Feeding and Digestion in Some Ants
(*Veromessor* and *Manica*)

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Ants are among the most fascinating creatures to observe, whether one is a zoologist, botanist, psychologist, or curious child. Geologically speaking, ants are quite ancient. More than 100 million years ago they were already in existence in societies. After man, they have the most complex social organization, their food habits are among the most varied in the animal kingdom, and together with rodents, they present the greatest potential threat to the hegemony of man on earth. In the following account we want to record what happened when a botanist met with two myrmecologists and jointly watched ants; a harvester ant (*Veromessor*) in the southwestern deserts and montane ants (*Manica*) in the Nevada mountain forests.

The harvester ant *Veromessor pergandei* (Mayr) lives almost entirely on seeds and other plant parts which it collects and brings to its underground nest. One finds the nests of this ant almost anywhere in our hot deserts, except where excessive salinity excludes plant growth. But wherever plants appear, be it only *Allenrolfea occidentalis* (Wats.) Kuntze, the ink-weed, or *Atriplex confertifolia* (Torr. & Frém.) Wats., the salt bush, this harvester ant occurs.

The following information about *Veromessor* was gathered mostly in Death Valley, in the immediate surroundings of our mobile laboratories, which, from early 1967 on, were stationed each winter and spring at the north end of Death Valley National Monument, in a side valley near Grapevine Ranger Station, at an altitude of 800 m in the *Larrea tridentata–Franseria dumosa–Atriplex hymenelytra* vegetation.

Except for foraging and the removal of sand and waste from the nest, which occupies them at most a few hours each

day, these harvester ants live entirely underground in their extensive nests. These nests consist of wide corridors sloping downwards, and of horizontal 0.5-1.0 cm high nest chambers. We have not yet excavated a complete nest, but the chambers reach into the permanently moist lower soil layers where the temperature is practically constant the year around. On cool winter days any foraging is done during midday; when in spring and summer the midday air temperatures reach 30 C and above and the ground surface becomes even warmer in the sun, foraging is restricted to a few early morning and later afternoon hours, starting in or lasting into darkness. Therefore, these ants live an air-conditioned life, never are exposed to extremes in temperatures, and stay in a dry atmosphere for only short periods; even in a dry desert soil, at some depth the relative humidity remains high throughout the year.

Observing a nest near our laboratory trailer in Death Valley, it was found that each day the direction of the food-gathering column of workers was shifted clockwise about 15°. In such a column the worker ants continued in closed ranks with no scouting along the edge, fanning out only in the last 10 m of journey. Since most workers returning to the nest carried a seed, fruit, flower stem or other object of prospective food value, an ant continued in the collecting column until she found a "usable" object and then immediately returned.

The foragers go out and bring in almost anything: sticks, leaf segments, good and empty seeds, dead insects, petals, moth wings, mouse and reptile droppings. These foraging workers are probably conditioned by smell as to what they bring to the nest. Tevis (1958) found that most workers of one nest of harvesters on a particular day brought in *Plantago;* they brought not only seeds (which are usable), but also leaf segments, dry flowers, stems, peduncles − all of *Plantago*. Therefore anything which smelled like *Plantago*

was brought to the nest on that particular day. But he also found that 0.5-21.5% of the ants returning from a foraging foray carried inedible objects. On other days they brought *Geraea,* the desert sunflower. Then he found not only the large seeds, but also yellow segments of the corolla, moving towards the nest in the mandibles of the foragers. This is perhaps not so remarkable when this behavior is compared with that of bees, in which the workers from one hive may collect just clover nectar, or sage nectar, or orange nectar; other foragers are informed concerning the kind of plant by the odor of the returning foragers.

Foraging Columns

Usually during the middle of the desert winter, i.e., in December and January, there was little activity around harvester nests. During the middle of the day some ants might carry out sand from a new entrance of an old nest, but we did not see workers move out in dense columns to collect seeds. This harvesting started in February and March. After a cold night there was no activity beyond the nest crater until the sun warmed the ground. Then a column of ants left the nest at a very slow pace, which quickened as the temperature rose. They all moved in the same direction and kept that direction regardless of the terrain, whether there were any seeds or other plant parts to be collected, whether the ground was rocky or sandy. In one case a column travelled 40 m over an asphalt road, finally reaching a gravel pit where there was collectable food. Only when very large boulders were in the way did the column become deflected, but beyond the boulder it resumed the original direction. Creighton (1953) reported that the foraging column needed sunlight to orient itself and that a patch of shade of more than half a meter length caused many of the foragers to break out of the column and wander aimlessly about. In Deep Canyon we placed a

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metal-walled trap across a foraging column, hoping to learn what each ant was bringing back to the nest. The workers went from the nest as far as the shadow cast by the wall, stopped and milled around. The next day they had made numerous new entrances outside our trap and continued seed-hunting without having to go through dense shade.

