CANNIBALISM DURING COPULATION IN THE BROWN BUSH CRICKET, *HAPITHUS AGITATOR* (GRYLLIDAE)[1]

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In 1902, W. S. Blatchley published the interesting observation that females of the brown bush cricket, *Hapithus agitator* Uhler, eat the forewings (or tegmina) of the males (p. 458): "Of all the males taken, over thirty in number, there was not one with perfect wing-covers [forewings], and, in almost every instance, the wing-covers as well as the rudimentary [hind] wings were wholly absent; while every female had both pairs un[h]armed. I at first ascribed this wing mutilation to the males fighting among themselves, but finally discovered a female in the act of devouring the wings of a male." Blatchley suggested three alternative explanations: "Possibly the females require a wing diet to requite them for their bestowed affections, or, perchance, they are a jealous set, and, having once gained the affections of a male, devour his wing covers to keep him from calling other females about him. . . . It is more than probable, however, that the mating of the sexes takes place in a similar manner to that of the striped tree cricket [*Oecanthus nigricornis* F. Walker] . . . the females gnawing away the tegmina of the males in order to more readily reach some seminal glands which lie beneath. The openings of these glands, located on the dorsum of the mesothorax [they are actually on the metathorax], are visible in dried specimens at hand."

Fulton (1932) published the second fragment of information concerning mating behavior in this cricket when he noted (p. 69) that: "It apparently seldom sings and the sound is so faint that it is doubtful if it could be heard where other insects are singing. A male caged with a female was once caught in the act of singing while following the female about the cage. Its song was a creaky, fluttering sound, continued for 15 to 25 seconds at a time, so weak that I had to hold one ear close to the top of the jar in which the insects were confined in order to hear it distinctly. The stridulatory vein of a specimen of *Hapithus* examined under a microscope showed only 35 rather widely spaced teeth."

Nibbling or palpating the dorsum of the male is a widespread behavior among the females of crickets, katydids, and cockroaches in which the female mounts upon the male's back during copulation (Alexander and Brown 1963; Alexander 1964). In at least one other orthopteran, a Russian katydid, *Bradyporus tuberculatus* Fischer-Waldheim, the female bites at the male's dorsum and causes bleeding, then feeds on the blood (Boldyrev 1928). In most other cases there are dorsal glands, single or double, either elaborate or else diffuse and obscurely differentiated, which occupy the female's attention while she is maneuvered into position, while the spermatophore tube is being inserted, and (sometimes) while the spermatophore is emptying the sperm into her spermathecal tube (Alexander and Otte in press). The glandular area on the metanotum of *H. agitator* is probably homologous with Hancock's gland in Oecanthinae (Fulton 1915); it is represented in dried specimens by a

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swollen area with two anterior depressions, and clusters of hair-like setae which may collect and harbor the secretion that interests the female.

The brown bush cricket, then, represents an interesting case for at least two reasons. First, in some localities it has almost lost its ability to produce stridulatory noises; and second, the male has both dorsal glands and wings to which the female is attentive during courtship and copulation.

Alexander (1962) included *Hapithus* in a table which summarized for comparison the principal aspects of mating behavior in several genera and subfamilies of crickets and, as noted by Alexander and Brown (1963), erred in indicating that the male does not possess dorsal glands. Observations had been made on a colony of *H. agitator* in Columbus, Ohio, during the years, 1956-57, including witnessing the eating of the male's wings by the female many times in both caged and uncaged individuals, but no complete copulation had been seen. No noise could be detected when the males from this colony vibrated their wings, even when a male inside a jar was held close to the ear and watched in a mirror while he vibrated his wings in response to a female. This Columbus colony was about 20 miles north of the presumed northern border of the species' range, near Circleville, Ohio.

In 1958, Alexander heard but was not able to tape-record a soft, sputtery trill made by a male from Raleigh, North Carolina, courting a female. In 1961 and 1962, we tape-recorded the noises made by Pickaway and Ross County, Ohio, males (Fig. 8). The Columbus colony may be aberrant in evidently having some entirely mute males.

Because of the questions surrounding the details of the mating act in this insect, we obtained four males and three females from Ross County, Ohio, in August 1962, for laboratory observations. The sexes were kept separate for five days, during which time the females were provided with stems for oviposition from the plant on which they had been collected, great ragweed, *Ambrosia trifida* L. Two males and two females were then placed together. Although both females were parasitized by large larvae of *Rhopalosoma* wasps, two complete copulations occurred, and provided some answers to questions as well as some new questions. Photographs were made of these and other mating pairs collected in Alabama and North Carolina in 1964; all were too poor to reproduce, but were used by Otte along with sketches made by both authors of pairs in copula to complete the drawings, Fig. 1-7.

