PSYCHE

Vol. 65 June-September, 1958 Nos. 2-3

A CHEMICAL RELEASER OF ALARM AND DIGGING BEHAVIOR IN THE ANT *POGONOMYRMEX BADIUS* (LATREILLE)

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INTRODUCTION

The complex social behavior of ants appears to be mediated in large part by chemoreceptors. If it can be assumed that "instinctive" behavior of these insects is organized in a fashion similar to that demonstrated for the better known invertebrates, a useful hypothesis would seem to be that there exists a series of behavioral "releasers", in this case chemical substances voided by individual ants that evoke specific responses in other members of the same species. It is further useful for purposes of investigation to suppose that the releasers are produced at least in part as glandular secretions and tend to be accumulated and stored in glandular reservoirs. In support of this hypothesis one such releaser, the trail substance of fire ants, has been described elsewhere (Wilson, 1959). This agent effects short-range exploratory behavior and also serves as the chief orienting stimulus. Goetsch (1952) has suggested the existence of another class of chemical releasers in ants, the *Fernalarm* substances ,which are said to be released by excited workers to communicate a state of excitement within the colony. According to this author, workers of certain deserticolous species of the dolichoderine and formicine genera *Forelius, Tapinoma, Iridomyrmex, Dorymymex,* and *Camponotus* apparently can discharge abdominal secretions that create this effect among other workers through the air over short distances. Goetsch's interesting observation has not yet received experimental verification. The purpose of the present paper is to report on yet another chemical releaser, a secretion of the mandibular glands of the harvesting ant *Pogonomyrmex badius*. This agent is especially interesting, because it operates to release two seemingly unrelated complex behavior patterns, general alarm behavior and digging.

MATERIALS

Observations were made chiefly on colonies collected at Ocean Drive Beach, South Carolina, and Gulf Shores, Alabama, and maintained in artificial nests in the laboratory. Since the mother queens of *Pogonomyrmex* colonies are notoriously difficult to find in the field, a note on the collecting method employed would seem to be in order. The best results were obtained by excavating small nests during the early morning, preferably following rainfall. The upper portions of the nests were simply dug out with a spade and scattered over a ground-cloth until the queen was sighted. Under such conditions, roughly half the nests opened yielded queens during the first ten minutes of search. Other methods tried, including deep lateral excavations and the use of sieves, proved relatively inefficient.

The colonies were housed in the laboratory in vertical, multistoried, plexiglas nests. The horizontal galleries were fitted with sliding plexiglas walls that could be moved to allow cleaning and to give access to the interior of the nest. The floors of the galleries were made of softwood strips. Curved plastic tubes led from the outside to the ends of the wooden floors to allow periodic watering of the nest interior. A single opening led from the bottom gallery outside to a walled foraging arena. The ants had been gradually habituated to strong light, so that it was possible at all times to keep the nest interior brightly illuminated. The foraging arena was illuminated during twelve hours of each day by fluorescent lamps turned on and off by an automatic timing device. A more detailed description of this type of artificial nest, which has proven successful in the pursuit of a variety of behavioral problems, is planned in a later report. During the present study, the adult population of the captive colonies ranged between 63 and 124, which is smaller than that of large juvenile and adult colonies in the wild.

Description of Alarm Behavior

When workers of *Pogonomyrex badius* are disturbed by alien mechanical or chemical stimuli, they show the following characteristic alarm response. *Low intensity*: rate of locomotion increases, with the ant moving in wide, poorly defined loops and circles; the head and antennae are periodically lifted high and the antennae waved about; the gaster may be periodically lowered so that its long axis is approximately perpendicular to the ground surface. *High intensity*: rate of locomotion increases still more, with the ant tending to move in tighter and more geometrical circling patterns; the head and antennae are periodically raised a moderate distance, but not as high as during lower intensity alarm; the mandibles are held partly open; the gaster may be periodically bent downward.

