On the other hand, whenever speciation has occurred, the resulting species have evolved different repertoires. We have tape-recorded about 350 signals from a total of more than 200 cricket species, in 10 subfamilies and 50 genera, brought together from all parts of the world. In this entire assemblage there are only three pairs of species, one group of three species, and one group of four species that have any identical signals among them.

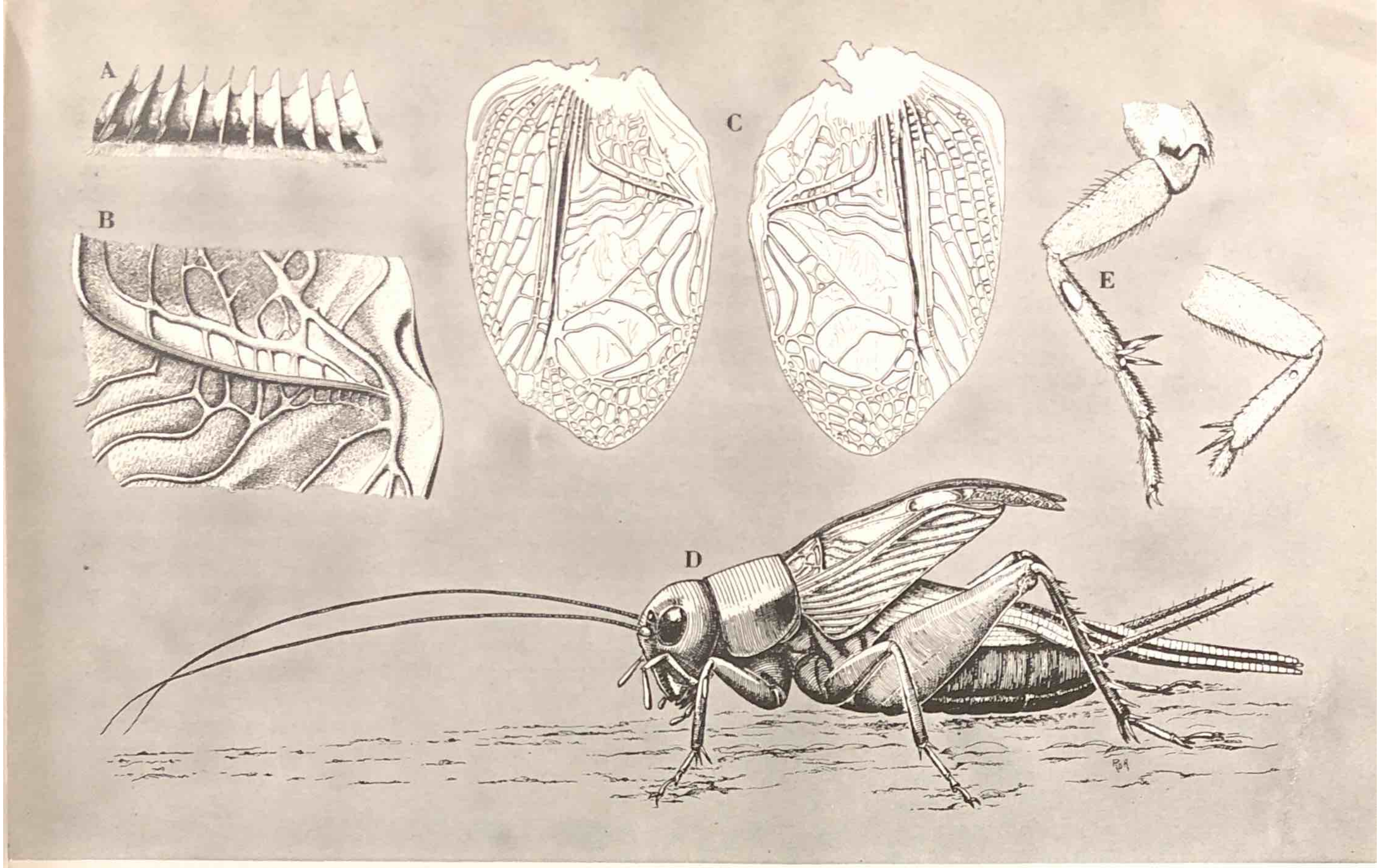


Figure resembling row of saucers set on edge, A, is enlargement of stridulatory file. Its position in wing venation is shown by B and C. In most cricket stridulation, file on right wing rubs portion of left while both wings are raised, D. Oval area on forelegs, E, is auditory organ. Section of leg at right is inner view.