In the case of our harvester, the direction of the column was apparently also determined internally as was the width of the outgoing column. Sometime in the darkness (when the night was warm) or after sunrise (on cool mornings), we saw the early stages of column formation. It was then a solid ribbon of ants of all sizes (majors, medias and minors) all outward bound in the same direction and at the same speed. There were no scouts preceding the column, nor were there any before the column formed. This differs greatly from the food gathering of some other ants, where, once a scout has located a food source, she marks a backtrail, which is then followed by a horde of workers.

In *Veromessor* the column remained a coherent rank about 5 cm wide until the collecting ground was reached 15-50 m from the nest. This coherence was probably due to lack of interference; the emerging column being much more compact than an older column, where going and returning ants seemed to be in continuous collisions since there was no left or right hand traffic. In an older column each returning ant carried an object proportionate to its size. Majors carried material matching, and occasionally exceeding, their body weight; minors carried much smaller particles such as individual *Oenothera* seeds.

To judge the number of ants in this *Veromessor* nest, we estimated the number which were working above ground. At 0700 daylight time on 14 June 1971, with a temperature in the shade of 29 C, there were about 200 ants working inside the nest crater. The column of harvesters, going in a northeasterly direction on a mountain slope, was 40 m long, with about 400 ants per meter of column. This amounted to about 15,000 ants, since the end of the column widened and thinned out. The other column, much wider, went along the bottom of the canyon in an easterly direction, but was only 20 m long. Since there were about 1000 ants per m in this column, a total of 20,000 ants were harvesting there. This meant that in the

early morning 35,200 ants, all from the same nest, were working above ground at the same time. Therefore the total nest population was probably 50,000 ants. This nest was many years old, since last year's nest crater was of about the same size as this year's (see Fig. 1). There are larger nests, but most are smaller. The above is only an estimate; yet it gives us some information about the total biomass of these ants in the desert. A minor worker weighed about 2 mg, whereas a major weighed about 10 mg. This meant that all ants in this nest weighed about 250 g or half a pound. Per hectare, this amounts to several kilograms. For the same area we have a figure of 63 kangaroo rants (*Dipodomys*) and pocket mice (*Perognathus*) per hectare, which amounts to about the same total biomass. Larger animals (birds, rabbits, foxes and coyotes) are rather scarce and their biomass per hectare is less.

Lizards, living off other animals, are scarce, with a biomass of a fraction of a kilogram per hectare. And the soil microanimals such as mites and *Collembola*, which live on litter and are not frequent under dry desert conditions, have a biomass less than 1% of that of the ants.

These figures fit the general picture of the food pyramid. The primary consumers (ants and small rodents) each have about the same biomass, 2-10 kg/ha. The secondary consumers; lizards, birds, foxes and coyotes have a combined biomass of less than 10% of the primary consumers. And there are no tertiary consumers, such as mountain lions in our area.

Underground Activities

Thus far we have only reported on the above-ground activities of *Veromessor*. Since they do not eat outside the nest, and since they spend 80-90% of their time underground, the picture just presented concerns only a small fraction of their activities. The rockiness of most of the Death Valley soils prevented us from making extensive excavations of nests, and the dryness of the soil made it impossible to unearth intact nest chambers. Threfore the major conclusions about nest-life of *Veromessor* have to be drawn from indirect evidence.

Apparently *Veromessor* does not drink liquid water. It occurs in deserts without waterholes. When water was available, the workers were never ob-

served to use it as bees do. They were not attracted by sugar water, or sweet pulpy fruits, nor did they ever collect honey, nor were they found near sugar secretions from aphids or leafhoppers like honey ants. Their food collecting was restricted to dry to green seeds (Fig. 2), fruits and dry petals, dry stems, rodent or reptile droppings and to a limited extent dead insects. This was deduced both from what workers brought towards the nest and from their refuse dumps.

Veromessor nests are completely below ground, i.e., they do not build a mound, usually have one main opening surrounded by a crater, with sometimes subsidiary openings or craters within a perimeter of several meters. The crater shape is produced because all sand they dig out of the nest is neatly stacked at an angle of about 18° around the nest opening. This sand was carried out by the workers to or beyond the rim of the crater; one never saw a sand grain roll back into the nest because the angle of repose of the sand is about twice the angle of the crater wall.

