A case of Müllerian mimicry of sound

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Synopsis

Stridulation and behaviour displayed by *Necrophorus investigator* is described and compared with that exhibited by the Bumble-Bee.

Stridulation by the Burying Beetles of the genus *Necrophorus* F. is a well-known phenomenon. Two transversely striated files set at an angle, one on each side of the median line on the dorsal surface of the fifth abdominal tergite, are rubbed against the tips of the elytra to produce a rasping or sawing noise. These files have the distinction of figuring in *The Descent of Man* (Darwin, 1891, p. 463, fig. 25). A good photograph was published by von Frankenberg (1936). The underside of the tip of the elytra, which acts as a serrator, is figured on Plate I (figs. 1 and 2). Recordings of the stridulation (Plate III, fig. 6) show that the sound consists of a series of pulses, the number of pulses depending on the number of transverse ridges on the files. The majority of the sounds produced are audible to the superior human ear, since the frequency ranges from approximately 300 to 8000 c.p.s. It is the usual simple frictional type of mechanism common to most beetles.

The function of the stridulation of *Necrophorus* has, however, never aroused much interest, although Dumortier in Busnel (1963, p. 605) assumes it is a "protest sound" since, like so many of the Coleoptera, these insects stridulate only if handled roughly. *Necrophorus investigator* Zetterstedt is an aposematic species, which, when molested, emits a nauseous, stinking irritant froth from the anus (Plate I, fig. 3), and it was originally assumed by us that the stridulation was a straightforward warning sound accompanying the discharge. Closer observation of the behaviour of *N. investigator* convinced us that the sound production is part of an elaborate display by which the beetle mimics—almost caricatures—the Bumble-Bee (*Bombus*). This has probably escaped notice hitherto because, if the beetle is handled or picked up, the display pattern is disrupted.

If *N. investigator* (or *N. fossor* Erichson) is poked or seized with a pair of forceps in the head region, and then quickly released, it will often turn on its back and begin to stridulate (*see* Plate II, fig. 4). In this position, the first pair of legs is held upright at an angle to the body, and the second and third pairs (Plate II, fig. 4) are pushed out laterally like oars. This is characteristic and oddly reminiscent of the movements of the legs made by the Bumble-Bee if disturbed while resting or sleeping in a semi-torpid state (*see* Plate II, figs. 4 and 5). Meanwhile the beetle works the tip of the abdomen vigorously in and out, thereby rubbing the files against the serrators and producing a series of short bursts of stridulation. These movements resemble the stinging movements of the semi-torpid Bumble-Bee, and the noise emitted is a fair imitation of its short bursts of "peevish" buzzing. Furthermore, during the display, the tip of the beetle's abdomen, which becomes covered with brownish froth (in *N. investigator*) or whitish froth (in *N. fossor*), together with the light coloured belt of hairs on the abdomen, and the reddish-brown edge of the elytra seen from below, give a general if rather crude resemblance to the colour scheme of a Bumble-Bee such as *Bombus terrestris* L. or *B. lucorum* L. It should be remembered that many foragers

