

PSYCHE

Vol. 69

JUNE, 1962

No. 2

DEFENSE MECHANISMS OF ARTHROPODS. X. A PHEROMONE PROMOTING AGGREGATION IN AN APOSEMATIC DISTASTEFUL INSECT.¹

By T. EISNER AND F. C. KAFATOS²

Department of Entomology, Cornell University, Ithaca, N. Y.

A striking feature of many aposematic insects is their habit of maintaining dense and often conspicuous aggregations (Cott, 1957). Rather than spacing themselves more or less evenly throughout what is seemingly a uniformly favorable habitat, they occur in distinct, sporadically distributed clusters. Many meloid and coccinellid beetles, as well as a variety of pentatomid, coreid, and lygaeid Hemiptera, among others, are well known for this habit. These insects possess chemical defense mechanisms that protect them against predators, and their tendency to advertise themselves to visually oriented predators such as birds by pooling their aposematic resources in a collective display, appears to have obvious adaptive value. Moreover, by restricting themselves to a few relatively widely-spaced sites, the insects are exposed to but a fraction of the total number of predators in the area. This is likely to be of particular importance with respect to predators such as birds, which are known in many cases to have well-delimited foraging territories, and each of which may be expected to inflict a toll upon the insect population during the training period when the bird is learning to discriminate against the insect. Clearly, the fewer the foraging territories occupied, the greater will be the number of insects spared.

Hitherto no studies have been made on the mechanism by which such aggregations are established and maintained. The purpose of

¹This study was supported by Grant E-2908 of the U. S. Public Health Service. The work was done at the Southwestern Research Station of the American Museum of Natural History, Portal, Arizona. We are indebted to the director of the Station, Dr. Mont A. Cazier, for his generosity with equipment and facilities, and to Miss Abby Rockefeller, who assisted ably in this and related studies.

²New address: Biological Laboratories, Harvard University, Cambridge, Mass.

Manuscript received by the editor January 9, 1962.

this note is to present evidence indicating that in at least one case, a gregarious beetle of the family Lycidae, the clustering behavior of both sexes seems to be mediated by a volatile attractant produced by the males alone.

Lycids are widely distributed through the tropics and subtropics, commonly are aposematic, are known to be distasteful to many vertebrate and invertebrate predators, and frequently figure as dominant Müllerian elements in mimetic associations. They form dense aggregates, sometimes being found by thousands, closely spaced on the exposed inflorescences of the host plants on which they feed and mate.

The particular species on which we worked, *Lycus loripes* (Chevrolat), is abundant on the grounds of the Southwestern Research Station of the American Museum of Natural History, Portal, Arizona, where this study was made. The locality has been described in some detail elsewhere (Linsley et al., 1961), and it will suffice here to mention that, at the time of the experiments (July 15-25, 1961), the lycids were found almost exclusively on a patch (ca. 80 x 160 ft.) of sweet white clover (*Melilotus alba*) directly facing the principal laboratory building of the Station (Plate 3, fig. 1). Over 3000 *L. loripes* inhabited the patch at the time, distributed more or less irregularly in dense clusters. These lycids are uniformly yellow-orange in color (except for some black on the appendages), and are conspicuous on the white flowers of the clover, particularly on those branches where they are densely aggregated (Plate 3, fig. 2). They are sluggish and do not take readily to flight when disturbed. They fly relatively little even on their own initiative, and when they do, it is usually during the noon hours.

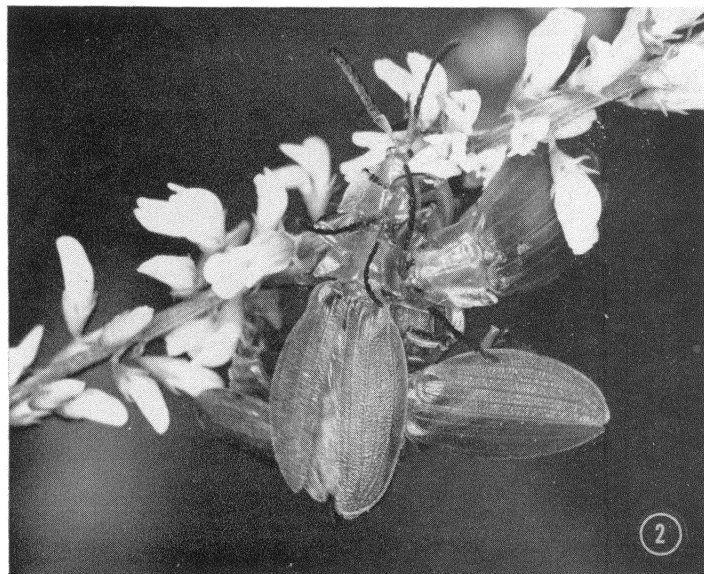
Behind the laboratory building there was a second stand of *Melilotus*, roughly equal in area to the front patch, but almost entirely devoid of lycids. This uninhabited patch became the test arena in which formation and growth of aggregations was experimentally induced.