Northern males of *Hapithus agitator*, lacking a calling song, behave differently from the males of other stridulating orthopterans. They are not sedentary, calling the females to their singing locations; instead, they roam about until they locate a female. Upon touching a female with their antennae, and possibly receiving some chemical stimulus as a result, since their behavior indicates that they seem to differentiate between males and females at this time, they immediately raise the forewings to about a 60° angle with the body and begin their near-silent, courting wing vibrations. Even if the female is unresponsive and moves off, the male remains with her, following her about and retaining antennal contact, maneuvering in front of her and beginning courtship with lifted wings whenever she stops for a moment. Occasionally even a seemingly unresponsive female is cornered and detained by these kinds of attention by the male. In this way, several males and females caged together become paired off and remain so, often retaining the original pair formation for hours or possibly days. In the field, colonies are very compact: one can sweep with a net across large areas of seemingly

suitable habitat and capture no *Hapithus,* then secure 20 or 30 individuals from a few sweeps across a few plants. Repeated sweeping in the precise locality where specimens have already been taken is the most certain way to secure more specimens, and Alexander has re-located a small colony in exactly the same spot near Circleville, Ohio, on great ragweed on four different years between 1955 and 1962. Except in dense colonies, it would seem that pairs formed through accidental meetings might persist for days, possibly through repeated bouts of copulation and oviposition.

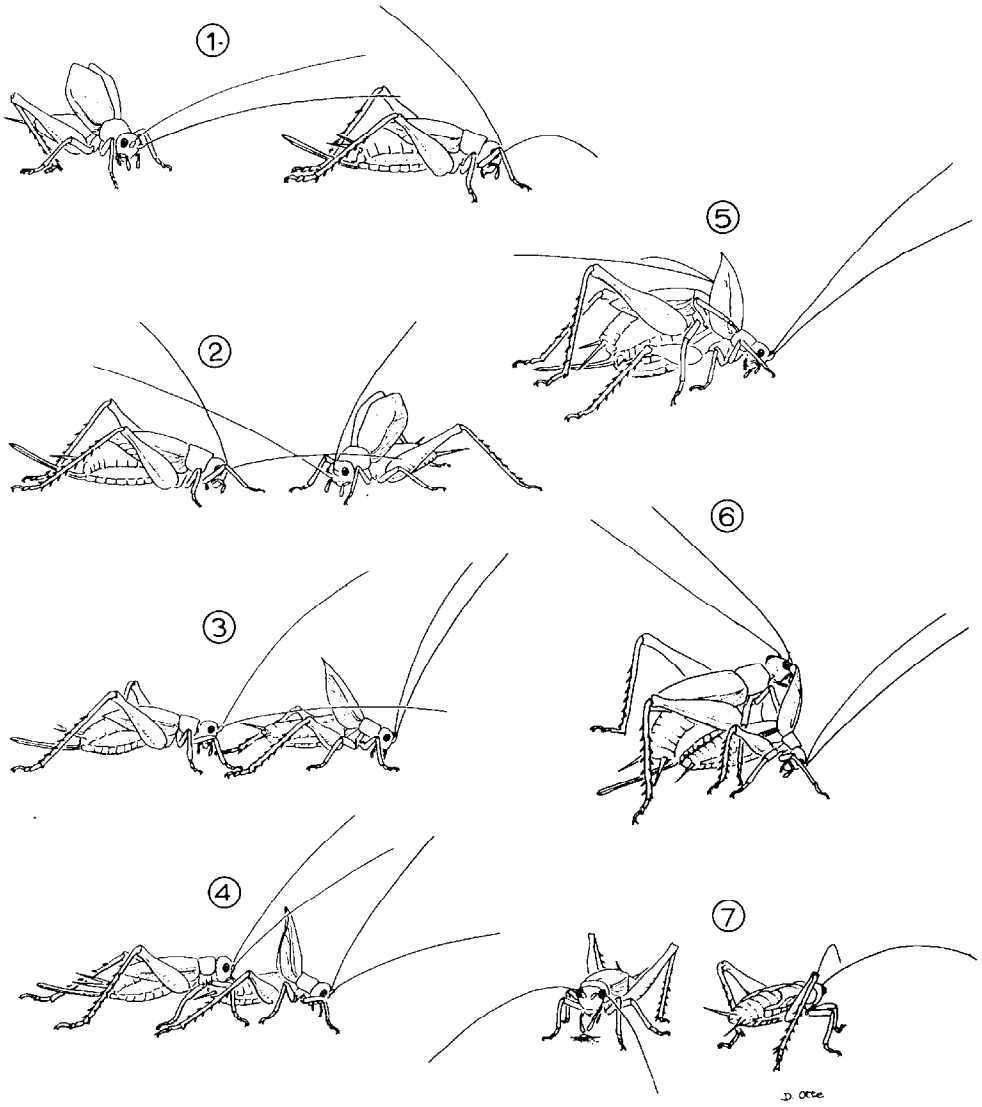


Fig. 1-7. Courtship and copulation of *Hapithus agitator.* See text for explanation.