What kinds of variations occur among cricket signals? First, crickets can never produce sustained tones: because they make all their sounds by oscillatory motions of the forewings, their sounds must be successions of "pulses," each produced by one stroke of the forewings. So far, all crickets recorded appear to sonify only during the closing stroke of the wings (against the slope of the teeth on the stridulatory file) and, except rarely, to open the wings silently.

A cricket can produce one pulse at a time or a few together (a "chirp" in either case, by common definition), or he can deliver a long series of pulses that may be regularly, irregularly, or not at all interrupted (a "trill"). The fastest pulse rates known are about 250 per second at 80 degrees Fahrenheit in some North American bush crickets in the subfamily Eneopterinae. Cricket sounds can also vary in frequency (cycles per second, roughly equivalent to "pitch" in human terms), and this usually relates to the size of the insect. Ordinary house and field crickets, about one-half inch long, all chirp at 4,000 to 5,000 cycles per second; some of the tiniest crickets, 1/16 to 1/8 inch long, chirp at more than 10,000 cycles per second; and the large mole crickets, an inch or more in length, chirp at about 1,500 cycles per second, which is about the pitch of the third G above middle C on the piano.

With one exception, all known cricket chirps are associated either directly or indirectly with the reproductive function. A student of mine, Daniel Otte, has found that one of the giant, burrowing *Brachytrupes* species, known as "bull crickets" in South Africa, makes an "alarm" or "disturbance" squawk, as do many other insects, when seized or harassed in its burrow. Aside from this exception, six functional kinds of cricket signals have been identified, and a single North American species, the short-tailed cricket, *Anurogryllus muticus*, appears to possess all of them. This is a greater variety of acoustical signals than is known for any other kind of insect, or for any fish, amphibian, or reptile, and even for many birds. Actually, relatively few mammals have been shown to have as many as six different acoustical signals, although this surely is because of inadequate study in practically all cases.

The six acoustical signals functional in the reproductive behavior of crickets may be described as follows:

1. *The calling song* attracts sexually responsive females from considerable distances—outside the range of other senses—and elicits aggressive behavior in hyperaggressive males. It is almost certainly important in the spacing of territorial, singing males.

2. *The courtship song* stimulates the female to move forward and into the mating position.

3. *The aggressive sound* causes other males to fight, chirp, or retreat, depending on the situation.

4. *The courtship interruption sound* has no proven function. It may call females back to males after accidental separation.

5. *The post-copulatory sound* may keep the mating pair together for subsequent copulation.

6. *The recognition sound* has no

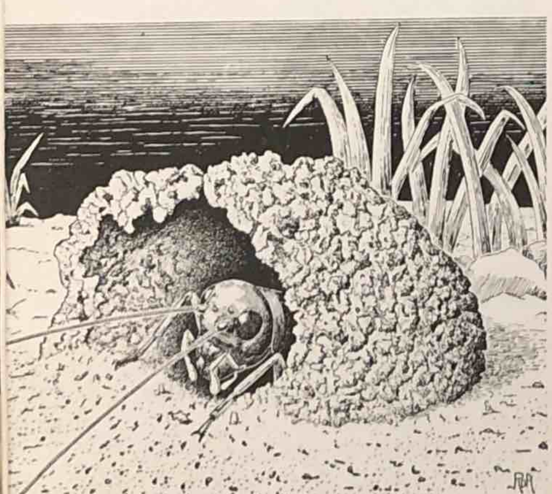
proven function. Possibly it keeps groups or pairs of subsocial individuals together in burrows.

The first acoustical signal in the cricket system, produced perhaps 150 million years ago, must have been a soft sound that operated only between individuals in close proximity. Otherwise both the auditory organ and the signalling device would have had to appear suddenly, not only in complex form, but already tuned together—a possibility too remote to be worthy of serious consideration. The only soft, close-proximity signals among modern crickets are courtship sounds, and it is likely that this reproductive context was the one in which the first cricket chirp was produced. All the other signals are probably outgrowths of this fundamental situation.

