proximately the same when the order of the addition is altered or the impalements are carried out after the additions.

Figure 1B shows a fast-sweep oscilloscope trace of an impalement in the presence of succinate. The rate of increase in potential is very rapid (about 1 msec), consistent with the rapid advance of the electrode and the absence of a decay. Also, this rate of increase is consistent with the theoretical expectations from microelectrodes with a sharp taper (*17*). The membrane potentials are independent of the resistance of the electrodes used (and hence tip diameter and electrode taper), suggesting that these measurements are not the result of the leakage of salt from the electrode tip. The mean potentials measured in 30 impalements under identical conditions (1 m*M* KCl, 10 m*M* tris, 0.3 osmolal sucrose, *p*H 7.4, with the potential recorded within 4 seconds) were 16.3 mv. The standard deviation from this value was ± 0.9 mv, although the electrode resistances varied from 10 to about 80 megohm. The constancy of the recorded potentials with time (for example, compare A and B in Fig. 1) also supports the notion that diffusion of electrolyte from the microelectrode tip does not play a significant role in the measured potential.

We have developed an assay to measure the accumulation of calcium phosphate under the conditions of massive loading described by Greenawalt *et al.* (*18*) and, hence, the transducing ability. The accumulation is detected with quantitative interference microscopy. The measurements were made with a ×40 objective and matching condenser (numerical aperture, 0.65) (Jamin-Lebedeff system, Zeiss) according to the deSenarmont method of compensation (*19*). We made measurements by eye to the point of maximum darkness (extinction) for the mitochondria and calculated the optical path difference as described by Forer and Goldman (*20*). The results were consistent with an increase in mitochondrial dry mass of 10.6 ± 0.9 percent ($N = 15$) for one experiment and 12.9 ± 0.8 percent ($N = 22$) in another, under conditions facilitating calcium phosphate accumulation. These mitochondria show a granulation with an apparent formation of small granular inclusions as seen with differential interference optics after Nomarski. This response requires both succinate and adenosine triphosphate. In our experiments, this response is blocked by antimycin A or oligomycin.

The mitochondria are still viable after impalement since they can undergo these characteristic changes (see Fig. 2). The potential does not change during the accumulation (*21*).

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## Weaver Ants: Social Establishment and Maintenance of Territory

*Abstract.* *Workers of the African weaver ant* Oecophylla longinoda *recruit nestmates to previously unoccupied space by means of odor trails laid from the rectal gland, a hitherto unrecognized musculated organ located at the rear of the rectal sac. When enemy ants and other intruders are encountered on the territory, the* Oecophylla *assemble nestmates into small resting clusters by dispensing an attractant-arrestant pheromone from the sternal gland, a second newly discovered organ located on the last abdominal sternite. Under prolonged stress, additional forces are recruited to the combat area with the aid of the rectal-gland trail substance.*

The weaver ant genus *Oecophylla* consists of two living species, *O. longinoda* of tropical Africa and *O. smaragdina* of southeastern Asia and Melanesia. These insects are renowned for their habit of constructing arboreal nests out of leaves bound together with larval silk. The workers hold small larvae in their mandibles and move them back and forth between the leaf margins like shuttles. Weaver ants are also exceptionally abundant, aggressive, and territorial, a circumstance that makes them of significance in tropical forest ecology and agriculture (*1*). We report here the discovery of a remarkably complex communication system by which *O. longinoda* workers acquire and subsequently control new territorial space. The ants engage in two modes of recruitment, during which they

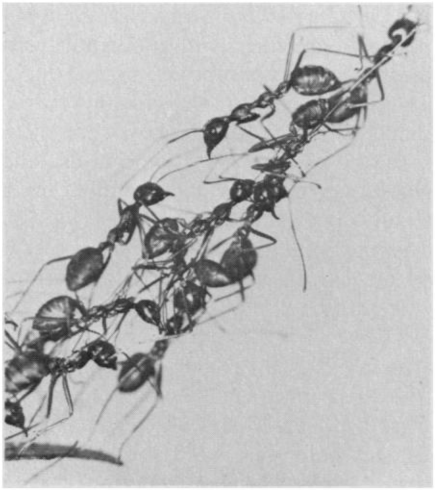

Fig. 1. Workers of the weaver ant *Oecophylla longinoda* form living bridges by linking their bodies into chains. The worker seen running over the upper portion of this bridge is laying an odor trail from her everted rectal gland directly onto the bodies of her nestmates. The trail will guide other members of the colony to a newly available foraging space.

dispense pheromones from two previously unreported exocrine glands.

