Stridulation in Leaf-Cutting Ants

Abstract. *The leaf-cutting ant* Atta caphaloes *L. stridulates whenever it is prevented from moving freely. Although audible to the human ear, the airborne sound produced has its main energy concentrated between 20 and 60 kilocycles per second. However, it is not the airborne, but the ground-conducted stridulation sound that acts as a distress alarm: a stridulating ant attracts other workers, and if the "calling" ant is covered by earth, intensive digging is released in the attracted nest mates.*

Although it has been recognized for almost 100 years that ants of the subfamilies Ponerinae and Myrmicinae can produce stridulous sound by moving the sharp posterior rim of the third abdominal tergite over a fine-ribbed area on the front of the fourth abdominal tergite, not much is known about the physical quality of the sound that is produced nor of its perception by the ants, nor whether it has any biological function (*1*).

I have studied the leaf-cutting myrmicine ant *Atta cephalotes* L. in Trinidad, West Indies. Workers of this species stridulate whenever prevented from moving freely. This occurs under natural conditions when ants are fighting and especially when they are buried under an earth slide. When the gaster is moved about a transverse axis against the postpetiole the scraper glides over the ridges of the file and produces pulses (Fig. 1). The duration and repetition rate of pulses and pulse groups of three soldiers are given in Table 1. Analysis of tape recordings of stridulation by playback through a bandpass filter and by sound spectrograms showed that the frequency spectrum of the airborne sound extends from the upper range of human hearing to more than 100 kc/sec, the main intensity being concentrated between 20 and 60 kc/sec (*2*). At 1 cm from the microphone the sound intensity is approximately 80 db referring to 0.0002 μbar.

If the stridulation fulfills any purpose in the social life of the *Atta* colony, a stridulating ant must be able to influence the behavior of nest mates. Since stridulation is produced almost exclusively when an ant is in distress, reactions of other ants might be either to escape or to approach. In all experiments care was taken to control communication by alarm odor produced in the mandibular glands of *Atta* (*3*). Ants running to and fro on their "streets" were offered test objects, such as a piece of filter paper (2 by 2 cm) or *Atta* soldiers that were able to stridulate and to produce alarm odor or that were selectively impaired in these abilities. Two sets of objects were offered simultaneously, one serving as control for the activity of the ants at the chosen place (*4*), and the number of soldiers and workers touching the test object in a standard time interval was counted. Since decapitated ants stridulate as well as intact animals, they serve as test objects with the alarm odor excluded. Table 2 shows that a stridulating soldier attracts other ants (I and III in the table) though less than does one producing alarm odor (II), and that stridulation adds its alarm effects to those of the odor (IIa and IIIa). Counting soldiers and workers separately (including data not given in Table 2) revealed that a significantly higher proportion of soldiers is attracted by a stridulating ant and/or by an ant producing alarm odor than by an empty paper, the relation being 1.6 : 1.

In another type of experiment, I induced ants to come out of their nest entrances during daytime, when they were not active outside the nest, by using various combinations of stridulating and/or odor-producing soldiers as "bait" at the entrances. In 39 cases, an average of two ants per 5-minute test period were counted when a decapitated soldier with blocked abdominal joints was pinned to the ground before the hole as a control. An odorant and stridulating soldier, however, attracted 12 ants per 5 minutes when it had no contact with the ground (the average of five experiments), and 25 ants (the average of ten experiments) when it touched the ground. Stridulation of headless ants, free of the ground, attracted an average of two ants per experiment (11 experiments), the same as the nonstridulating controls, whereas ten ants on average (18 experiments) were attracted when the same soldiers were pinned to the ground. This difference is statistically highly significant and shows that only ground-conducted vibration elicits behavioral responses.

Table 1. Average and standard deviation of data characterizing the stridulation sound of three soldiers of *Atta cephalotes*, from recordings taken at 27°C.