We have seen seven complete copulations in *H. agitator* from Ohio, and the general sequence of actions occurring in each case is illustrated by Fig. 1-7. A male following a female (Fig. 1) moves in front of her with lifted forewings if she pauses (Fig. 2). If she remains more or less motionless

during this behavior, the male eventually produces a spermatophore, then turns about in front of the female and begins to back toward her head (Fig. 3). The female, if responsive, finally begins to palpate the male's cerci, spermatophore, and dorsum, moving slowly up on his back (Fig. 4). Eventually the female moves so far forward that her head is hidden beneath the male's wings at their base (Fig. 5), and at this time the male makes upward and forward "hooking" motions with the tip of his abdomen, which is turned upward against the venter of the tip of the female's abdomen. Evidently at just the moment that he engages the genitalia and pulls the female's abdomen and her ovipositor downward, the female starts to raise her head slowly until her mouthparts are near the tips of his raised tegmina, which she then begins to eat (Fig. 6). The condition of the male's tegmina following one copulation is shown in Fig. 7.

Time between appearance of a spermatophore on the courting male and initiation of copulation varied in our observations from 67 seconds to 12 minutes; time from initiation of copulatory actions to female starting to eat the wings varied from 25 to 42 seconds; time from female beginning to eat the wings until the pair separated varied from six minutes and 50 seconds to 12 minutes. One male produced another spermatophore 12 minutes after copulating, and once a female initiated copulation with a second male 12 minutes 30 seconds after copulating. After separating, in two instances the female found the spermatophore on the ground a few seconds after it had dropped from her abdomen or was rubbed off by her, and ate it (Fig. 7). In one case another male found the spermatophore and started to eat it, dropping it eventually; the female found and ate the remaining portion. In another case the female found and ate the spermatophore several minutes after copulation had terminated. After copulation the male and female in all cases stayed together, and the male was aggressive toward other individuals that approached, as in most other crickets.

In Florida, the populations most closely resembling *H. agitator* (described from Baltimore, Maryland), have often been referred to under the name *H. quadratus* Scudder (described from Cuba and central Texas); sometimes the Florida populations have been treated as a subspecies of *H. agitator*. We have collected and tape-recorded this cricket near Homestead, Florida, and watched two copulations in the laboratory. In neither copulation did the female eat the male's tegmina. However, Blatchley states that spring-collected adult males at Dunedin, Florida, had partly eaten wings. Of 92 Florida males, 31 Georgia, Alabama, and Mississippi males, and 18 Virginia, West Virginia, North Carolina, and South Carolina males in the University of Michigan Museum of Zoology, only one male from Conecuh County, Alabama, and two from Putnam County, Florida, have damaged tegmina. The Alabama male was collected 2 September, the Florida males 2 and 14 October; seven other Florida males were collected in October, two in November, one in December, one in May, nine in July, and all the rest in August and September. Of 61 Florida males in the Florida State Collection of Arthropods, Gainesville, only two, collected in December in Clay County, have tegmina apparently damaged by feeding (Thomas J. Walker, personal communication).

In contrast to these southeastern males, the proportions of males from more northern and western states with tegmina partly eaten away to males with complete tegmina are as follows (University of Michigan Museum of Zoology): Ohio, 6:2; Indiana 8:0; Illinois, 1:0; Missouri, 3:7; Arkansas, 15:2;

Oklahoma, 1:0; Louisiana, 5:0; Texas, 3:2; Kentucky, 2:2; West Virginia, 0:4; and Tennessee, 6:14. Fifteen males collected in St. Frances, Ouachita, and Prairie Counties, Arkansas, 23-24 October 1957, by I. J. Cantrall, T. J. Cohn, and D. C. Eades, all have their tegmina eaten completely away. Probably wing-eating occurs in all populations north of peninsular Florida; most of the open circles in Fig. 18 are based on single specimens, frequently a female.