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from the nests of these bees—nearly a quarter of the total (Free & Butler, 1959) in the latter species—remain away from home at night, some resting in a semi-torpid condition on the flowers they have been visiting, and others not infrequently sheltering under grass and leaves on the ground. After a heavy dew these Bumble-Bees are incapable of flight and can do little more than wave a leg in the direction of a disturbance or roll over on their backs, moving the tip of the abdomen in and out in a threatening manner, buzzing if further molested and not infrequently squirting a fluid from the anus at the source of the disturbance (Plate II, fig. 4). Such Bumble-Bees must greatly outnumber Burying Beetles and it is, perhaps, not really surprising that several members of *Necrophorus* have developed into mimics of the somnolent *Bombus*, even though their efforts result in a rather crude imitation of the model. Since the beetle is distasteful to predators (Morton Jones, 1932) and has a defensive fluid with a nauseating stench, which can persist for over a year on inanimate objects with which it has been in contact, this type of behaviour is most accurately described as a form of Müllerian mimicry. Although the angle of the legs, movements of the abdomen, rasping sound of the stridulation and general colour scheme, if considered as individual components of the display, are by no means exactly similar and give the impression there is something "wrong" about the whole performance (for example, the abdominal movements of the beetle are limited to an in-and-out movement and have none of the sideways twists characteristic of the last abdominal segments of *Bombus* when attempting to sting, and the imitation "buzzing" is too regular), the general impression is remarkably effective (Plates II–IV, figs. 6–9). Since there have been very few observations of audio-mimicry among insects, recordings were also made of the Bumble-Bee (*Bombus hortorum* L.) buzzing (after a few moments cooling in the refrigerator) for purposes of comparison. Dr. Peter Haskell and Mr. John Moorhouse very kindly made oscilloscope recordings from these tapes (Plate III, figs. 6 and 8), which were subsequently analysed on a sound spectrograph by Dr. W. H. Thorpe. A comparison of the sonographs of the two species shows that the sounds have the same general form (Plate IV, figs. 7 and 9), although there are approximately twice as many hubs over the same frequency span in the bee as in the beetle. The length of the bursts of sound are roughly comparable, but in artificially chilled specimens those of the bee are frequently longer. The same applies to the gaps between sound bursts, and it is probable that, in nature, the stridulation of the beetle is far more uniform than the "peevish" buzzing of the bee. Nevertheless, although the mechanism of sound production is entirely different in the two insects, there are definite similarities between the two types of warning sounds.

Darwin (1891) suggested that this stridulatory mechanism of beetles may have originally evolved as an intraspecific form of communication, a suggestion which has been developed by Haskell (1961); this is an attractive idea, particularly in connection with a social species like *Necrophorus*. Such mechanisms, no doubt, serve several different purposes, but it seems probable that in this instance the display is also directed against crepuscular ground predators as well as birds, the latter appreciating the bright red or orange aposematic markings on the dorsal surface, whereas mammals are more receptive to warning sounds. It is perhaps worth noting that, although *N. humator* (Goeze) possesses stridulating files (the ridges are much less pronounced than in *N. investigator* and *N. fossor*), we have not heard this large, uniformly black, species stridulate, nor could we stimulate it to display by molestation. Darwin (1891) also drew attention to the fact that throughout the order Coleoptera stridulating mechanisms were widespread, wonderfully diversified in position, but exhibited a great uniformity of structure.

Captive tits are very frightened by the presence of these beetles in their cages, although they were not heard to respond by a warning call to their presence as they do with certain other aposematic insects (Rothschild & Lane, 1960) and, indeed, it may not be a coincidence that the insects' bursts of stridulation are curiously reminis-

cent of the warning chatter of tits (Plate III, fig. 10), although, in this instance, analysis with a sound spectrograph demonstrates that the two sounds are fundamentally different and that the resemblance is superficial. Warning mechanisms such as sound, scent and colour have little if any phylogenetic significance, and the same general effects are produced not only in different families and orders but in different phyla. In *Necrophorus* and the Bumble-Bee, the red or yellow background markings, stridulating and behaviour combine to advertise the rather different chemical defences of the two insects. Although the beetle secretes a powerful defensive fluid, it has in addition evolved a resemblance to the Bumble-Bee, which presumably affords it added protection. The bee probably receives a very minor share of the benefits accruing from this particular situation. On the other hand, we are lamentably ignorant of the habits of the predators involved; some animals may be especially repelled by the beetle's defensive fluid, and consequently the advantages may not be as one-sided as they appear.

SUMMARY

Stridulation in *Necrophorus investigator* Zetterstedt is found to be part of an elaborate pattern of behaviour reminiscent of that exhibited by the Bumble-Bee when disturbed in a semi-torpid state.

Analyses of recordings of the stridulation of *N. investigator* and of the buzzing of a Bumble-Bee show that the sounds have the same general form.

It is suggested that this display of mimicry by the beetle is directed against crepuscular ground predators as well as birds.