Early in the season only sand grains were carried out and very carefully fitted on top of the crater wall between the other sand grains, giving the crater considerable solidity and preventing the wind from blowing the grains away. Besides, the sand carried out was not of uniform size like the grains of dunes, and large as well as small grains were mixed together. Whereas the sand was deposited evenly around the nest opening, the refuse was carried beyond to one side of the crater. This was not determined by the prevailing wind since it reversed regularly over a 24 hour period. Even strong winds did not blow the refuse away, because most of the fruits and seeds harvested were spiny or hairy. These spines and hairs bound the refuse heap into a coherent mass, which soon became further consolidated by the hyphae of fungi developing on this organic medium. Thus a 1-year old refuse heap from a *Veromessor* nest could sometimes be pulled off like a thick blanket, which was easily broken into separate segments, yet had an amazing integrity. The separation of sand crater and organic refuse may be a historical accident, because during the first stage of crater building, during the first month of activity in January and February, mainly sand was dug from the nest, whereas seed collecting was most active in the later months of the year,

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after the winter annuals had finished their life cycle.

The organic matter around the crater of a harvester nest consisted of everything that was brought in by foragers and what was not used in the nest, or what had been used and was of no further importance to the ants. The bulk was formed by fruits, fruit coats, seed coats, tiny twigs, and leaves, in other words, what was left after the usable seeds had been extracted. We see therefore two entirely different activities of workers; foraging, which is not particularly selective, and seed extraction, which requires a high degree of selectivity.

The workers inside the harvester nest did a most remarkable job. In the first place they removed the seeds from the burs or fruits. This was done by cutting them, and in different nests different cutting methods were used. In one nest, the involucres of *Chorizanthe brevicornu* Torr. were cut at the base and a flap of the involucre was then pulled off to extract the seed, very much as a banana peel is pulled off. In other nests, the involucre was cut all around to expose the seed. Comparable differences were found in dealing with the burs of *Franseria*, or the involucres of *Chorizanthe rigida* (Torr.) T & G. which become very woody and very hard to cut. These differences between nest actions suggest that the method of cutting fruits and burs may be modified by learning.

Whereas the foraging workers are apparently guided by smell alone, the nest workers were far more discriminating. They selected usable seeds from useless leaf or stem segments, the latter being discarded. But far more remarkable was their ability to distinguish good from empty burs of *Franseria*. The latter were discarded and were found intact on the refuse heap, suggesting that they did not need to be opened to determine whether the seeds were edible. The good burs were cut open at either end and the one or two seeds were exposed without being extracted.

When the nest workers were cleaning seed, this seemed for quite some time their sole occupation, for the workers brought out only chaff, i.e., no sand. An occasional mouse dropping was included in the rubbish, and unusable sticks and leaf fragments were discarded too, but everything thrown out was organic.

In older nests part of the refuse carried out by the workers was entirely different; a mixture of sand grains and coherent masses of finely comminuted organic matter, which we will call ant pellets (Figs. 3-5). This refuse was so matted together that most of the components could not be recognized, but they seemed to be chewed plant tissues. Usually, however, many contorted seed coats were present, apparently of chewed seeds. The whole mass clung together and sometimes hyphae could be seen between the particles. These hyphae were usually thick, colorless, phycomycetous, very different from the dark-colored mycelia found in other litter and soils.

These pellets resemble the discarded portions of the fungus cultures of *Atta* nests, and one might ask, whether these harvester ants may also have fungus cultures. This one might conclude from their harvesting behavior, for, in addition to seeds, petals, flowerbuds and other soft plant parts are brought to the nest by the foragers. Sometimes about half of all material brought into the nest was such soft tissue, but it was usually dry. Recognizable flower parts were petals of *Larrea, Geraea, Nama, Phacelia* and disc flowers of composites, stamens of *Larrea*, and unopened flowerbuds of *Larrea*. Since none of these petals could be recognized in the refuse dumps, they must be used in the nest. We suspect that they might be the major component of the ant pellets and this means that either they were eaten or that they were digested by fungi. If they were eaten by adult ants, they would have to be far more comminuted to pass through the digestive tract. Eisner and Happ (1962) reported that *Componotus pennsylvanicus* (DeGeer), a much larger ant, rejected particles over 100 μ in diameter. We found particles about 25 by 60 μ in the content of the midgut in *Veromessor*. Larvae can swallow much larger particles, but they do not excrete solid wastes, which remain in the larval stomach as the meconium. Therefore, digestion by fungi is likely since these pellets were usually tightly tied together by hyphae, as was the soil of the floor of the nest chambers. These fungi were quite different from the common soil and litter fungi of the desert, which all have dark-olive mycelia, either sterile, or belonging to *Ulocladium* (with dictyospores) or *Phoma* and *Coleophoma* (with pycnidia). From the floor of chambers from a *Veromessor* nest they were *Rhizopus, Mucor* or *Penicillium* (Fig. 6) and from ant pellets they were

different species of *Penicillium,* or light brown sterile mycelia.