When colonies of *O. longinoda* are transferred from the field and confined to potted citrus and fig trees in the laboratory (*2*), the major workers patrol the available surrounding space restlessly. If a large object is placed near the nest tree, groups of workers, orienting visually, mass on the nearest twig or branch and attempt to reach the object by forming living bridges with their bodies. If they succeed, those crossing over begin to lay trails back and forth across the new space. Many return all the way to the nest, and while so doing lay trails directly across the bodies of nestmates making the living bridge (Fig. 1). When a trail-layer encounters a nestmate, she often greets her with a tactile signal. The signal is quite variable, ranging in intensity from antennation of the recipient's body to a back-and-forth waggling of her body against that of the other ant. The combination of the chemical and tactile signals (but not the chemical trail alone) excites workers and induces them to move outward along the trail. This mode of communication, which we have termed long-range recruitment, results in an outpouring of additional workers onto the fresh space. Long-range recruitment is also directed to food sources and territorial enemies, although in these contexts it differs in certain details of the tactile signal and locomotory behavior. Recruitment to new space is virtually identical to recruitment during emigration, when a colony moves from a poor to a superior nest site.

Trail-laying is achieved by an eversion of what we propose to call the rectal gland (*3*). This organ is a musculated invagination of the lower rear surface of the rectal sac (Fig. 2). In order to lay a trail the ant lowers her abdomen, rotates the terminal segment downward, and extrudes the rectal gland. The gland is then dragged lightly over the substratum, apparently resting on a "sled" composed of two pairs of long bristles that lead back from the upper edge of the acidopore. In an attempt to identify the origin of the trail substance, we prepared ether extracts of the following body parts: rectal gland, remainder of hindgut, sternal gland, Dufour's gland, poison gland, and all remaining parts of the abdomen. The extracts were then used to constitute artificial trails drawn from baits of honey water at the base of the nest tree outward over the surface of a foraging arena (*4*). Weak-to-moderate, short-lived following was elicited by the preparations of sternal and poison glands. Because the behavior had aggressive components, including raising of the abdomen, opening of the mandibles, and rapid directed movement, we interpreted the result to be mostly or entirely a response to alarm pheromones in the two glands. In contrast, trails composed of rectal-gland extract induced prolonged following by much larger numbers of ants, which oriented in a calm manner indistinguishable from that displayed by ants traveling on natural odor trails. Preparations made from the remainder of the abdomen caused no perceptible reaction. The differences in response to the various organs were consistent during five replications employing two colonies. It was concluded that the trail pheromone used in long-range recruitment originates in the rectal gland and is dispensed when the ant everts the gland and drags it over the substratum.

A second form of communication, previously unrecorded in social insects, is referred to loosely as *short-range recruitment*. When workers encounter alien *Oecophylla* workers or other kinds of insects too large for them to seize and hold on the spot, they chase the intruders through distances of 15 cm or more while dragging the end of the abdomen (but not the anus or acidopore) over the ground. This response is entirely different from ordinary trail-laying employed during recruitment to new terrain and food discoveries. The ant's movements are rapid and jerky, of the kind usually associated with alarm. In contrast, nearby workers

Table 1. Clumping of *Oecophylla longinoda* workers after the introduction of five African tree ants (*Polyrhachis militaris*) into an arena patrolled by *Oecophylla* workers. The numbers reflect the changing pattern of spatial distribution of the *Oecophylla* over an array of 93 quadrats, 10 by 10 cm (*5*).

| Time (min) | Total number of ants | Mean number per quadrat | Variance | Variance/ mean | Spatial pattern (clumping) |
|---|---|---|---|---|---|
| 0 | 86 | 0.925 | 1.575 | 1.703 | Weak |
| 5 | 90 | 0.968 | 1.558 | 1.610 | Weak |
| 10 | 77 | 0.828 | 1.411 | 1.704 | Weak |
| 20 | 74 | 0.796 | 1.152 | 1.447 | Weak |
| Polyrhachis *introduced at 25 minutes* | | | | | |
| 30 | 87 | 0.935 | 4.039 | 4.320 | Moderate |
| 35 | 96 | 1.032 | 3.429 | 3.323 | Moderate |
| 40 | 108 | 1.161 | 4.673 | 4.025 | Moderate |
| 45 | 103 | 1.108 | 3.085 | 2.784 | Moderate |
| 50 | 123 | 1.322 | 3.960 | 2.995 | Moderate |
| 55 | 88 | 0.946 | 3.771 | 3.986 | Moderate |