Our grateful thanks are due to Dr. P. T. Haskell, Miss Barbara Lade, Mr. John Moorhouse and Dr. W. H. Thorpe for assistance with the analysis of the sound recordings, and we much appreciate their generosity in devoting so much of their valuable time to this problem. We would also like to thank the B.B.C. for the loan of their recordings of the alarm call of Tits shown in Plate III, figure 10.

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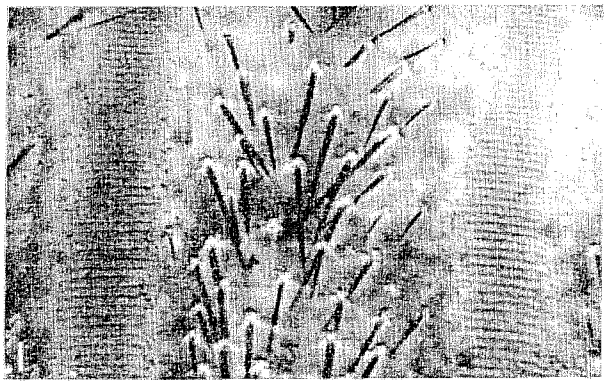
BOOK NOTICE

Charles Darwin and his world. By Julian Huxley and H. B. D. Kettlewell. 8vo. London: Thames & Hudson, 1965. Pp. 144, frontis., text illust. 25*s*.

Dr. Kettlewell has recently visited the places in Brazil that Darwin visited on his famous voyage in H.M.S. 'Beagle', and he has collaborated with Sir Julian Huxley to produce a popular account of Darwin's life and of his theory of the origin of species. This study contains many illustrations chosen to illumine both the personal and scientific aspects of Darwin's life. The volume concludes with a chronology, notes on the illustrations, and an index.



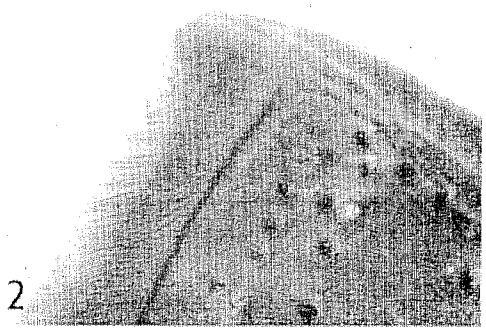


FIG. 1.—Stridulating files of *N. investigator* (×120). The number of ridges varies from specimen to specimen. Some individuals examined had less than 100 ridges per file whereas others had over 200. The width of the ridges is approximately 0·16 mm. (thickness approximately 0·017 mm.); these gradually become thinner and narrower towards the two ends of the files.

FIG. 2.—Tip of an elytra of *N. investigator* showing the serrator. The elytra are held motionless but slightly parted while the beetle stridulates. The in-and-out movement of the abdomen thus draws the files briskly against the serrators. The angle of the files exactly coincides with the angle at which the wings are held.