These two states of activity are not discontinuous but merely represent points on a gradient of intensity that is a function of the magnitude of the stimulus applied. Essentially the same pattern of behavior is exhibited both inside the artificial nest and outside it in the near vicinity of the nest entrance. Under laboratory conditions, the intensity of response outside the nest is inversely related to the distance of the locus of stimulation from the nest entrance. At the outer limits of the foraging arena, approximately one meter from the nest entrance, high-intensity responses have been difficult to induce, and workers have frequently shown instead a simple escape reaction.

A highly excited worker is a potential cause of a wave of alarm behavior among other workers. Under natural conditions a single worker exhibiting high-intensity alarm just outside the nest entrance can initiate general excitement that spreads centrifugally over the entire surface of the nest crater, along a radius of fifty centimeters or more. As the first worker commences a circling movement, it encounters other workers, which are stimulated to take up smiilar movement, in turn exciting other workers, and so forth. The wave of excitement seems to diminish in intensity away from the original stimulus in a roughly logarithmic fashion.

These results can be closely duplicated in laboratory colonies. When waves of excitement caused by a continuing stimulus at a single locus inside the nest are measured, a pattern of alternating expansion and contraction through the linear galleries is noted. The maximum range of the wave expansions is a function of the magnitude of the stimulus. During the first several minutes the maximum range achieved by successive waves tends to be stable. This is evidently due to the fact that expansions are ordinarily led by no more than one or two workers that break away momentarily from the zone of continuous excitement close to the stimulus; these individuals run outward, creating lesser, shorter-lived excitement among workers they pass, then turn back in the inevitable looping pattern that characterizes alarm behavior. After several minutes the workers in the zone of continuous excitement begin to adapt

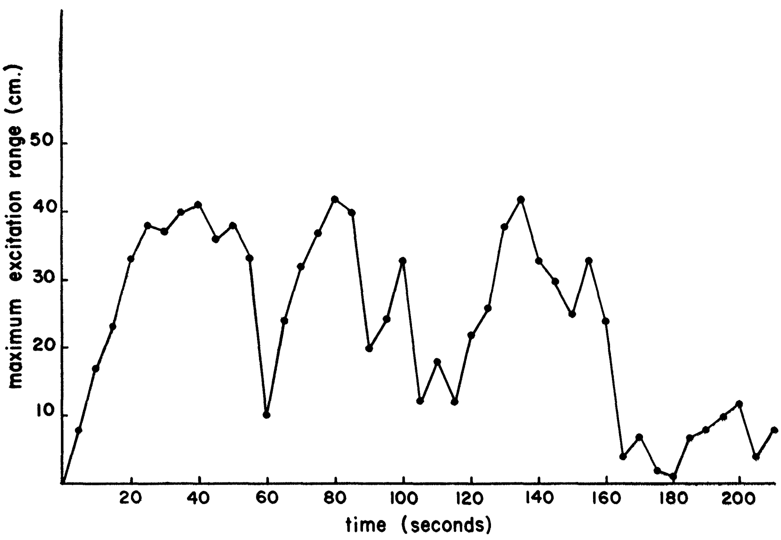

Figure 1. Spread of excitation through a laboratory colony of *Pogonomyrmex badius.* The continuing stimulus in this instance was an injured, immobile *Camponotus pennsylvanicus* (DeGeer) worker pinned to one spot in the nest interior. The maximum range of excitation was measured at five-second intervals in one direction only outward from the stimulus through the linear galleries of the artificial nest. Nest temperature: 30° ± 2° C. Further explanation in the text.

to the stimulus, the alarm behavior grows generally less intense, and the waves of expansion grow ever shorter (See figure 1).

THE RELEASE OF ALARM BEHAVIOR BY THE MANDIBULAR GLAND SECRETION

It has been noted repeatedly that purely mechanical stimulation of one worker by another is not ordinarily adequate to effect alarm behavior of significant intensity. Workers falling accidentally from the nest walls have been observed to push heavily against other workers without creating noticeable excitement. The same is true when injured workers occasionally manifest abnormally high locomotory activity for sustained periods and repeatedly bump against nestmates. Workers within the nest can also be pushed about lightly with clean glass rods, providing the ants are allowed to adapt to the immobile rods for a short time beforehand. Two other kinds of stimuli have proven most effective in eliciting alarm behavior: sound, especially that transmitted through the solid medium of the nest walls, and alien chemical substances.