In Table 1, the distribution of the various fungi from different Death Valley sources is presented. It is based on over 150 isolations of fungi, of which 142 produced pure cultures. Of these more than half (80) were sterile mycelia, seemingly related to *Ulocladium* and *Phoma,* and if we include the latter two genera, over 100 out of 142 were slow-growing brown, dark olive or black mycelia, able to break down organic litter. Only 25 out of 142 mycelia were fast growing, best adapted to nutrient-rich media, the types we are best acquainted with in our human environment. In the litter and soil they seemed to be accidental infections, but in ant pellets and in the walls of the ant nest chambers they predominated, and the slow-growing dark mycelia occurred because the basic pellet and soil material contained them. The fast growing mycelia were apparently present due to the activities of the ants.

Components of Refuse Dumps

We learned much more from the refuse dumps of the *Veromessor* nests. Depending on where the nests were located, the major components of the chaff were:

A. Nests in washes, away from canyon slopes
1. *Franseria dumosa* Gray, burs
2. *Hymenoclea salsola* T. & G., burs
3. *Atriplex hymenelytra* (Torr.) Wats., fruiting bracts
4. *Larrea divaricata* Cav., nutlets
5. Seed coats of annuals like *Mohavea breviflora* Cov., *Cryptanthe* sp., *Eriogonum trichopes* Torr., etc.

B. Nests near canyon slopes
1. *Chorizanthe rigida,* lignified involucres
2. *Chorizanthe brevicornu,* involucres with attached stem
3. Seed coats of annuals like *Cryptanthe, Eriogonum reniforme* Torr. & Frém.

In the case of *Chorizanthe rigida* both freshly ripened and one- or two-year-old involucres were collected. They become lignified, like root and stem, just before the death of this annual plant, and the single seed in each woody and spiny involucre is permanently
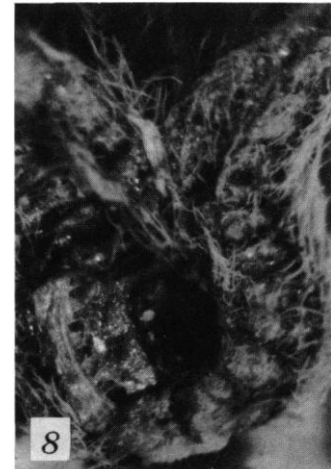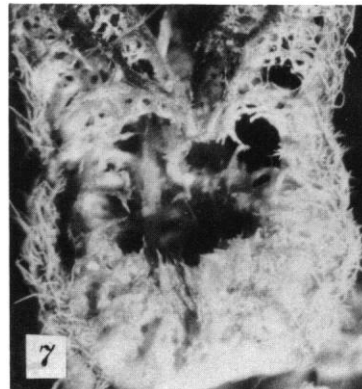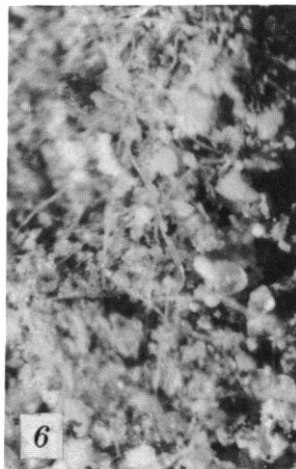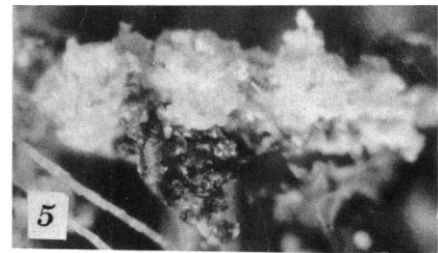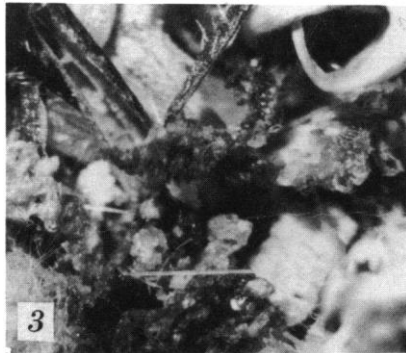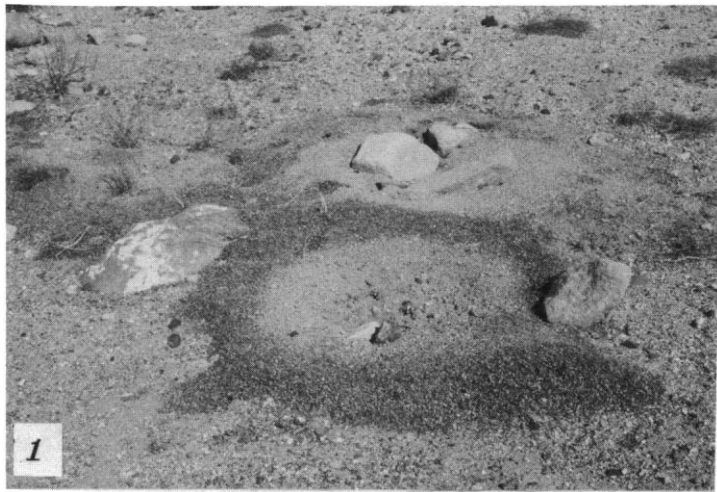
Fig. 1. Nest of *Veromessor pergandei* showing well developed new craters with distinct refuse dumps nearly encircling the craters at the left and center front (crest 65 x 75 cm). Immediately behind the front crater is an older abandoned crater with the refuse becoming indistinct. Fig. 2. *V. pergandei* cutting open fruits of *Oenothera clavaeformis* Torr. & Frem. and removing the immature seeds. Natural size. Figs. 3 and 4. "Ant pellets" showing sand grains and seed coats clinging together, X20. Fig. 5. An ant pellet of finely macerated material, X30. Fig. 6. Material from floor of chamber 38 cm below ground level in *Veromessor* nest in Death Valley. Note numerous hyphae, X36. Fig. 7. *Chorizanthe rigida* one-year-old involucre from refuse dump of *Veromessor*, X20. Fig. 8. *Chorizanthe rigida* from *Veromessor* refuse dump with left hand nutlet coated with partially dissolved cell material, X20.