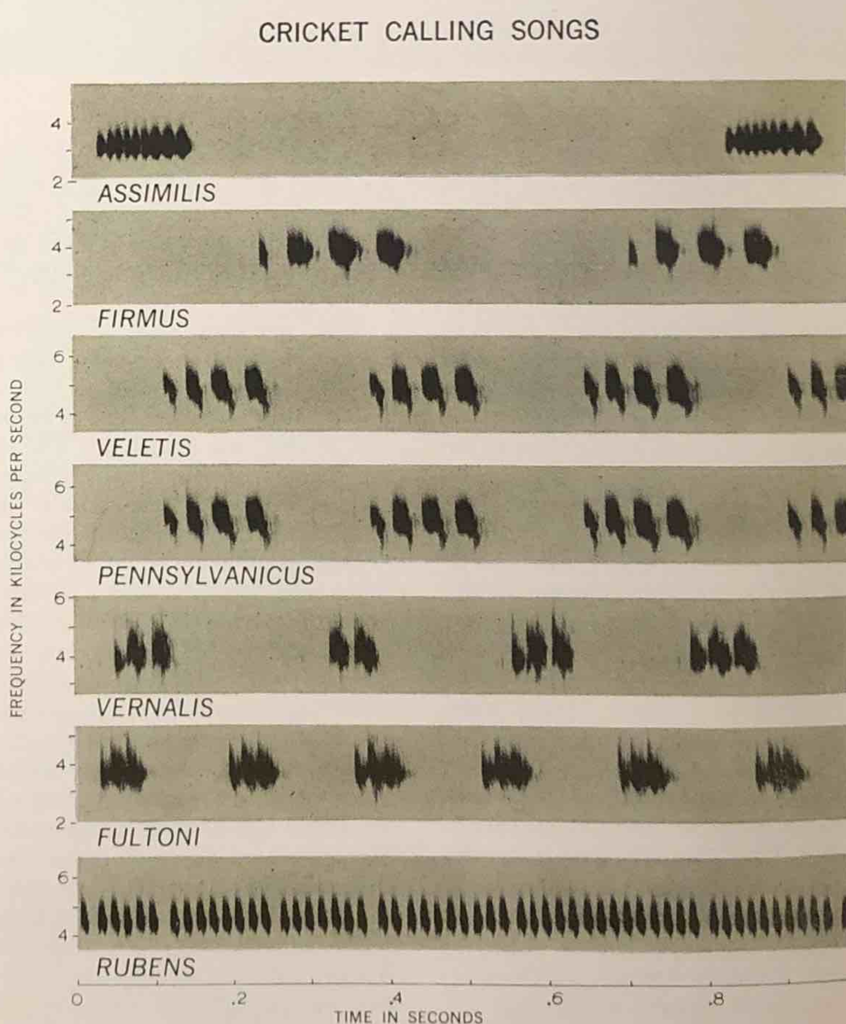
The close functional relationships between courtship and calling suggest that the calling song is principally an absentee courtship signal; it arose as a result of an original courtship signal becoming more intense and of longer duration, finally being produced in the absence of the female and attracting her without the tactual and chemical signals usually present during courtship. Special aggressive signals probably arose as modifications of the calling song after it had already become a mediator of male–male interactions, as well as of male–female interactions. There seem to be two ways in which such duality in function could have developed. One is by having the same structural sound units affect two different kinds of individuals differently (here, the male and the female). The other is by developing two separate components in the signal, one with an aggressive effect for other males, and the other a calling effect for females. The two different components can then be produced alternately during singing. Only a few crickets in Africa and Australia, among those studied, seem to have taken the second alternative, although many long-horned grasshoppers, katydids, and cicadas have done so.

Post-copulatory signals appear to have evolved from courtship singing in tree crickets. The female tree cricket stays on the male's back after the initial copulation and feeds on the secretions of a gland under the uplifted wings. Post-copulatory signals in the few field crickets that have them have evidently evolved from the calling sound. Post-copulatory sounds in these two cases are still similar to the courtship and calling sounds, respectively. Only a few crickets have post-copulatory sounds; it surprised us when we first saw a male cricket singing right after copulating, since the usual field cricket male cannot call again until he has developed another spermatophore, or sperm sac, and is ready to copulate again. That a single sound can function in these two different contexts, calling (pair forming) and post-copulatory, may result from the great difference between the two situations, which reduces the likelihood of confusion.