The presence of a chemical releaser of alarm behavior was suspected when it was noted that greatly excited *Pogonomyrmex badius* workers discharge a highly volatile, pungently odorous substance. When workers of another species, *Solenopsis saevissima* (Fr. Smith), were allowed to invade a *badius* nest, the substance was discharged continuously for several hours and was associated with a state of high excitement among the *badius* workers.

Dissections of anesthetized workers revealed that the substance is concentrated, perhaps exclusively, in the reservoir of the mandibular gland of the head.[1]

In a majority of workers that have been removed care-

[1] The morphology of the mandibular gland of ants has been described by Janet (1898) and more recently by Whelden (1957a, 1957b). As shown by these authors, the gland reservoir lacks constrictor muscles, and it seems likely that contraction is achieved through an increase in the surrounding hemolymph pressure. The gland and its reservoir are best exposed by splitting the head sagittally and removing the pharynx and associated tissues. Direct removal of the mandible by extraction almost always results in the collapse of the gland reservoir and loss of its contents.

fully from the nest, anesthetized, and dissected, the gland reservoirs have been partly or completely filled with a colorless fluid. When the reservoir walls are ruptured this fluid evaporates within several seconds and the characteristic pungent odor can be perceived by the human observer over a distance of 50 centimeters or more.

The releaser effect of the mandibular gland secretion was demonstrated in the following way. When workers were seized with forceps and held about two centimeters above groups of resting workers just outside the nest entrance, alarm behavior was induced in the resting workers after an interval of several seconds. The captive workers were not stridulating, thus eliminating the possible complication of this additional stimulus, but they were releasing sufficient quantities of mandibular gland secretion to be discernible to a human observer a short distance away. Freshly killed workers, which were not producing discernible amounts of the secretion, elicited no response when held above resting workers.

When workers were crushed between two pieces of glass above groups of resting workers, large quantities of the mandibular gland secretion were released, and high-intensity alarm behavior was elicited. That the effect was in fact proluced by the mandibular gland substance and not by other substances released by crushing was tested in the following experiment. In separate trials various parts of an anesthetized worker were isolated and crushed above groups of workers in the manner described. Each body part was tested from a total of ten workers. The sequence of presentation was randomized to eliminate possible special sequential effects. Also, the trials were spread over a period of several days to reduce the decline of response due to adaptation. The results, presented in Table 1, show that the relatively minute mandibular gland produces more effect than any other part of the body, no matter how large. No attempt has been made to determine the extreme distance over which the contents of a single gland can act; the experiments described here suggest that it it not less than five centimeters at room temperature (26° C).

TABLE 1

LOCATION OF OLFACTORY ALARM RELEASERS IN
Pogonomyrmex badius WORKER

Body part	Percentage of positive responses	Intensity of effect	Delay in onset of effect (range in secs.)	Duration of effect (range in secs.)	Duration of effect (M±s.e.)
entire head	100%	moderate to high	3-13	15-150	50.7±17.6
entire body minus head	30%	very low	4-8	10-15	13.3±1.4
mandible plus mandibular gland	100%	moderate	4-9	10-40	28.0±2.3
mandible alone	0	—	—	—	—
lateral half of head minus mandible and mandibular gland	0	—	—	—	—

Table 1. The effect on resting groups of workers of volatile substances artificially released from various body parts by crushing. Each selected part was separately crushed between two pieces of glass and then quickly exposed at a point four to five centimeters above groups of resting workers collected just outside the nest entrance. The results given in this table come from ten replications of the experiment. The lag in onset of behavior was measured to the nearest second, the duration of effect to the nearest five seconds. In the case of a negative response, the crushed material was held in position one minute before being withdrawn. In the course of dissection it was found expedient to leave the mandibular gland attached to the mandible in order to preserve the contents of the reservoir intact. Further explanation in text.