Males from peninsular Florida have a rather loud chirp, evidently a calling sound since it is heard abundantly and is produced by lone males. T. J. Walker (personal communication) reports taping and hearing the calling song of *agitator* in southeastern Texas. Both males and females from southern states have larger auditory organs than those from Ohio, Indiana, and Illinois, where, particularly in some males, the tympanum is difficult to locate and may be non-functional.

Courting Florida males also produce a trill not too different from that of courting northern males, though definitely more rhythmical and perhaps louder. Fig. 9 is a trill made by a Cape Sable, Florida, male; Fig. 10-11 are trills made by one Homestead, Florida courting male; Fig. 12-13 are trills made by a second Homestead male just following copulation; and Fig. 14-15 were made by the same male when he was approached by another male following copulation. Fig. 16-17 are calling chirps made by Marco Island, Florida, and Homestead males, respectively.

Surprisingly, we could detect no difference between the stridulatory files of southern and northern males; two Ross County, Ohio, males had 38 teeth each, and five Homestead, Florida, males had 28, 35, 36, 36, 39 teeth. These include all the males whose sounds are illustrated in Fig. 8, 10-15, 17, and all the males observed in copulation.

If, as seems most likely, these various populations represent members of a single, geographically varying species, then the following characteristics evidently change from south to north.

1. Colonies are more compact, and more pair formations occur by accident.
2. Males are more roving and once they locate a female follow her for long periods.
3. The calling sound is lost.
4. Auditory organs are reduced and probably either less sensitive or, in the extreme, non-functional.
5. The male's tegmina are eaten during copulation and between copulations.
6. Courtship and post-copulatory sounds are fainter and less consistent.

Beginning with a calling ancestor resembling the southern Florida populations today, these changes must have occurred during evolution in approximately the above order. Our data are inadequate to determine whether they now change abruptly or gradually from south to north, or in what way changes in any characteristic coincide with changes in others. We cannot, therefore, guess in what way northern populations with mute and near mute males were geographically isolated from southern populations with calling males during their divergence. But this view of related changes during the degeneration of acoustical communication may give insight into the conditions favoring the evolution of stridulatory calling signals.

The above evidence suggests that, of Blatchley's somewhat amusing interpretations, the second and third, at least, were almost exactly wrong: it is not

that jealous females eat male's wings to keep them from calling other females, since the males no longer "call" the females anyway. Neither has the eating of the wings anything to do with exposing the male's dorsal glands, for it occurs while the wings are lifted. Instead, it evidently became advantageous