The so-called recognition signal of crickets is too poorly understood for much speculation about its origin, but where it occurs it seems structurally similar to courtship signals. This signal is made only by burrowing crickets that have developed elaborate parental behavior, and it is the only one supposedly produced by females as well as males.



A burrowing cricket, Valerifictorus micado, *sits in entrance hood of burrow.*



Audiospectrographs show calling songs of seven cricket species (genus Gryllus*).* G. rubens *"trills"; other species "chirp."* G. veletis *and* G. pennsylvanicus *have identical song but avoid confusion since they become adults in different seasons.*

This suggests that its function may be interchangeable between the sexes.

Perhaps the most significant pressure for evolutionary change in cricket songs is the advantage of distinctiveness in the calling signals of species that are reproductively active in the same places at the same times. As many as 30 or 40 cricket species may be calling together in a single habitat in North America, and if a female could not distinguish the sounds of her own males, her performance would be inefficient, to say the least. As we might expect, no two species that live together in this way have the same songs. Furthermore, some closely related species that do not live together, because they are either seasonally or geographically isolated, do have the same calling songs—in fact, almost exactly the same repertoires!

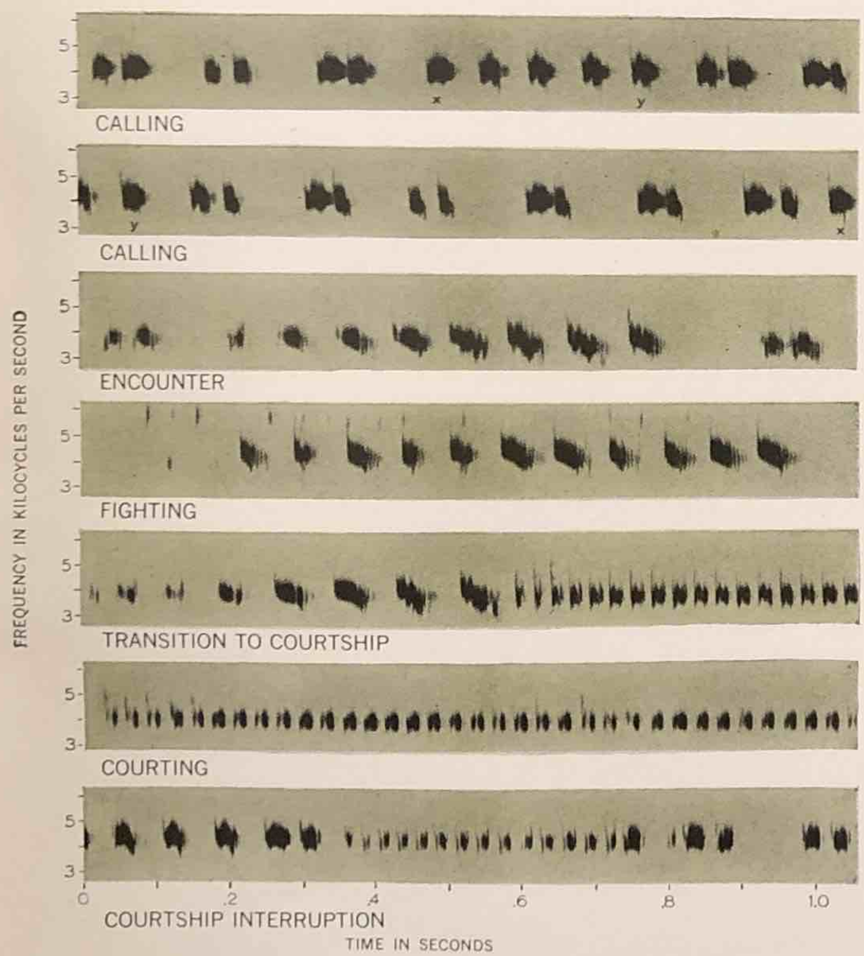
The consistent song differences between species that live together provide an extraordinarily powerful tool for the taxonomist. Using song as his single initial clue, he can obtain specimens of every species in an area within a short time. As a result, a great many puzzles in distribution patterns, morphological variation, and complexities in life histories are being solved, and some hope can be held out for accurate recognition of all cricket species in the near future, at least in the regions where field study and behavioral work can be carried out.