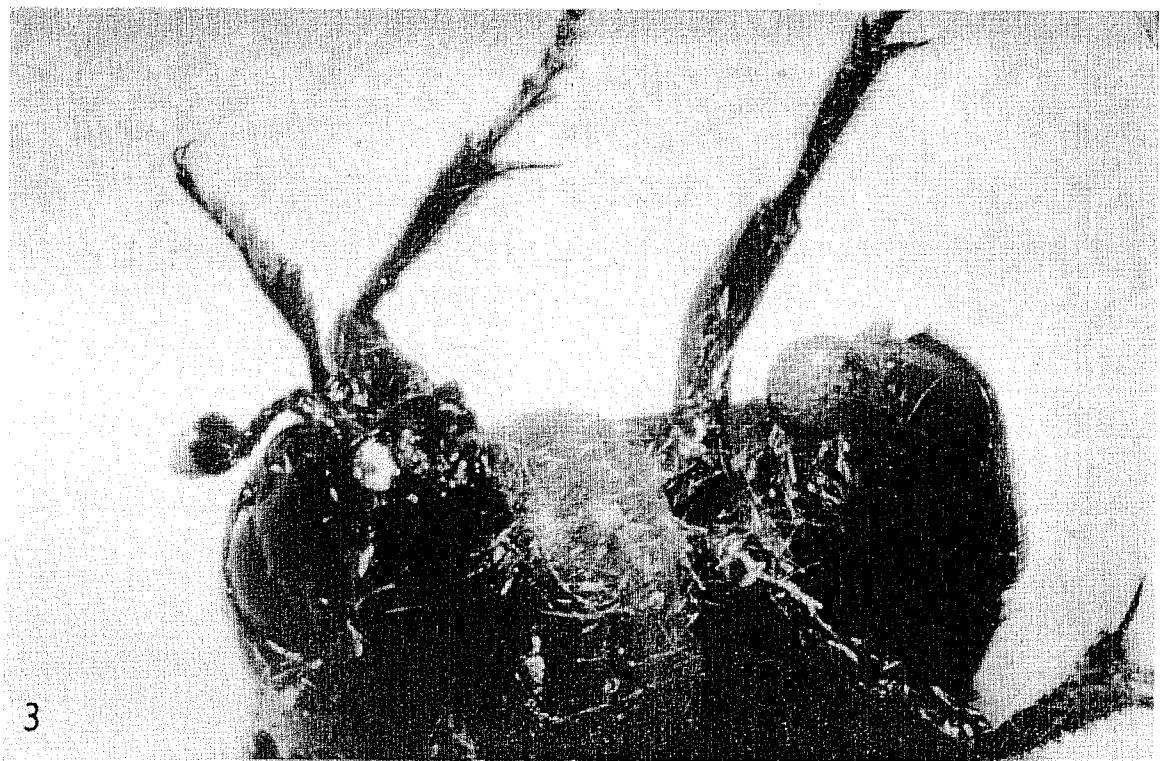


FIG. 3.—*N. investigator*, showing the secretion of anal defensive fluid.