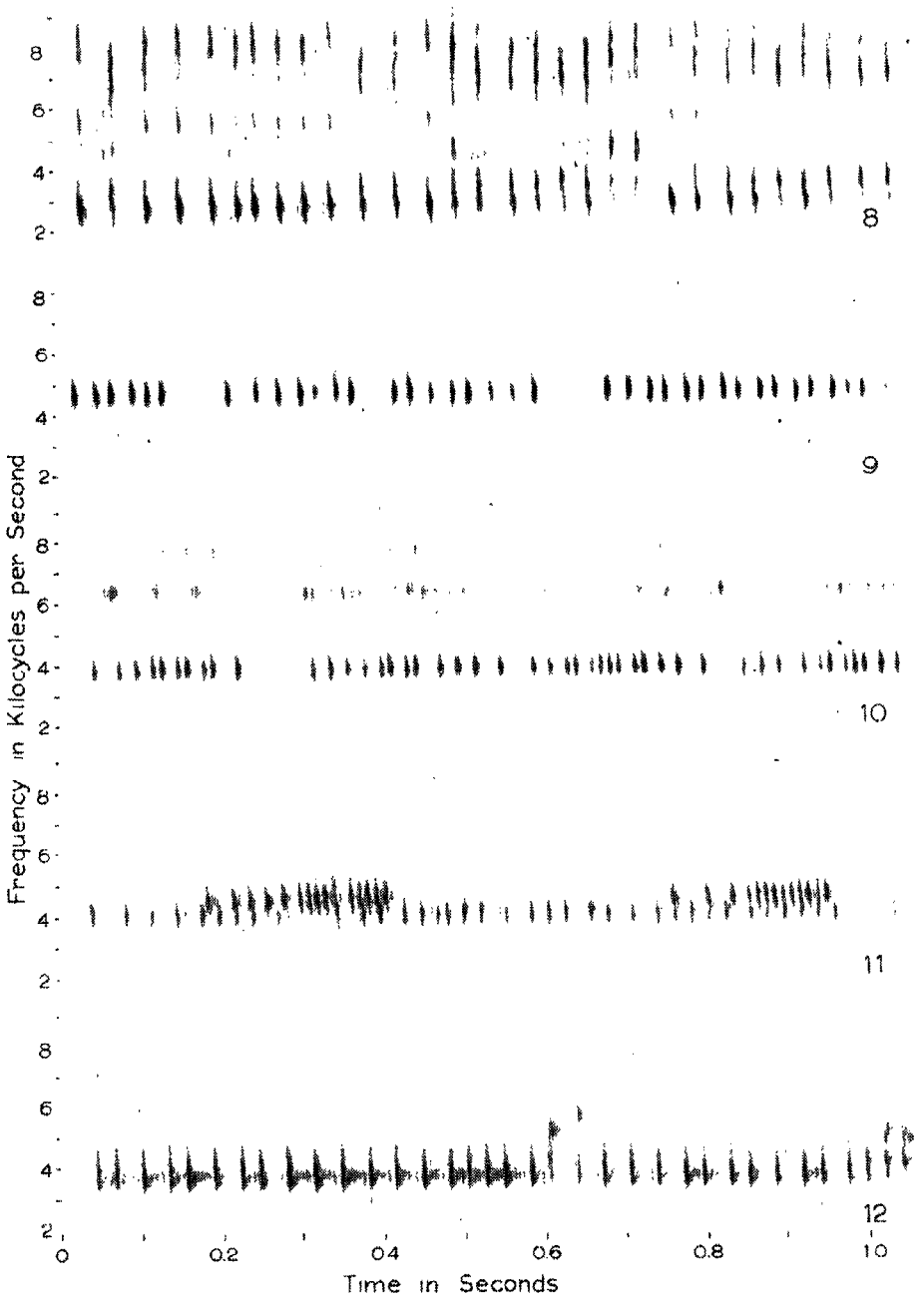
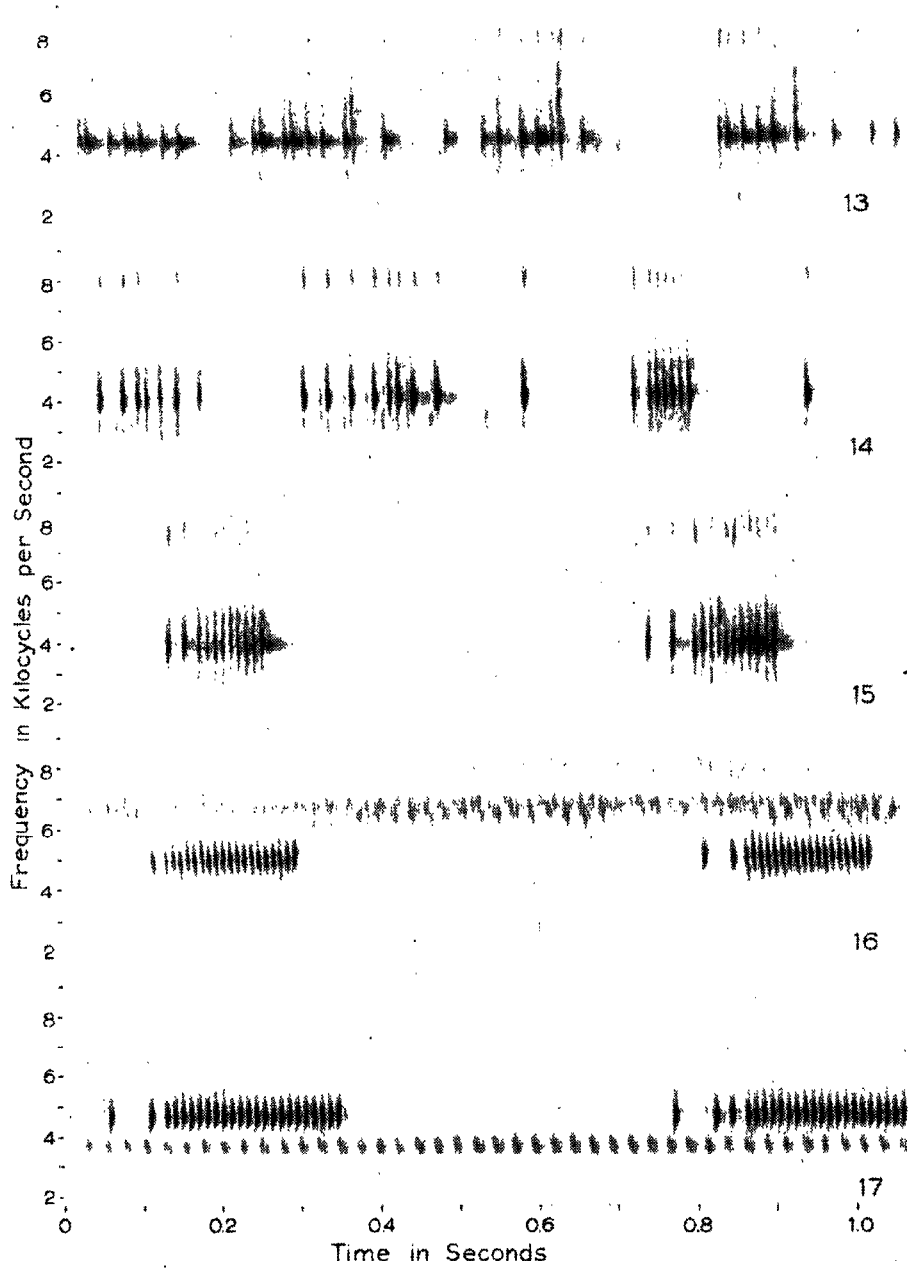