The above observations show that the mandibular gland secretion from a single worker is adequate of itself to release alarm behavior. The social excitation waves characterizing alarm behavior in *Pogonomyrmex badius* are evidently propagated by means of excited workers exposing other workers to the secretion as they dash outward in their looping movements. Since the active component of the secretion is highly volatile, mass excitation tends quickly to die down when the primary external stimulus is removed. Finally, it is interesting to note that workers suddenly killed by predators under natural conditions are still capable of producing the alarm effect, since their secretion will be released when the head is crushed. One is reminded of the observation made commonly by students of ants (e.g., Carthy, 1951; Sudd, 1957) that crushed workers induce alarm or avoidance behavior in their nestmates. In the case of *Pogonomyrmex badius*, this effect can be ascribed specifically to the mandibular gland secretion.

The Release of Digging Behavior by the Mandibular Gland Secretion

During the experiments described in the preceeding section, it was discovered that workers exposed several times in rapid succession to mandibular gland secretion frequently began to show digging behavior. The complex motor activity involved appeared to be identical in all respects to normal digging behavior observed during "nest work", except that it tended to be undirected, i.e., unrelated to any particular topographic feature, and hence inconsequential in results. Excavation started in this fashion furthermore involved little interaction among workers, it ceased when the exposure to the secretion ceased, and it was not followed up by later nest work. No attempt was made to determine the primary causation of the behavior. At least two explanations seem possible: (1) prolonged exposure to the secretion induced the behavior directly, (2) the behavior was a physiological by-product of a prolonged state of excitement caused by exposure.

One is tempted to refer to the seemingly functionless digging behavior as a "displacement activity", in the sense employed by vertebrate ethologists (Tinbergen, 1951). It arises out of what can properly be called a conflict situation, during which workers become highly excited but encounter no object against which aggressiveness can be released. However, it should be noted that such behavior may well be functional under certain conditions. Experiments with substitute chemical agents, described in the next section, show that the digging becomes directional when the stimulus is confined to a single locus. It is probable that a worker buried by a cave-in will release mandibular-gland secretion; this becomes virtually certain if the cave-in is caused by the intrusion of some larger animal. As a result, it can be predicted that excavation following a major disturbance of the nest will tend to be directed toward those parts of the nest where workers are trapped. This hypothesis remains to be proven experimentally.

The Effects of Alien Chemical Stimuli

Apparently a wide variety of relatively volatile chemical agents are capable of inducing behavior patterns similar or identical to those released by the mandibular gland secretion. When groups of workers were allowed to come into direct contact with small amounts of formic acid, ethylamine, *n*-butyric acid or *n*-caproic acid absorbed in one- centimeter-square pieces of filter paper, they responded immediately with alarm behavior and in time with digging behavior. Further, the digging was concentrated around the paper squares. The ants made no attempt to remove the squares but instead tended to dig shallow trenches around them. When triethanolamine, ammonium sulfide, phenol, and oleic acid were tested in the same way, the ants either showed no reaction or (in the case of oleic acid) removed the paper square to the refuse pile of the foraging arena. When ethylamine and *n*-butyric acid were allowed to evaporate in the near vicinity of resting ants, so that these substances could be detected only by olfaction, the ants again responded with alarm and digging behavior. But in this case the intensity of the behavior was distinctly less than that following direct contact with the absorbed chemicals. It was also significantly less than that following exposure to comparable amounts of the evaporated mandibular-gland secretion.

Summary

The secretion of the mandibular gland of the myrmicine ant *Pogonomyrmex badius* (Latreille) contains an unidentified component that acts as a releaser of both alarm and digging behavior. This substance is highly volatile, so that the contents of a single mandibular gland reservoir can act through the air over at least five centimeters; at 26° C alarm behavior was effected over this distance within four to nine seconds under the experimental conditions used. Highly excited workers discharge the secretion during the characteristic looping movements of alarm behavior and in so doing tend to set up waves of excitement that spread among other workers through the nest galleries and over the nest surface. Prolonged exposure to the secretion induces characteristic digging behavior, which may be directional if the stimulus is confined to a single locus. The hypothesis is advanced that directional digging thus induced functions at least in part to expedite "rescue" work following nest cave-ins. Similar alarm and digging behavior can be induced through the air by some other relatively volatile agents, e.g., formic acid, *n*-butyric acid, and ethylamine.

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