Ant	Pulse repetition rate (per sec)	Pulse duration (msec)	Pulse group repetition rate (per sec)	Pulse group duration (msec)
1	715 ± 160 ($N = 77$)	0.12 ± 0.02 ($N = 41$)	4.8 ± 0.65 ($N = 16$)	50 ± 7 ($N = 10$)
2	606 ± 156 ($N = 30$)	.3 ± .07 ($N = 28$)	5.0 ± .7 ($N = 11$)	45 ± 5 ($N = 11$)
3	909 ± 179 ($N = 73$)		7.3 ± .6 ($N = 19$)	39 ± 3 ($N = 19$)

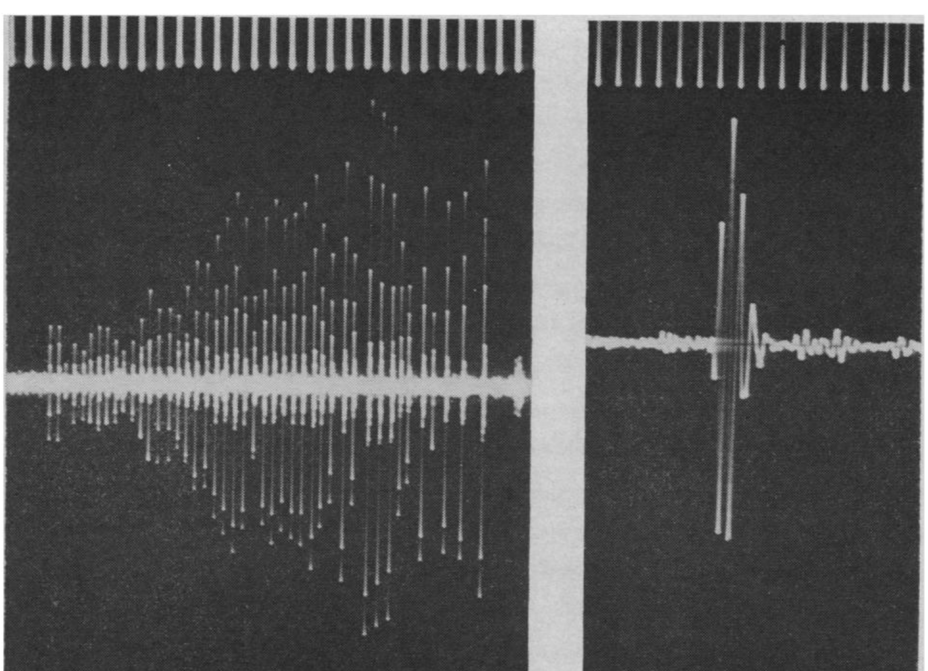

Fig. 1. Oscillograms of airborne stridulation sound of an *Atta cephalotes* soldier. (Left) Pulse group; time marker 2.5 msec. (Right) Single pulse; time marker 0.05 msec.

Table 2. Number of workers and soldiers of *Atta* which are attracted by the test objects listed in the first column. Objects a and b are offered simultaneously. The last column shows the ratio of the number of attracted ants (workers plus soldiers) in the "a" experiments to the number attracted in the corresponding "b" experiments, when the ratios are significantly different from 1 : 1 ($p \leq 0.01$).

Objects offered to the ants	No. of expts.	Ants attracted: Workers	Ants attracted: Soldiers	Ratio of attracted ants (a : b)
I a. Decapitated soldier	10	173	27	3.6 : 1
b. Empty paper		51	5	
II a. Normal soldier	10	451	95	1.6 : 1
b. Soldier with blocked abdominal joints		301	50	
III a. Normal soldier	10	447	93	2.2 : 1
b. Decapitated soldier		205	41	
IV a. Decapitated and non-stridulating soldier	6	24	0	Not significant
b. Empty paper		15	0	

Table 3. The efficiency of stridulating workers and soldiers of *Atta cephalotes*, in closed glass vials, of attracting other ants and releasing digging behavior. Average values per minute of observation are given. S vial: vial containing stridulating ants; M vial: "mute" control vial: S/M ratio: ratio of the number of responses to the S vial to the number of responses to the M vial.