Fig. 8-17. Audiospectrographic samples of *Hapithus* sounds from different regions and in different situations. See text for explanation. All temperatures approximately 75°F.

in some localities for males of *H. agitator* to "sacrifice" (use) their tegmina keeping the female in place during insemination, largely because the calling function had already been reduced or lost and the tegmina were serving chiefly (1) to cover the abdomen and the metanotal glands and (2) perhaps to attract the female into the copulatory position through their vibrations during courtship, as either tactual or visual stimuli. Such a male would not as severely reduce his chance of subsequent matings by allowing his wings to



be eaten as he would if the wings were necessary to call other females. Likewise, the cannibalistic female in a population of near-mute, near-deaf males that find their females without song is not interfering with the reproductive chances of her male offspring when she causes them to be fathered by a male that allows his wings to be eaten during copulation.

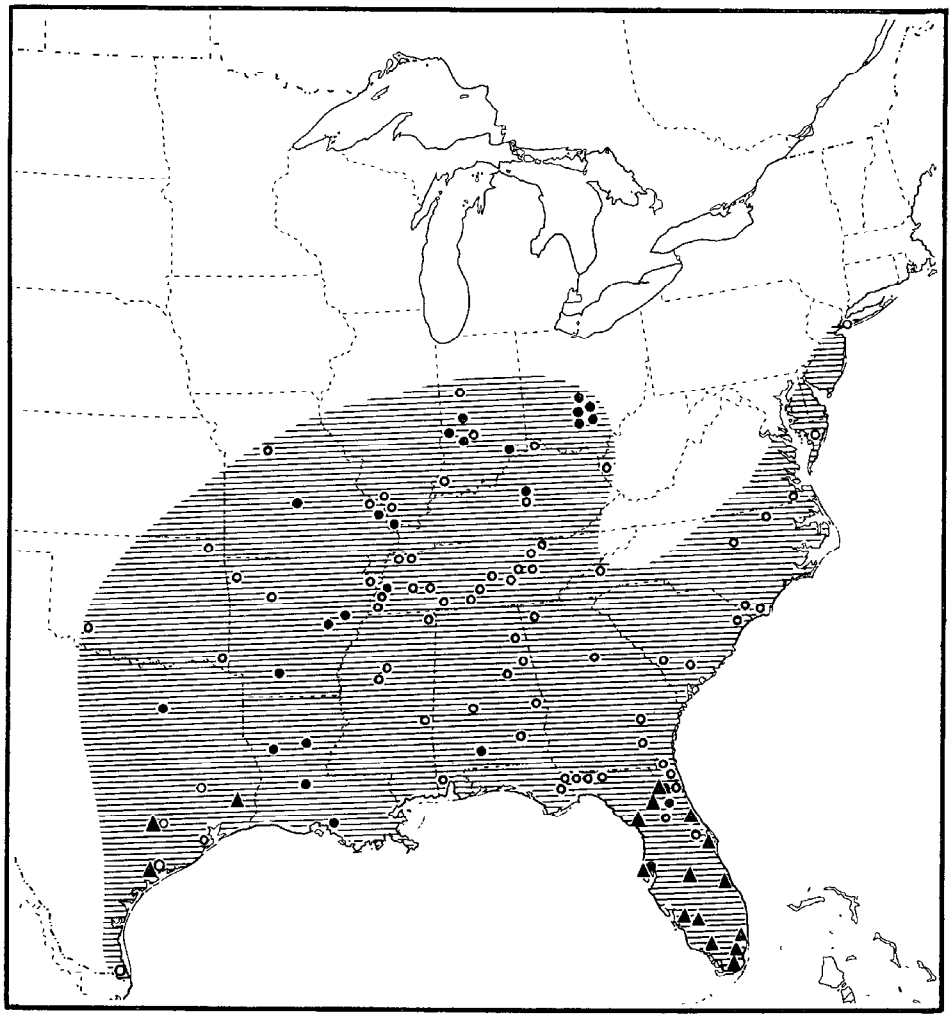


Fig. 18. Distribution of *Hapithus agitator* in the United States (including *H. quadratus*). Hatched area is predicted general distribution; black triangles are localities where calling songs have been heard; black circles are localities where some or all collected males have damaged tegmina; open circles are all other localities. One symbol is plotted for each county record. Texas records were supplied by Thomas J. Walker.