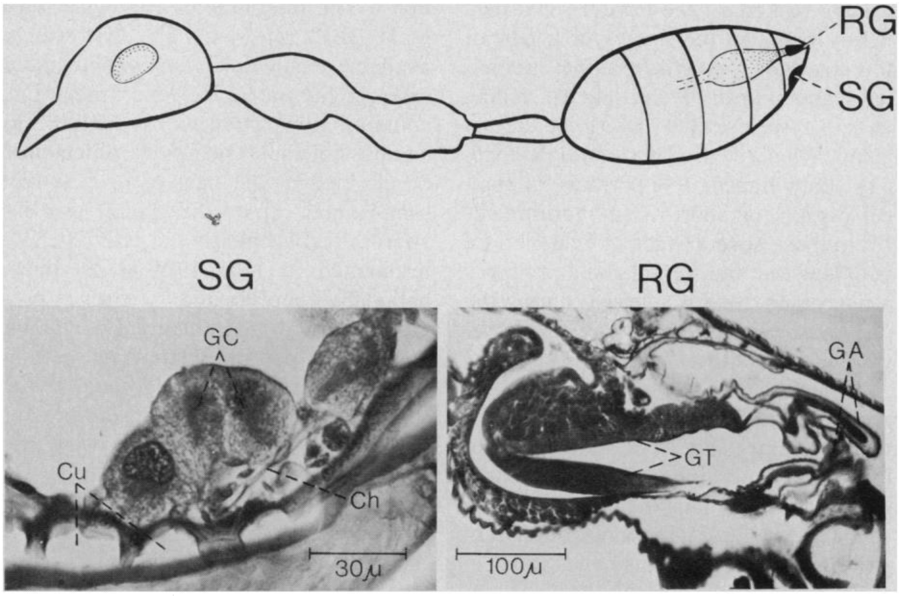

Fig. 2. The two newly discovered exocrine glands of *O. longinoda* are depicted in this diagram of a major worker. The lower photographs show longitudinal sections of the glands. The sternal gland (*SG*) consists of cells (*GC*) lining the inner wall of the terminal abdominal sternite; they are connected by intracellular channels (*Ch*) to outer cups (*Cu*) in which the pheromone accumulates. The rectal gland (*RG*) is an infolding of the rectal wall that includes glandular tissue (*GT*) and an eversible gland applicator (*GA*).

respond in a relatively calm manner. They are attracted over distances of up to 10 cm to the area where the display occurred and tend to settle there in loose clusters. The result is a change in the overall spatial pattern of *Oecophylla* workers in those portions of the territory through which the intruders move, from random or weakly clumped distributions to moderately or strongly clumped distributions (*5*). An example is given in Table 1. In laboratory trials clusters of workers were able to retain and subdue invaders in much shorter periods of time than were single defenders.

Because short-term recruitment involves touching the substratum with a portion of the abdomen anterior to the anus and acidopore, with no sign of an extrusion of the rectal gland, we searched for another pheromone source farther along the ventral abdominal surface. And indeed a promising new gland was discovered near the center of the last abdominal sternite. This structure, which we call the sternal gland, is illustrated in Fig. 2. When preparations of the gland (*4*) amounting to approximately one-gland equivalent each were placed in dummies of folded filter paper and presented to *Oecophylla* on their territories, the ants responded in a manner indistinguishable from that attending natural short-range recruitment. Similar preparations of poison glands and Dufour's gland induced aggressive attraction, which was not followed by clustering in the manner observed during short-range recruitment (*7*). When *Oecophylla* workers are picked off the territory and held lightly between the fingers or a pair of forceps, they rotate the terminal abdominal segment upward exposing the shining cuticular surface that covers the sternal gland. When released back onto the territory, they immediately perform the typical display of short-range recruitment. From these several lines of evidence we conclude that the sternal gland produces a pheromone that is released during the display and induces the workers to aggregate into small local clusters.

When foraging *Oecophylla* workers encounter intruders repeatedly at short intervals, some shift from short-range to long-range recruitment, laying rectal-gland odor trails back to the nest. The result is the gradual increase of worker density on the territory, also illustrated in the data of Table 1. This increase, enhanced by local clustering caused by continued short-range recruitment, results in a greatly increased rate of capture of the intruders.

The use of pheromones in the establishment and exploitation of colonial territories is only part of a remarkably complex system of recruitment behavior in *O. longinoda*. In fact, our current studies suggest that communication in this species may be the most elaborate yet to be recognized in ants as a whole (*8*).