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enclosed. Only in the course of years, as the woody tissues decompose through fungal activity, can the freed seeds germinate. This happens usually in or near the mother plant, although the woody involucres may become detached from the mother plant before they themselves are sufficiently decomposed to allow germination of the seed. The harvester ants seemed to collect mostly the detached involucres. In the nest they were then opened by lifting one side of the involucre after cutting the exceedingly tough vascular bundles. The nutlet inside was removed and the involucre was carried outside the nest (Fig. 7, a 1-year-old involucre). In the case of fresh seeds the nutlet was digested after cutting a hole in the involucre (as suggested in Fig. 8, where the inside of the nutlet is coated with only partially dissolved cell material).

In *Chorizanthe brevicornu* the plant fragments collected by the foragers consist of internodes, each carrying apically a cylindrical involucre. One side of the involucre was cut away, or in other nessts the involucre was slit lengthwise, to remove the seed. Then in practically every case the cortex of the upper portion of the stem was cut open, and a strip of bark was pulled off over a distance of a few millimeters, baring the brilliantly white pith. This was either eaten or chewed out (we found pieces of this pith in the refuse dumps occasionally). In many cases the exposed surface of this pith was overgrown by a coarse mycelium (*Rhizopus?*) which ceased growing once the internodes were dumped outside the nest (Fig. 9).

Both *Franseria dumosa* and *Hymenoclea salsola* are Compositae of the Ambrosieae tribe, and have their 1 or 2 achenes enclosed in a stone-hard mature bur of a size easily carried by major workers. Inside the nest one end of the bur was cut off, exposing the achenes, which were never removed from the bur. By a digestive process the embryo was dissolved out of the achene, leaving the black achene coat enclosed in the bur. After solution of the embryo the empty bur was ejected from the nest.

In a few cases burs were ejected before the seeds were completely digested and this made it possible to deduce how the digestion took place. The embryo had dissolved in an irregular pattern, the remains having a very smooth surface, consisting of a layer of macerated intact cells. This suggests that a protopectinase (presumably produced

by the ants) was involved in dissolving the middle lamellae.

Several tests were carried out. In all cases burs of *Franseria* and *Hymenoclea* were cut open crosswise. When placed in a moist chamber (in petri dishes on pure agar) both ends of the embryo started to swell and the cut surface remained ivory-colored. After 2 days at 15 C embryos and cotyledons had completely emerged from the bur halves. On some of the cut surfaces liquid was squeezed from the gaster of living workers of *Veromessor*. These surfaces became dark-brown (Figs. 10 and 11) and the embryos and cotyledons did not enlarge. After 2 days at 15 C the cut surface of the cotyledons was soft, and could be smeared on a slide. It was found to consist of detached rounded cells with more or fewer oil droplets, apparently freed from cells which had burst. Figures 14 and 15 show such macerated cotyledonar tissue of *Hymenoclea*, and Figure 16 the same of *Franseria*.