Ants used in the vials (body size in mm)	No. of expts.	Minutes of observation	Touch responses: By workers*: S vial	M vial	S/M ratio	Touch responses: By soldiers: S vial	M vial	S/M ratio	Digging responses by workers*: S vial	M vial	S/M ratio
5 S† (12–15)	18	210	1.76	0.43	4.1	0.23	0.04	5.7	0.99	0.13	7.6
5 W‡ (8–11)	9	70	2.34	1.10	2.1	.39	.16	2.4	1.50	.47	3.2
10 W‡ (5–8)	5	40	2.10	1.00	2.1	.25	.10	2.5	0.88	.42	2.1
10 W‡ (3–5)	6	45	1.67	0.93	1.8	.18	.09	2.0	.87	.40	2.2
15 W‡ (1.5–3)	6	45	1.20	.69	1.7	.16	.13	1.2	.64	.24	2.7

* Smaller than soldier caste. † Soldiers. ‡ Workers.

About the same number, nine ants (average of six experiments), were attracted when the stridulating ants were enclosed in a tightly closed glass vial, partly buried in the ground, which definitely excluded any olfactory communication.

How do the attracted ants react when arriving at the source of vibration? A glass vial, 1.5 cm in diameter and 8 cm long, containing stridulating ants pressed down gently by a vapor-tight piston, and a "mute" control vial were buried 1 to 2 cm in the ground at a distance of 3 to 10 cm from an entrance hole. The control vial was either empty or contained the same number of ants rendered mute by cutting off the gaster. For 5 to 15 minutes the number of soldiers and workers touching the vials and the number of digging responses shown by the ants were counted. Every taking up of a soil particle at the vial was regarded as a digging response, and so was the moving of particles with mandibles or legs. Since the total time of observation varied in different experiments, Table 3 gives the number of touches and digging reactions of workers or soldiers at the "stridulating" vial and at the control vial divided by the minutes of observation, that is, the average number of actions per minute. Furthermore, the proportion of reactions at the two vials is given to eliminate the bias caused by differing levels of general activity of the ants at the different experimental locations. The number of digging reactions of soldiers was too small for inclusion in Table 3.

A glass vial containing five stridulating soldiers attracted four to six times as many ants as the "mute" control and released nearly eight times as many digging responses. The smaller the ants, the less effective was their stridulation, the decline being more pronounced in the number of ants attracted than in the number of digging responses. Combining the results of 55 experiments (including some not shown in Table 3), comprising 495 minutes of observation, shows that about four times as many digging responses occurred at the stridulating vial and about three times as many ants were attracted by it. If one compares the relation of the number of soldiers and the number of smaller workers touching the "stridulating" vial, namely, 1 : 6.2, with the relation of digging responses shown by these two groups, namely, 1 : 20.6, one sees that almost all the digging is done by smaller workers (5). The comparison between the relation of the number of touches to the number of digging responses at the control vials (2.8 : 1) and the same relation at the "stridulating" vials (1.9 : 1) shows that there is not only more digging at the source of stridulation because there are more ants attracted, but also that the digging is specifically increased where stridulation occurs. (The difference is statistically significant.)

For *Atta cephalotes*, which dig nests several meters deep in soil (5), the danger of earth slides trapping parts of the population is evident under conditions of tropical climate. Besides this function as an "ant SOS," which is apparently the primary one for the worker caste, stridulation can add its alarm effects to the alarm odor, causing workers to concentrate at places where it is necessary to fight a predator or other ants. The apparent redundancy of alarm devices finds its explanation in the fact that underground emergency communication by vibratory signaling is more effective than by olfactory means. Further investigation will be necessary in order to determine whether stridulation may also function in courtship or in predator-prey relationships.

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References and Notes

1. For summary, see B. Dumortier, in *Acoustical Behaviour of Animals*, R. G. Busnel, Ed. (Elsevier, Amsterdam, 1963), pp. 346–373 and 583–654; see also H. Autrum, *Z. Vergleich. Physiol.* **23**, 332 (1936).
2. Condensor microphone: Bruël and Kjaer, model 4135; tape recorder: Precision Instrument Co., model PS-202; filter: Krohn-Hite, model 310-AB; sound spectrograph: Kay Electronic Co., "Missilyzer."
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5. H. Eidmann, *Z. Angew. Entomol.* **22**, 185, 385 (1935); W. Goetsch, *Zoologica (Stuttgart)* **35**, 1 (1939).
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