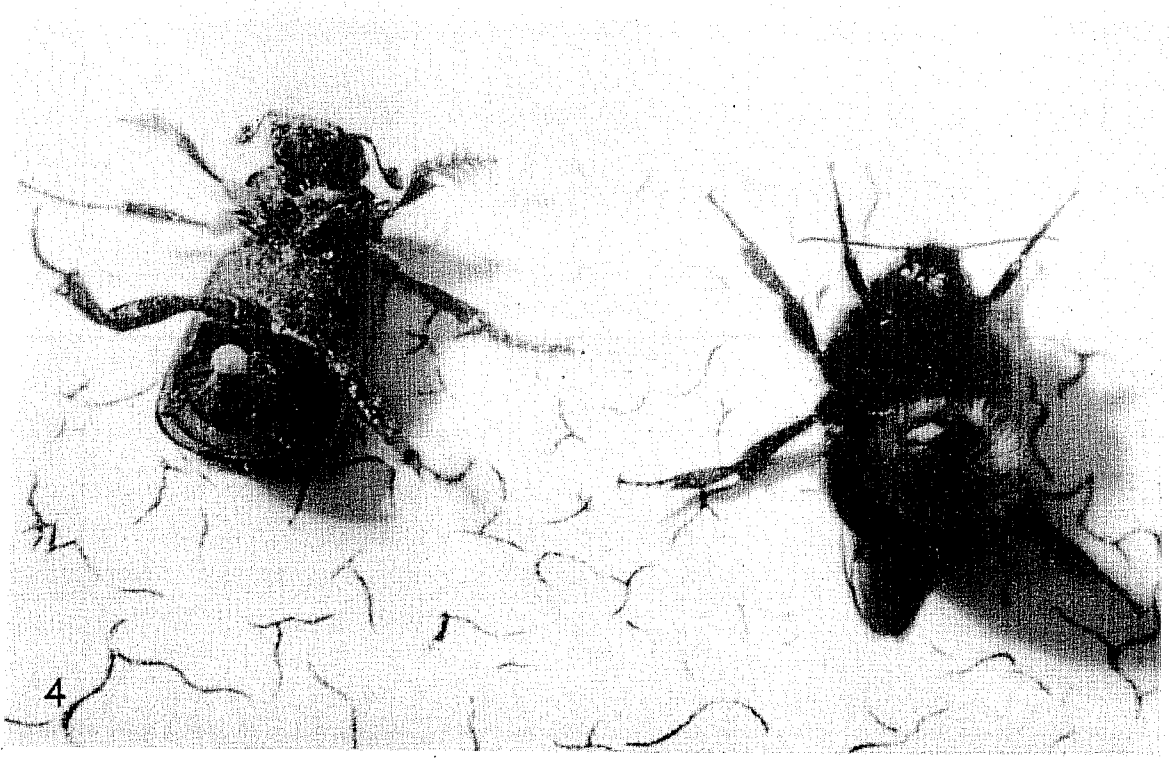


FIG. 4.—*Necrophorus investigator* and *Bombus hortorum* L. displaying together on a kitchen table, thereby illustrating the general resemblance of the display. The beetle has been seized with a pair of forceps and is in the act of stridulating. A drop of defensive fluid is oozing