The most important species differences in cricket songs are in their rhythm patterns. In some cases, the stridulatory rhythms have become complex, involving pulse pairing, gradual increases and decreases in the rate of pulse delivery, and progressive, program-like changes requiring a minute or more for completion. *Teleogryllus commodus* has one of the most complex repertoires known among crickets. Its calling song is a remarkable alternation of chirps and trills, pleasant to the human ear. Among the various species from Africa, South America, Hawaii, Jamaica, and other exotic places that are continually singing in my laboratory, I particularly enjoy listening to this Australian species and reflecting that this must have been one of the loudest and most persistent sounds in the environment of the Australian aborigines all during their evolution.

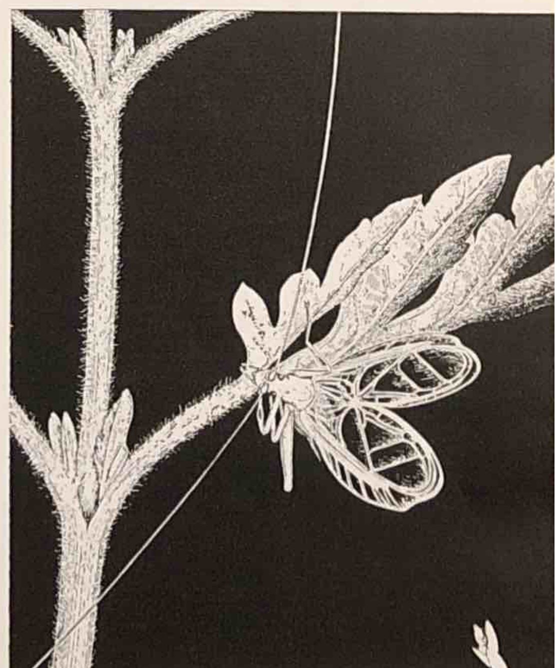
European man had the fairly simple chirps of the European field cricket, *Gryllus campestris,* and the house cricket, *Acheta domesticus;* the American Indians had a whole array of chirping and trilling species. It is not difficult at night, with the light off in my laboratory—where there are often 40 or 50 species chirping and trilling together—for me to close my eyes and imagine myself alone in some primeval habitat thousands of years prior to the advent of civilization, surrounded, as men were then more than now, by the cheery bedlam of countless crickets chirping messages more than a hundred million years old.

If I sent you a message by the
crickets, through the thickets,
How'd you answer better?
American Negro Folk Rhyme