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2. The *O. longinoda* colonies were collected from several localities in Kenya, mostly in the vicinity of Mombasa. Each colony was maintained on a tree surrounded by a moat of mineral oil and from time to time was given access by bridges to foraging areas 70 by 140 cm in extent.
3. The newly discovered rectal gland of *O. longinoda* is not to be confused with the rectal pads and rectal papillae that occur in ants and most other insects. These organs are entirely different in form and serve in the resorption of water.
4. Body parts from 10 to 30 major workers were placed in 0.5 ml of ether and chilled for an hour or longer; the number of parts was kept constant for a given replication. Artificial trails were drawn with hardwood applicator sticks for 40 cm over a paper surface, and the number of workers following for half this distance was recorded during four or more successive 5-minute intervals.
5. The spatial arrangement of *Oecophylla* workers was defined as either random or clumped by estimating, through the chi-square test taken to the 95 percent confidence level, the fit of their distribution to a Poisson distribution. In a series of more than ten such tests, with one or the other of four species of insects as invaders, the arrangement invariably shifted from random or weakly clumped to a more strongly clumped distribution (Table 1).
6. So far as we know, no homologs of the rectal gland and the sternal gland have yet been reported in other kinds of ants. S. M. Hammad [*Bull. Soc. Entomol. Egypte* **49**, 133 (1965)] reported a "scent gland" on the terminal sternite of the formicine *Cataglyphis bicolor*, but this structure consists of paired lateral clusters of cells evidently distinct from the *Oecophylla* gland. The sternal gland of *Oecophylla* is also different in location, structure, and function from the sternal gland of termites.
7. The mediation of aggressive alarm in *O. longinoda* by pheromones in the poison and Dufour's glands was previously reported by J. W. S. Bradshaw, R. Baker, and P. E. Howse [*Nature (London)* **258**, 230 (1975) and *Symposium of the International Union for the Study of Social Insects, Dijon* (1975), p. 61]. The same authors further discovered that a mixture of mandibular gland pheromones (hexenal, 1-hexanol, 2-butyl-2-octenal) induces aggressive alarm.
8. More detailed accounts of territorial and other forms of behavior involving recruitment in *O. longinoda* are being prepared for publication. We thank H. Engel for making the histological preparations and other technical aid, T. Hölldobler for Fig. 2, and K. Horton and R. Sekulic for collecting the live colonies of *Oecophylla*. The research has been supported by NSF grants BMS 75-06447 and BNS 73-00889. This article is dedicated to the memory of Alfred E. Emerson, eminent student of the social insects, who died 3 October 1976, in his 80th year.

14 October 1976

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## The Biome Programs: Evaluating an Experiment

The article by Mitchell *et al.* (*1*) reporting the results of the Battelle, Columbus Laboratories, analysis of three of the five biome studies in the U.S. contribution to the International Biological Program (IBP) represents the first widely available evaluation of these integrated research programs. However, the article contains some ambiguities, limitations, and possible misconceptions which must be clarified in the light of its potential significance. First, the timing was inappropriate. Although the IBP officially terminated in June 1974 as an internationally coordinated scientific program, the National Science Foundation (NSF) has continued to fund certain biome programs for an additional 3-year synthesis period. Therefore, the (potentially) most important results were not available at the time of the study.

Second, the evaluation is based on incomplete data. The analysis does not consider almost 500 internal reports, takes no account of the interbiome and international aspects of the program, and attempts to evaluate management effectiveness based on limited access to information on the decision-making process.

The third limitation is that, for purposes of the Battelle study, a simplified view of the programs was adopted. This can be paraphrased as follows: the biome program planners intended to produce an ecosystem model; projects were chosen to provide data to the model; data were to be submitted in uniform format to a computerized data bank which would produce model parameters; the parameterized model would then be of sufficient accuracy to be immediately useful for resource management. The authors conclude that the Eastern Deciduous Forest Biome program (EDFB) failed to meet these objectives. This is not surprising, since EDFB never adopted such simplistic goals. Nowhere in the IBP biome planning statements or project plans does the explicit goal of the biome programs, *to analyze ecosystems*, appear.

Further, we cannot agree that technical problems of mathematics or computer programming were limiting factors. Modelers now have the skills to translate biological understanding into the shorthand of mathematics, but the science of ecology simply does not possess a sufficient understanding of processes at the ecosystem level. The real heart of the matter lies in our understanding of the