from the anus. The bee, which had been left overnight in a pill box, was merely tipped out of the container alongside the beetle. Note that a drop of fluid is also oozing from the anus; one drop has already been ejected.

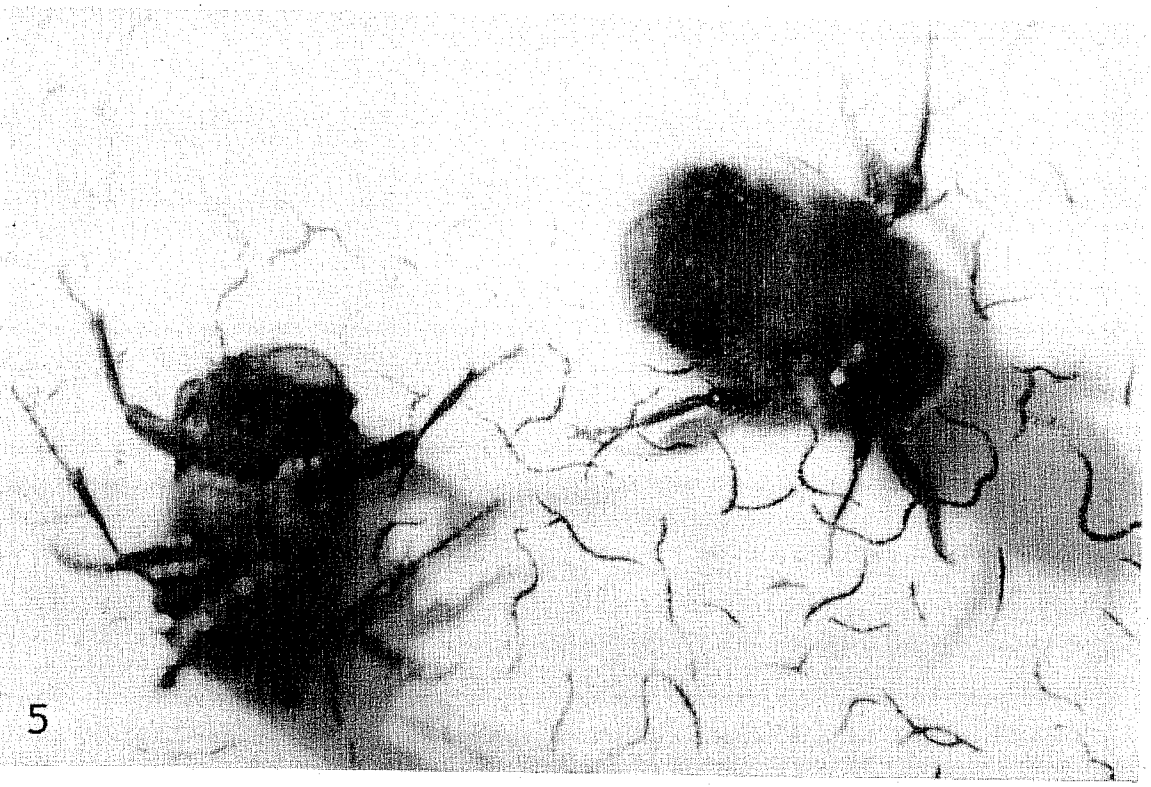


FIG. 5.—The same specimens photographed a few moments later.