Two points seem noteworthy. First is the probability that an advantage during post-copulatory (or, more properly, inter-copulatory) behavior has evidently guided development of the wing-eating tendencies of the female. By this, the significance of the two probable functions of this behavior is emphasized: (1) preventing the female from removing the spermatophore

before it has emptied its sperm into her spermatheca, and (2) keeping the pair together for repeated copulations. Second, the female-following behavior of northern males is also likely derived from post-copulatory behavior and must have developed, to some degree at least, as a pair-forming device prior to the loss of the calling function. In other words, the components of pair-forming behavior of non-calling males seem likely to have been "lifted" directly from the post-copulatory interactions.

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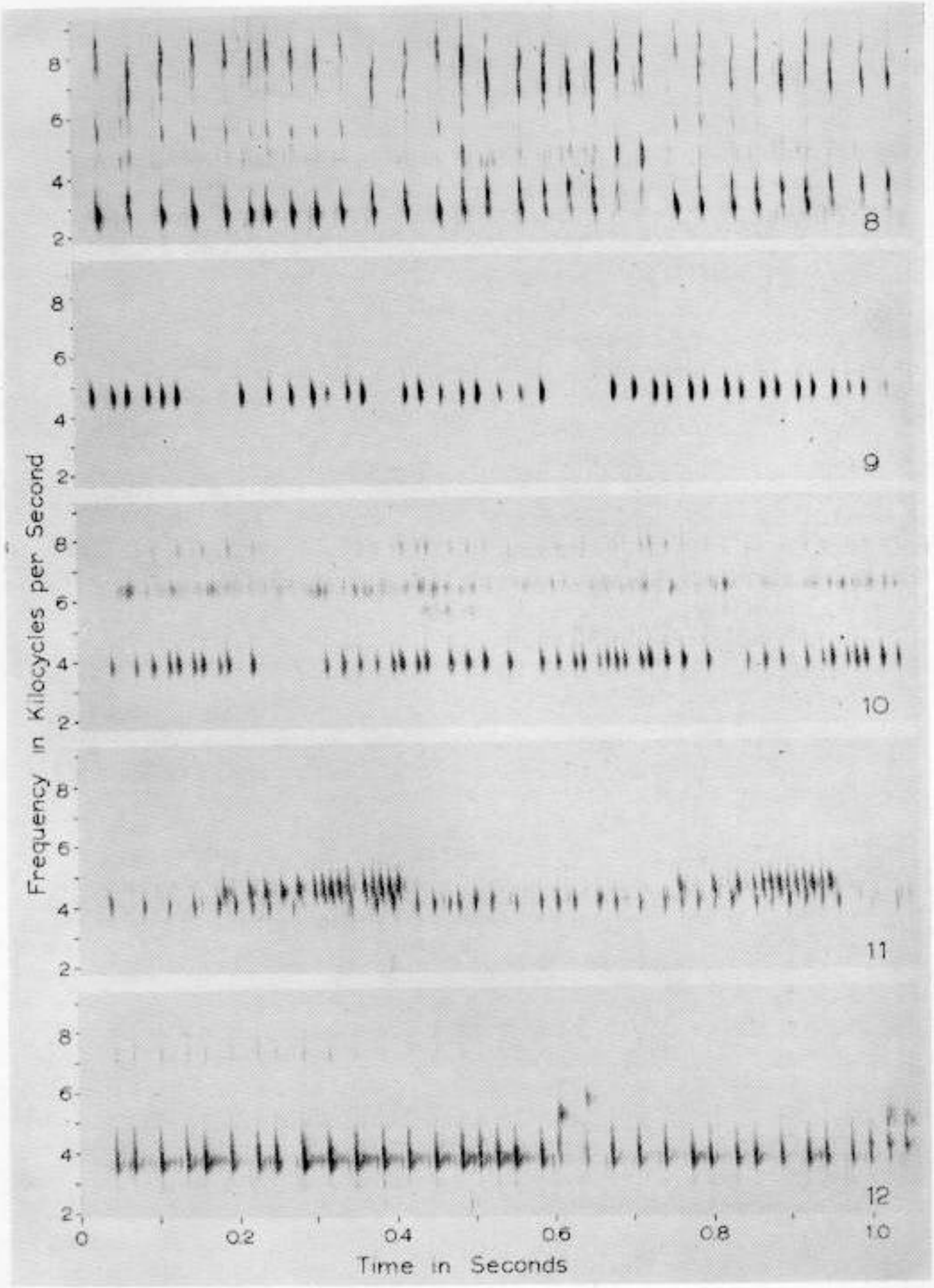
Frequency in Kilocycles per Second
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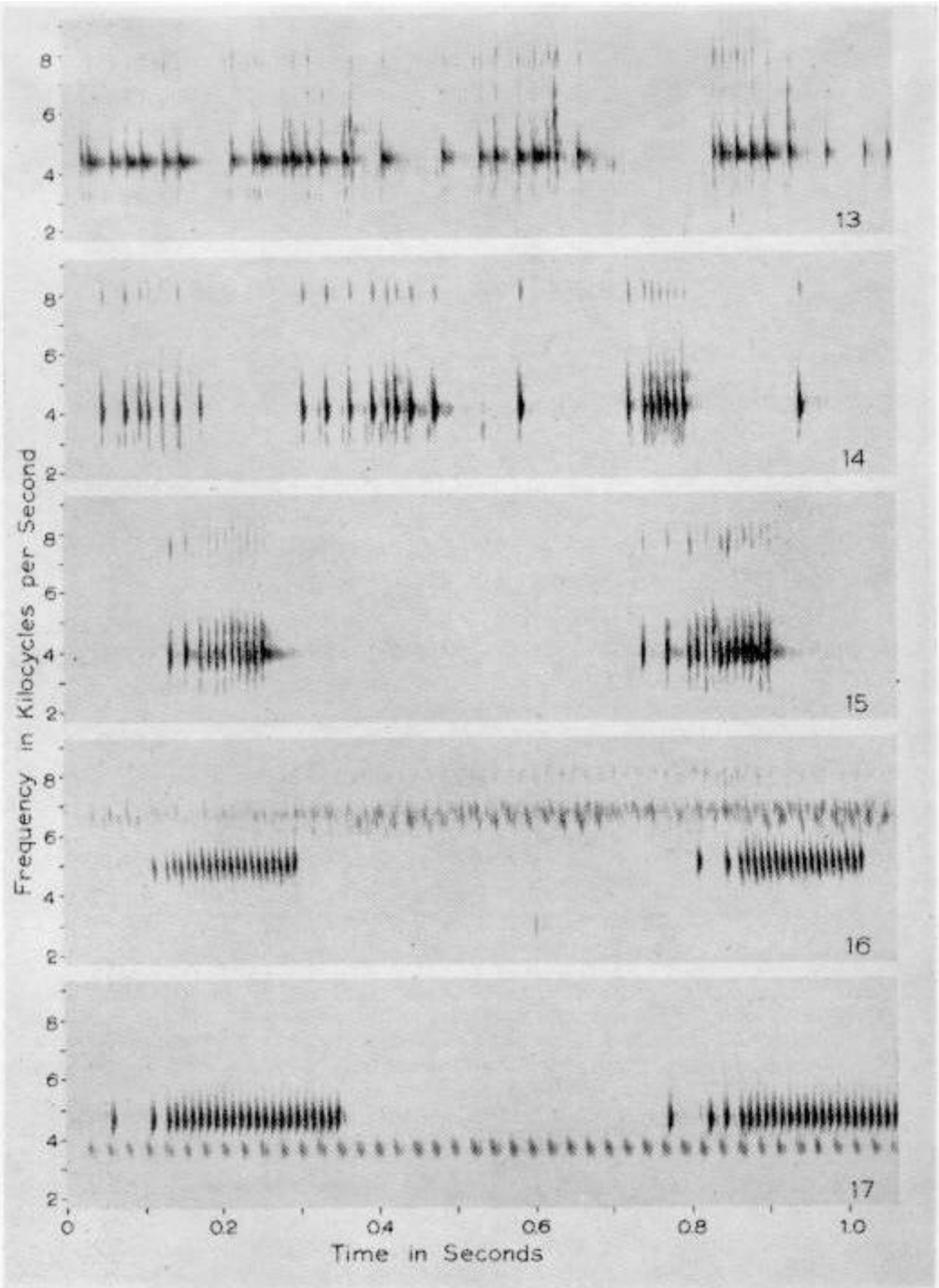
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