In another test the liquid squeezed from a *Veromessor* gaster preserved in alcohol was used; this caused darkening of the embryo cut surface, but no softening of the tissue. The liquid from the gaster of neither *Veromessor smithi* (Fig. 12) nor of *V. lobognathus* (Fig. 13) caused softening of the cotyledons of either *Franseria dumosa* or *Hymenoclea salsola*.

These tests allow us to draw the conclusions that (1) *Veromessor pergandei* workers produced a substance which darkened the cells of the embryo of *Franseria* and *Hymenoclea* and prevented them from swelling or germinating. (2) *Veromessor* workers produced an enzyme which acted as a

protopectinase and macerated embryonic tissue of *Franseria* and *Hymenoclea*. (3) *V. smithi* and *V. lobognathus* did not produce observable amounts of this enzyme; they are harvesters living in areas outside the range of *Franseria dumosa* and *Hymenoclea*. (4) The size of the head and mandibles of the workers of *Veromessor* (minimum width 1.0 mm) is such that they could not possibly cut up the seeds of *Franseria* or *Hymenoclea* inside the burs (maximum seed width at the cut surface 0.8 mm). (5) Neither could they extract the softened embryonic tissues from the seeds inside the bur because their heads cannot be inserted in the seed chamber. (6) Physically there is only one possibility for the ants to remove the softened embryonic tissue. The larvae have a narrow snout-like head (maximum diameter 0.3 mm), which could be inserted into the bur; with their mouth parts they could then remove the softened embryo.

Ant Nutrition

When we consider the above facts, some curious questions arise about ant nutrition, especially the nutrition of *Veromessor*. The larvae have wide enough digestive passages to ingest solid food, and much of their huge abdomens is filled with stomach. In contrast, an adult ant has a very slender esophagus and very small proventricular opening, which do not — and could not possibly — pass solid food larger than starch grains to the crop and stomach. Adult ants are long-lived and very active. Therefore they must eat a lot, but they can ingest mainly liquids. They have

TABLE 1. Fungi isolated from ant pellets, walls of ant chambers, desert soil and desert litter.

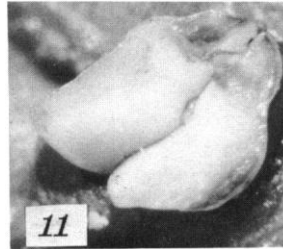|		Ant pellets	Ant chambers	Desert soil	Desert litter
Dark mycelia	Sterile	6 (35%)	2 (12%)	6 (17%)	51 (68%)
	Ulocladium	2 (12%)	1 (6%)	10 (28%)	10 (13%)
	Phoma, Coleophoma }	4 (24%)		3 (10%)	6 (8%)
Light mycelia	Sterile			8 (23%)	7 (10%)
	Aspergillus Penicillium }	5 (29%)	7 (44%)	4 (12%)	1 (1%)
	Phycomycetes		5 (32%)	3 (10%)	
	Actinomycetes		1 (6%)		

Fig. 9. *Chorizanthe brevicornu* stem and involucre from refuse of *Veromessor*. Mycelium can be seen on the surface, X30. Fig. 10. Cut surfaces of *Franseria* cotyledons on which the liquid from living *V. pergandei* gaster had been spread, X8. Note the dissolved surfaces. Fig. 11. The cotyledons of *Hymenoclea* one day after treatment with liquid from the gaster of *V. smithi*, X15. Only a slight darkening has occurred.

powerful mandibles which can pierce and chew fruits and seeds, but they have only a small external cavity, the infrabuccal pocket, in which they can keep solid food. Therefore a general consideration makes us question, what these mature ants really eat.

There are ants which live off liquid food, such as:

1) The honey ants. They collect nectar, e.g., *Myrmecocystus*. In Deep Canyon they can be seen to go from nectary to nectary of *Euphorbia setiloba* Engelm. and *E. polycarpa* Benth. to imbibe the liquid secretions. In the nest the workers can be seen to regurgitate the nectar they have collected to the "repletes," or honey-pots, which hang lethargically from the walls or ceiling of the nest chambers, and whose abdomens are monstrously swollen with the nectar they have ingested. This nectar is thus stored, apparently aseptically, in these repletes and is available to nest-mates on demand.