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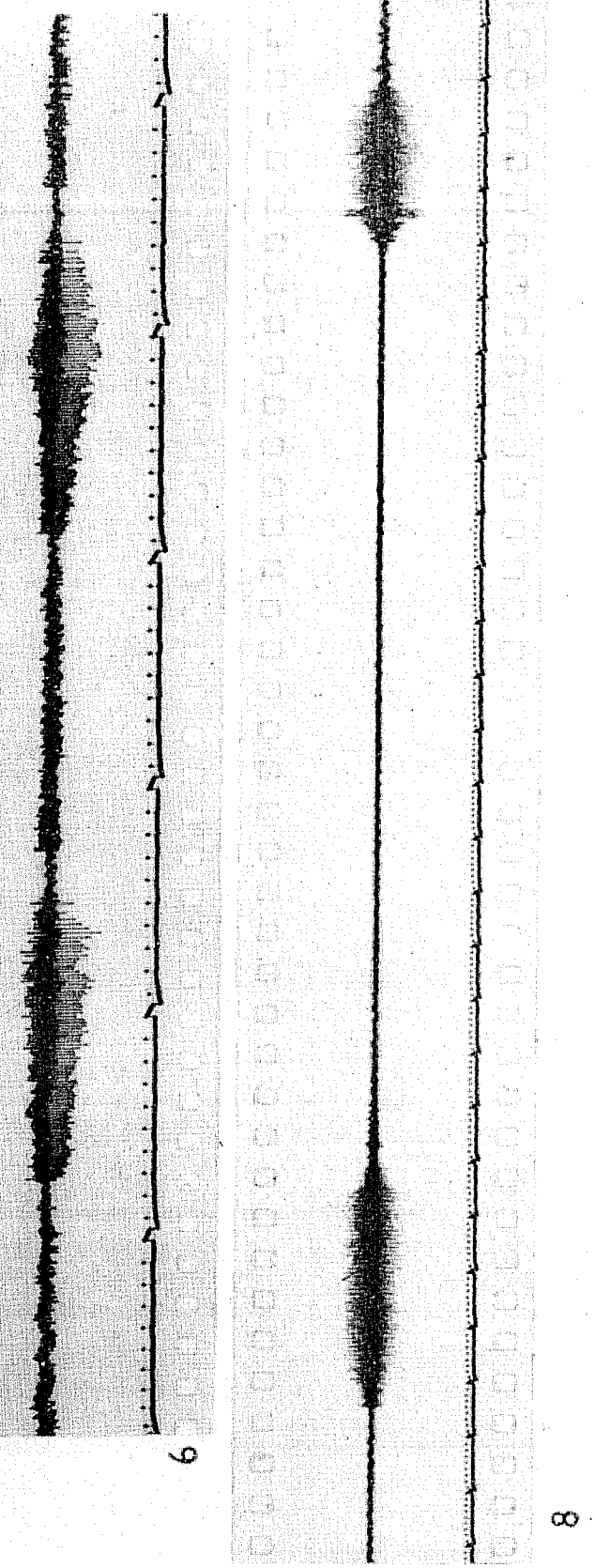
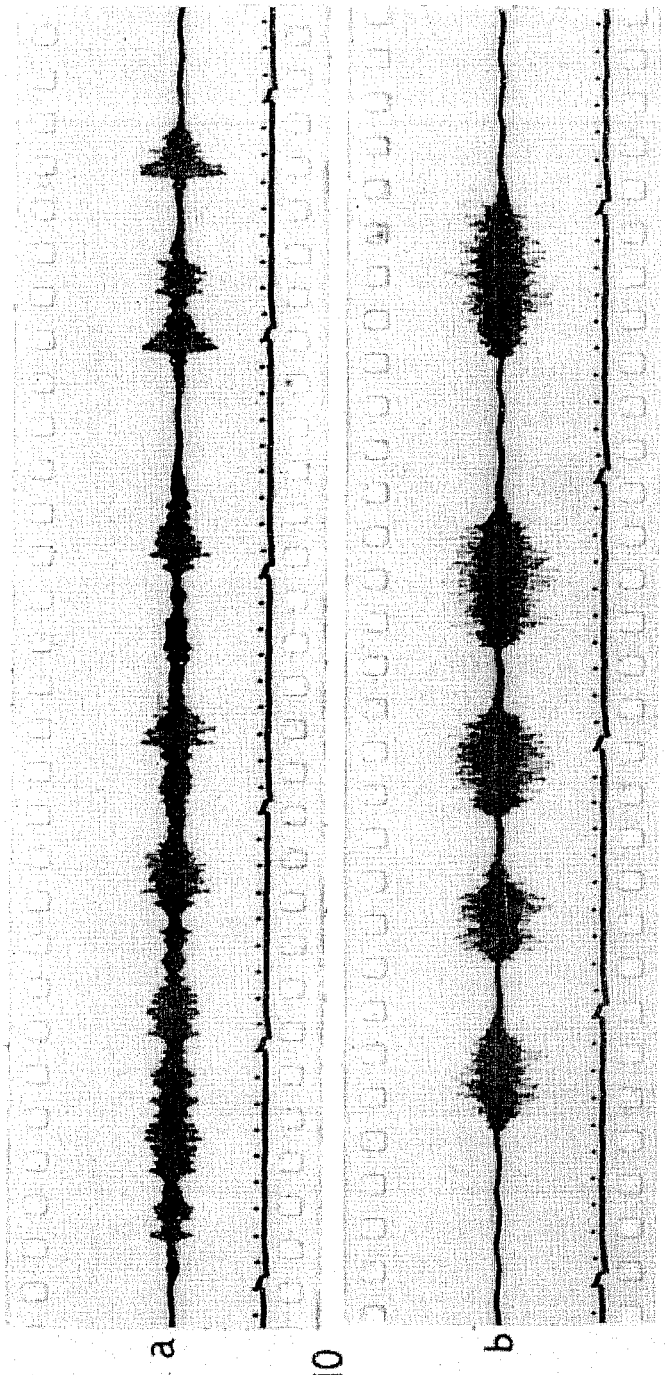
FIG. 6.—Cathode ray oscillogram of the typical stridulation of *N. investigator* showing first (forward) phase and second (recovery) phase and pause between stridulations. Timing trace, 1/10 + 1/100 sec.