Initial tests, designed to see whether one could induce lycids to aggregate after distributing them singly throughout the test area were bound to failure, since these lycids, rather than being attracted to one

EXPLANATION OF PLATE 3

Figure 1. The open field, densely overgrown with *Melilotus alba*, directly in front of the main laboratory building of the Southwestern Research Station, Portal, Arizona. On this field was found the main standing aggregation of *Lycus loripes*.

Figure 2. A cluster of *Lycus loripes* on an inflorescence-bearing branch of *Melilotus alba*. Within the main lycid aggregation, dozens of branches bore one or more such clusters, as well as isolated individuals and mating pairs.



EISNER AND KAFATOS — DEFENSE MECHANISMS

another, were lured back to the main standing aggregate in the front of the building. Instead of being scattered individually, the lycids were then put out in a number of isolated incipient aggregations to see whether these would tend to consolidate and attract newcomers. This they were found to do. Five groups of *L. loripes*, each comprising 75 individuals of both sexes, were placed on single *Melilotus* plants (or on compact clusters of branches) in such a way that three of the groups were closely spaced and roughly equidistant (5-6 m.), whereas the other two were spaced about 25 m. from each other and from the center of the triangle formed by the other three. Within five days (see Table I) the three closely spaced aggregations became consolidated around one of the loci, which now numbered 390 individuals. The two neighboring clusters had dwindled to 27 and 1 respectively. Recruitment had taken place also from the two outlying clusters, one of which had disappeared altogether, while the other now had only 15 lycids. Although the individuals of each lot had originally

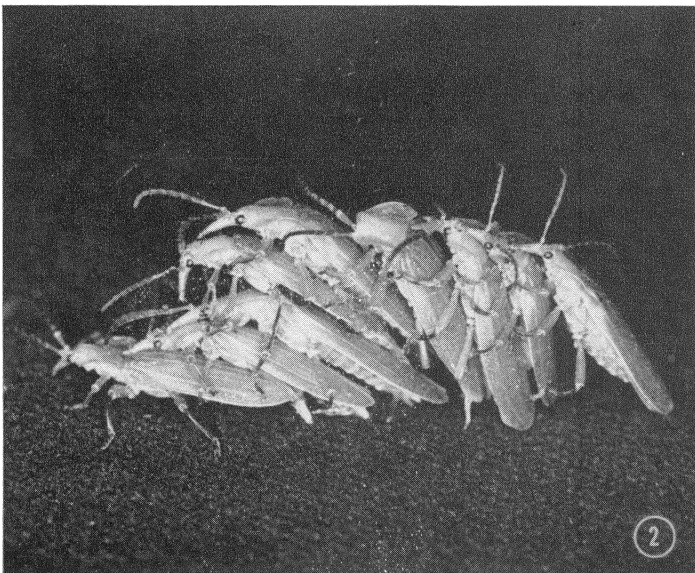
AGGREGATION						
	I	II	III	IV	V	
TIME (hrs.)	LYCID COUNT PER AGGREGATION					LYCIDS ELSEWHERE
0	75	75	75	75	75	5
4	22	23	35	35	82	5
30	2	21	30	9	178	30
56	2	21	26	3	309	24
119	0	15	27	1	390	30

Table I. Fate of five artificially-established incipient aggregations (each consisting of 75 lycids of both sexes) observed over a period of five days. Aggregations III, IV, and V were 5-6 m. from one another. Aggregations I and II were 25 m. from each other and from the center of the triangle formed by the other three. The times given for the various counts are measured from when the aggregations were first put in the field. The column on right gives the lycid count for the entire remainder of the *Melilotus* test patch behind the laboratory building.

EXPLANATION OF PLATE 4

Figure 1. One of the nets (enclosing *Melilotus* with lycids) used as a lure. This particular net, which held males alone, was one that successfully attracted other lycids (a few of the newcomers are seen on the net itself).

Figure 2. Group of male lycids, in the typical sequential arrangement they often assume when confined by themselves.



EISNER AND KAFATOS — DEFENSE MECHANISMS

been labelled with a distinct color marking, these tended to flake off after some days, and the exact course of the migration patterns could therefore not be followed. However, judging from the number of unmarked specimens present, which outnumbered by far the calculated maximum that could have lost its markings, it was clear that a substantial number of lycids were new arrivals in the test area, probably stemming from the principal aggregation at the opposite side of the laboratory building. Conversely, as expected, some marked individuals had been lured back to the front field.