2) The aphid milkers. They get a sweet liquid from the anal excretions of aphids.

3) *Manica bradleyi* (W. M. Wheeler) does very little foraging above ground and yet maintains what seem to be populous colonies (Wheeler, G.C., and Jeanette Wheeler, 1970). In the summer of 1966, we suspected that mycorrhizae might be a source of food for these ants

which spend so much time below ground. Soil around the galleries and brood chambers contained dense masses of mycorrhizal roots. (In the soil from nearby nests of *Formica sibylla* W. M. Wheeler we found no such masses.) All attempts to keep a part of a colony (workers and brood) thriving on the soil from the natural nest failed.

In 1969 attempts in the laboratory to feed adults of *M. bradleyi* on litter fungi tagged [1] with ^{22}Na failed because the ants seemed to be annoyed by the fungi and left the culture as quickly as possible. By the time the fungi were ready the larvae of *M. bradleyi* had matured to adults. We therefore substituted *M. hunteri* (W. M. Wheeler) which had larvae. The adult ants again left the fungus culture as quickly as possible. The larvae, however, fed if their mouthparts were placed on the hyphae. After five two-hour feeding periods the larvae showed significant radioactivity. The surprising thing was that the workers which had cared for the larvae but had had no direct contact with the radioactive fungi also showed

[1] Dr. N. Stark, of our Laboratory, prepared the radioactive fungal cultures and Dr. C. Blincoe, Prof. Biochemistry, University of Nevada, Reno, very kindly supplied the radioactive materials and made the counts for us.

considerable radioactivity. We are continuing to work on the food of *M. bradleyi*.

Ishay and Ikan (1968) reported that the workers of *Vespa orientalis* F. fed their larvae on animal protein and that only the larvae could digest the protein. The larvae used part of the protein for their own growth and fed the adults on sugars and amino acids produced from the proteins by gluconeogenesis. This food exchange is called trophallaxis. The above brief experiment with *Manica* suggests that mycorrhizal fungi may be eaten by the larvae only and after digestion fed to the workers. However, one big step is still missing, since we have not been able to find mycorrhizal roots which will attract the workers so that the larvae are brought in contact with the food source.

4) Most ants are known to feed their larvae by regurgitating their own food, in the form of liquid droplets, especially to the very young larvae. Males (who frequently cannot feed themselves), queens and workers beg food from the larvae. In the cases of *Veromessor* and *Manica* the above observations suggest
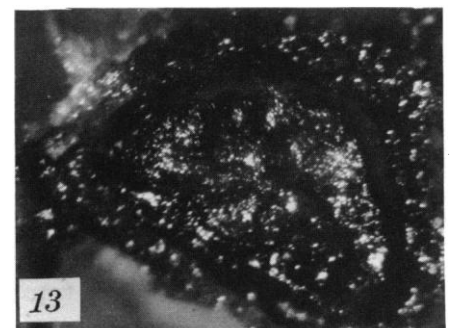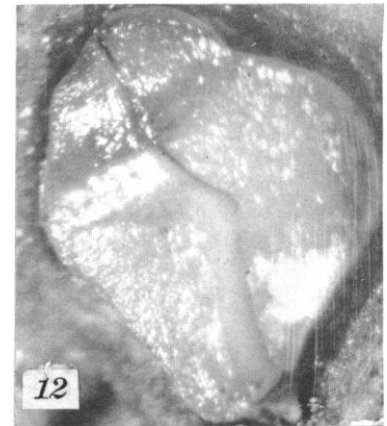