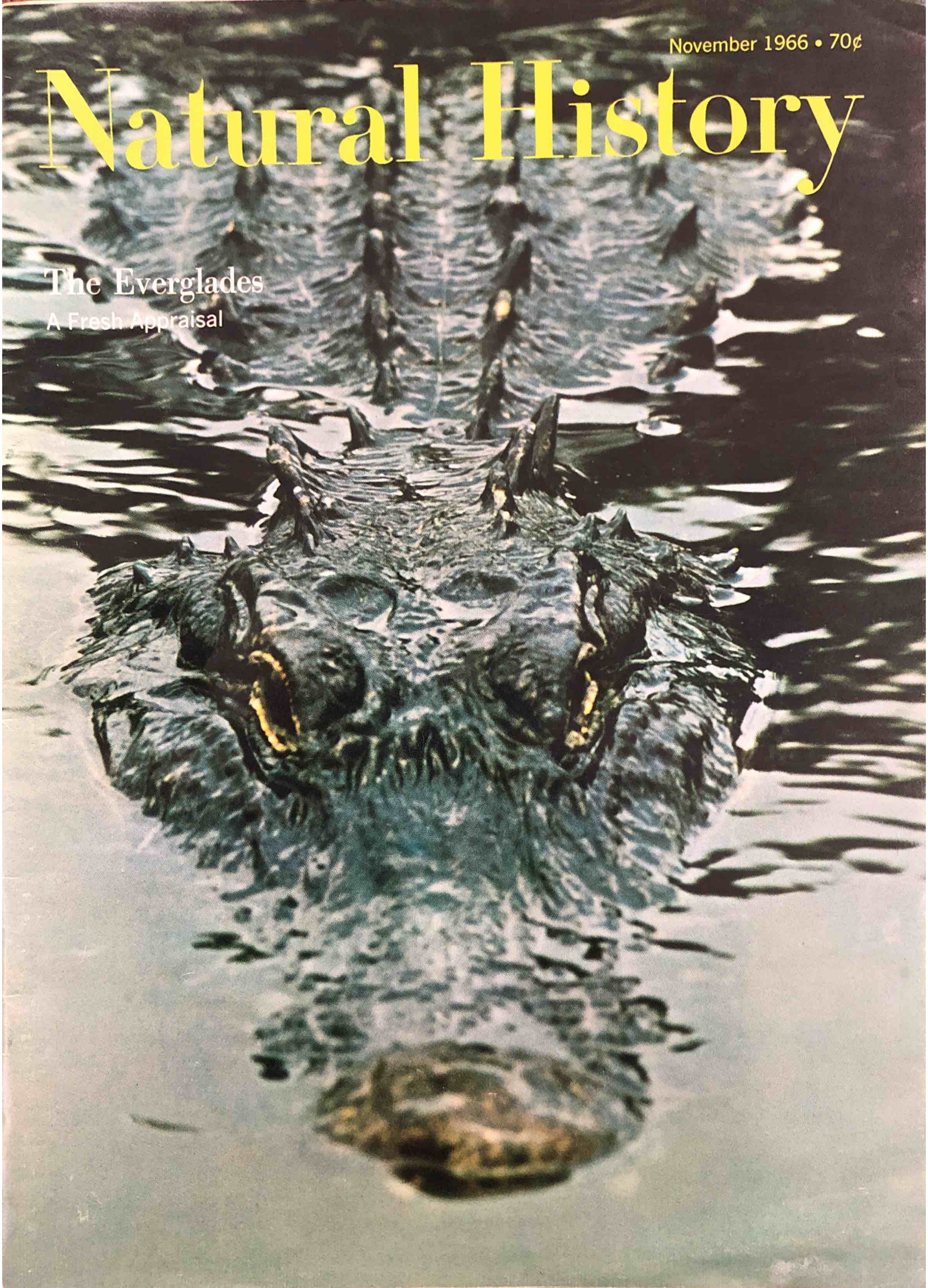
REPERTOIRE OF A CRICKET



The acoustical repertoire of the field cricket, Teleogryllus commodus, *contains two rhythms in calling song: trill (x-y) for male-male communication, chirp (y-x) for male–female. The repertoire is most complex thus far known for crickets.*



Wings raised in song, male Oecanthus quadripunctatus *perches on ragweed.*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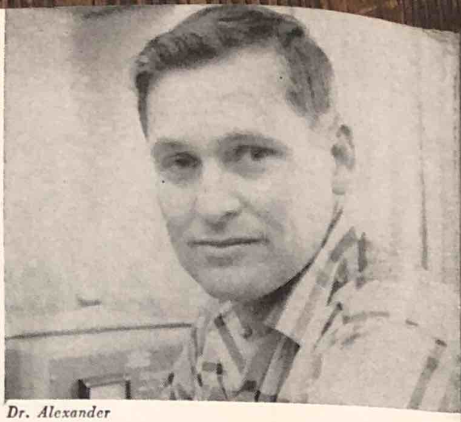

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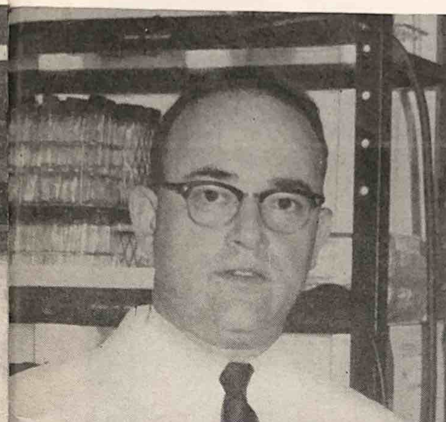

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