It remained to be determined what particular attracting stimulus is responsible for luring the lycids. Visual cues were eliminated by

DECOY GROUP

	A 150 ♂♂		B 150 ♂♂		C 150 ♀♀		D 150 ♀♀	
TIME(hrs.)	NEWCOMER COUNT PER DECOY GROUP							
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
20	39	7	65	13	4	2	4	3
45	41	16	25	8	0	1	0	0
72	29	17	19	5	0	1	0	0
	A 150 ♀♀				D 150 ♂♂			
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
96	5	2					23	12
119	0	0					31	7
145	0	0					26	13

Table II. Attraction of lycids to male and female decoy aggregates placed in nets. The four decoy groups (A - D) were placed at the corners of a square, roughly 25 m. to the side. The times given for the various newcomer counts are measured from when the decoy groups were first staked out. At 72 hours, the females from group D were exchanged with the males from A.

using porous nets of white cloth to enclose the groups of lycids, distributed as before on close clusters of *Melilotus* branches (Plate 4, fig. 1). The technique had the added advantage of preventing dispersal of the decoy group, while at the same time facilitating the count of newcomers assembled around the nets. Four nets were staked out with 150 lycids each, two of them containing only males, the other two only females. Spacing was maximized within the area available, each net being about 25 m. from its neighbors. The loci selected were known to have supported no previous aggregations. Table II summarizes the results. Only those lycids were counted as newcomers which were either directly upon the nets, or on *Melilotus* branches within a few feet around them. It is clear that the males, but not the females, exerted immediate and persistent attraction for lycids of both sexes. The fact that the newcomers included a preponderance of males should not be taken to reflect a greater susceptibility of this sex to the attracting stimulus, since the males were actually the more numerous in the population at the time (actual counts made, based on samplings from the main population site, showed the ratio to vary between 3:1 and 6:1).

The possibility was ruled out that ecological factors, rather than the males themselves, were the source of attraction. After the third day, the males from *net A* were exchanged with the females from *net D*. The other two nets were dismantled, and the lycids within them, plus the assemblages that had accumulated around both original male sites, were scattered at 1 m. intervals throughout the test area. Over the next three days only one assemblage built up, this time around the new male site (Table II). Clearly, the attracting stimulus is emitted by the males, and it is most likely a diffusible chemical factor.

An additional observation is worth mentioning. On two separate occasions, when artificially induced aggregations were allowed to persist over a period of several days, and were subsequently removed, the *Melilotus* branches that had harbored the beetles were found to retain the potential to lure lycids, presumably as a result of residual attractant with which the plants had been labelled. When the lycids that would subsequently accumulate on these branches were systematically removed once a day, and redispersed, the attractiveness of the plants dwindled to extinction within a few days.

The attraction of lycids to each other in the presence of males was also demonstrated in captive specimens. Mixed lots of males and females confined in glass-topped observation enclosures would soon distribute themselves into individual mating pairs or small clusters of

pairs. Females alone remained distributed singly and showed no attraction for each other. Males, by contrast, clustered closely, usually one on top of the other in overlapping sequence, as shown in Plate 4, fig. 2.

A chemical attractant of the type involved here may appropriately be called a pheromone. Pheromones, by definition (Karlson and Butenandt, 1959), are substances secreted by one individual to the outside, capable of eliciting specific behavioral or developmental responses in another individual of the same species. Among insects, these social chemical messengers include the sex attractants, the queen substance of honeybees, the trail substances of ants and termites, the releasers of alarm behavior in ants, etc. It is clear that the lycid attractant, aside from its obvious function in maintaining the aposematic population densely congregated, also serves appropriately in bringing together the sexes preparatory to mating. But since it lures both males and females with apparently equal effectiveness, there must be additional short-range stimuli operating within the aggregation to insure that males and females will ultimately be properly paired. One wonders what evolutionary justification accounts for the production of attractant by the males alone, rather than by the females, or by both sexes. Not enough is known about the life cycle of lycids, but the possibility that the males are the first to emerge in the season and hence are the ones that carry the aggregations through their incipency, is worth considering.

It is hoped, now that the groundwork of this problem has been laid, that additional more precise experimentation on this unusual type of attractant will be pursued. With *L. loripes* there are some especially intriguing aspects to the problem. This lycid is the dominant Mülleri-an element of an elaborate mimetic complex (Linsley et al., 1961) that includes among others, a congeneric sibling species of lycid [*Lycus simulans* (Schaeffer)], a cerambycid beetle (*Elytroleptus ignitus* LeConte), and a geometrid moth [*Eubaphe unicolor* (Robinson)]. Whether the attractant produced by *L. loripes*, which far outnumbers the others, exerts its action also on all or some of the mimetic associates, thus insuring that these are lured to "safety" within the aggregations of the dominant model element, remains unknown. Unfortunately all of these mimetic forms were extremely scarce at the time of our experiments, and could not be included for study.

Future work should concentrate also on some of the many other gregarious aposematic insects known, in which similar attractant mechanisms, or perhaps interesting alternatives, are likely to be at play.

REFERENCES CITED

- COTT, H. B.
1957. *Adaptive Coloration of Animals*. Methuen & Co. Ltd., London.
- KARLSON, P., AND A. BUTENANDT.
1959. Pheromones (Ectohormones) in insects. *Annual Rev. Entomol.*
4: 39-58.
- LINSLEY, E. G., T. EISNER, AND A. B. KLOTS.
1961. Mimetic assemblages of sibling species of lycid beetles. *Evolution*
15: 15-29.



Hindawi

Submit your manuscripts at
<http://www.hindawi.com>