FIG. 8.—Cathode ray oscillogram of the buzzing sound of a chilled Bumble-Bee. Timing trace, 1/10 + 1/100 sec.

FIG. 10.—Oscillogram of warning chatter or alarm call of various species of tits: (*a*) The Long-tailed Tit (*Aegithalos caudatus* (L.)) (tape recording by the B.B.C.). (*b*) Himalayan Crested Tit (*Machlolopus xanthogenys* Vig.) responding to the presence of a cat (tape recording by the authors).





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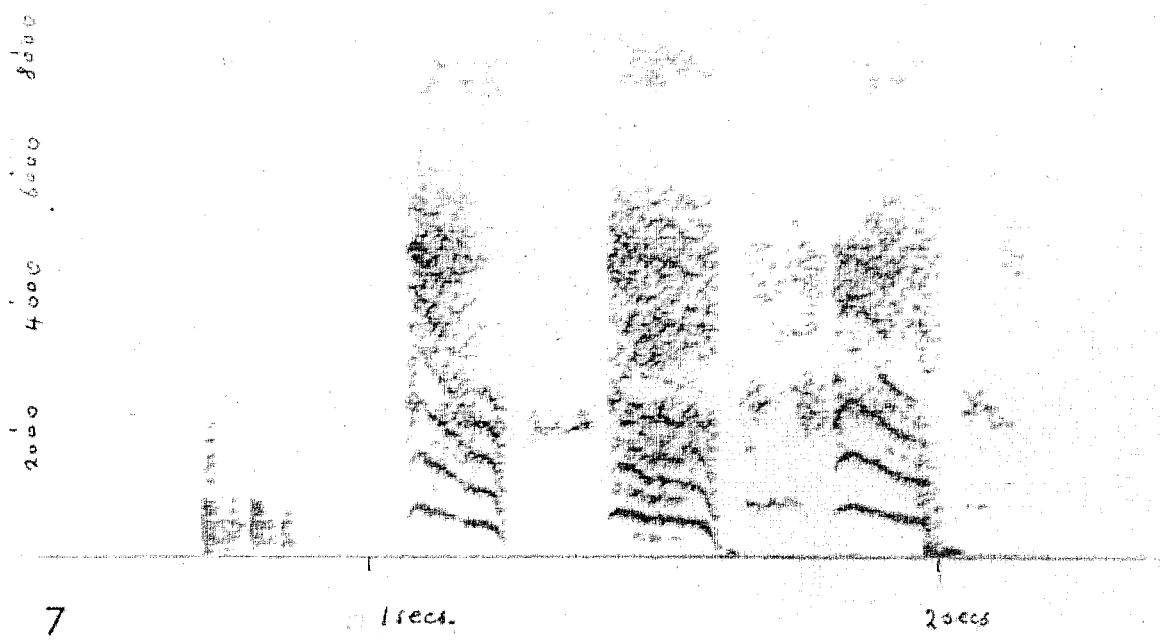

FIG. 7.—Frequency/time analyses of the tape recording of *N. investigator* (fig. 5) by a sound spectrograph.

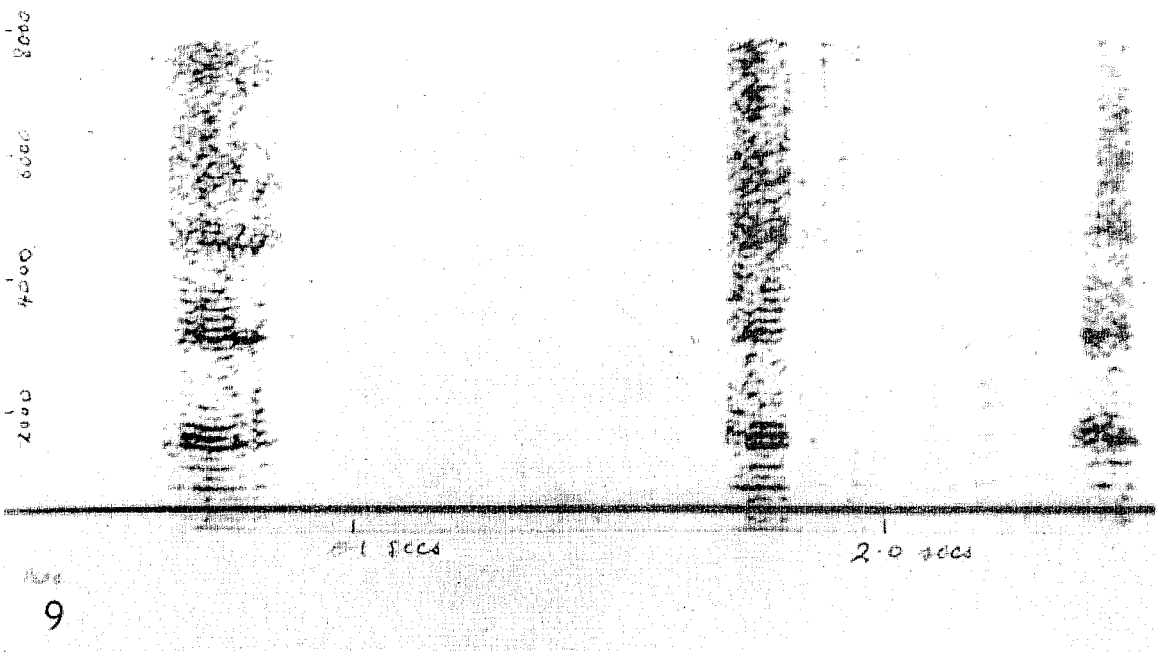

FIG. 9.—Frequency/time analyses of the tape recording of the chilled Bumble-Bee (fig. 8) by a sound spectrograph. (The heavy black line near the base is an artefact.)

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