Fig. 12. Untreated cut surface of *Hymenoclea* cotyledons, X30. Fig. 13. One cotyledon of *Franseria* one day after treatment with liquid from the gaster of *V. lobognathus*, X30. The surface is darkened but not swollen.
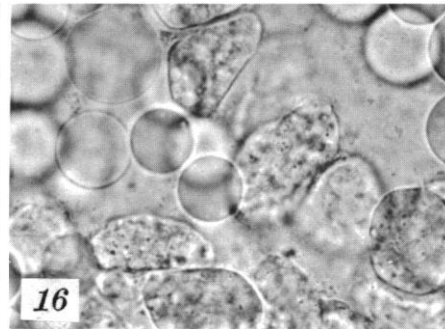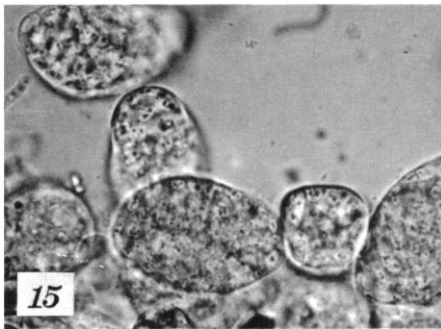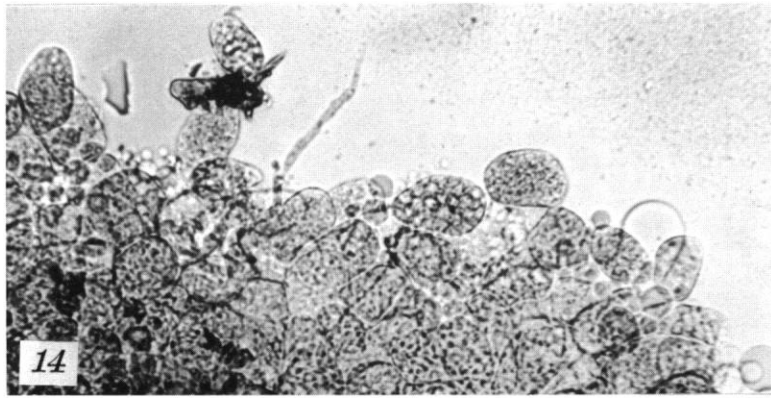
Fig. 14. Macerated cotyledonar tissue from surface of *Hymenoclea* treated with liquid from gaster of living *V. pergandei*, X400. Fig. 15. Same as Fig. 14, at greater magnification to show disassociated cells more clearly, X800. Fig. 16. Macerated cotyledonar tissue of *Franseria* treated with liquid from gaster of living *V. pergandei*, X800. Note oil droplets.

that it was the larvae which did some of the actual feeding, returning — as in the *Vespa orientalis* — digested food to the workers.

Since mature ants cannot ingest solid food, while larvae can, it is possible that the larvae ingest some of the food in *V. pergandei*, *M. bradleyi* and *M. hunteri*, digest it and feed the adults. This would alter considerably our ideas about the relationship of trophallaxis (food exchange) between young and adults. The ancestral ant larvae always had eaten solid food and such is the case with caterpillars. They are able to chew, ingest and digest plant materials, and transmit the excess food as stored material when they transform into butterflies. This of course requires a very large pupal and adult stage, which the ants do not have. We therefore suggest that in some ants (as in the butterflies) the larvae are the real food digestors and energy transformers. In ants the pupal stage is too small to transfer much food energy, particularly since the adult stage may last a year or more. This is very much like the situation in bees or wasps. There, too, the adult stage may last for many months, yet the pupae do not transmit any large amount of stored

food. And both bees and wasps feed as adults, but only on liquid foods, as in ants.

We so completely accept the idea that adult animals feed their young, especially in mammals and birds, that it takes some effort to think any other way. But after all, the number of adult animals which feed their young is very small; the behavior is found only among the two highest groups in the vertebrates. In practically all other animal classes the young do not get more than the reserve food the mother provides in the egg. They have to feed themselves through their whole life cycle up to the stage of sexual maturity; feeding and sexual functions are linked in the same individual.

In many other insects there is also a division of labor between feeding and reproduction. The mature stages of many flying insects do not eat or if they eat at all, their food is liquid and fully digested, such as honey or blood. But the larvae as in butterflies are mostly digestive sacs, in which the food is elaborated. It would be impossible to attach wings and navigational organs to caterpillars and make these digestive sacs take to the air. Therefore the larvae

of these insects digest a large amount of food, which they pass on to the adults in the form of stored food; most of the digestion has occurred in the larval stage.

Conclusion

We now suggest that in the evolution of some ants this process has gone one step further. The larvae are still the digestive sacs, as they are in most other insects. But being social insects, they can transfer the digested food to the adults by regurgitation instead of by body transformation. Thus a truly remarkable division of labor has occurred in these ants; the adults gather food, chew it and prepare it. Then they have it digested by the larvae, which regurgitate part of the elaborated food to their elders. When these ants are moving their larvae, they are just carrying their stomachs around. Therefore some ant colonies may not be able to live without larvae; they would starve to death.

If this general view is correct, one would expect that the larvae of the most primitive ants to be the most complex, whereas those of the most advanced groups of ants would be most nearly reduced to digestive sacs. In the primitive myrmeciines the prey is brought into the nest and scattered among the larvae, who feed themselves. Among the higher ants trophallaxis is common. The digestion of some food by larvae to feed the adults (Wilson, 1971) would certainly increase the importance of the role of trophallaxis and return it to the place which W. M. Wheeler held for it in the life of these social species.

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