The Biology of Honey Ants

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John R. Conway, associate professor of biology at the Univ. of Scranton, Scranton, PA 18510, earned his B.S. in Zoology from Ohio State Univ., his M.A. in Zoology from the Univ. of Colorado and his Ph.D. in Biology from the Univ. of Colorado. Before joining the Scranton faculty in 1985, Conway taught at Elmhurst College (1978–85) and Marycrest College (1976–78). He also was a visiting scientist for the Development of Galapagos and Dinosaur exhibits of the Chicago Academy of Sciences during the summer of 1985. Conway has published articles in many popular and scholarly publications including *Science Digest, Ranger Rick, National Wildlife, New Scientist and National Geographic World*. An excellent photographer (Conway took the photo on the cover of this issue), he has exhibited his work at major museums. During the summer of 1985, Conway co-led a Cincinnati Zoo collecting expedition to Southwestern Research Station in Arizona to bring back a living colony of honey ants for display.

Ants developed from a wasp-like form over 100 million years ago and have since become one of the most successful groups of social insects. They live in colonies containing at least three types of adults: queens, males, and workers. The honey ant is one of the most unusual of the 10,000 or so species of ants that exhibit different lifestyles.

At least six genera of honey ants live in the arid regions of North America, Africa and Australia. In every group, some workers, called "repletes," remain in the nest and act as living storage vessels for the nectar collected (Figure 1).

Figure 1. Repletes of the honey ant, *Myrmecocystus mexicanus*, hanging from the ceiling of a dome-shaped chamber in a nest in Colorado.

Repletes of the North American genus *Myrmecocystus* are of particular interest because they are among the largest in the world. For some years my research has focused on *Myrmecocystus mexicanus hortideorum* McCook. *Myrmecocystus,* the genus name, means "cyst- or sac-like ant," and refers to the swollen replete. The species name, *mexicanus,* refers to the distribution of this ant, which extends from the southwestern U.S. into Mexico. The subspecific name, *hortideorum,* is Latin for the Garden of the Gods, which is a park with spectacular rock formations near Colorado Springs, where Rev. Henry McCook (1882) first described in detail this species of ant about a century ago.

I first learned of this ant at the University of Colorado from my doctoral advisor, Dr. Robert Gregg, a well-known myrmecologist (ant specialist). To learn more about this insect and re-verify McCook's work, I moved to Colorado Springs and spent four years studying this ant in the laboratory and field. Since then many other scientists have studied honey ants and have discovered fascinating new aspects of their biology, such as tournament displays, intraspecific slavery and inhibition of foraging by stone-throwing ants. This article will review findings on this and other species of *Myrmecocystus.*

The Indians of the American Southwest and Mexico considered honey ants a delicacy. The Aztecs, calling the honey ant "*nequazcatl,*" dug them up and nipped off the honey-filled abdomen with their teeth. Mexicans also reportedly pressed repletes and used the "honey" in food, to treat diseases, or fermented it to produce an alcoholic beverage (Curran 1937; De Conconi & Moreno 1979).

Reproductives and the Mating Flight

Honey ants belong to the order of insects called the Hymenoptera. Ants live in colonies made up mainly of female workers. *M. mexicanus* queens resemble oversized workers with wings. The queen of each colony lays eggs that develop into winged males and queens. The male, which is smaller and darker, mates with a queen in the air and dies shortly afterwards. Males have poorly-developed jaws and do not seem to be able to feed themselves, but they do have well-developed eyes to locate a queen, and a complex copulatory apparatus to inseminate her.

Larvae of *M. mexicanus* queens appear in nests approximately ten months prior to the nuptial flight in late July. Queen pupae were unearthed about two months prior to swarming, and alate males and queens were uncovered in a nest about one month before the mating flight (Conway 1980a). Gregg (1963) recorded *M. mexicanus* males and females in colonies about two months prior to the mating flight, and Cazier and Mortenson (1965) reported reproductives of *M. mimicus* Wheeler in colonies five months prior to the nuptial flight.

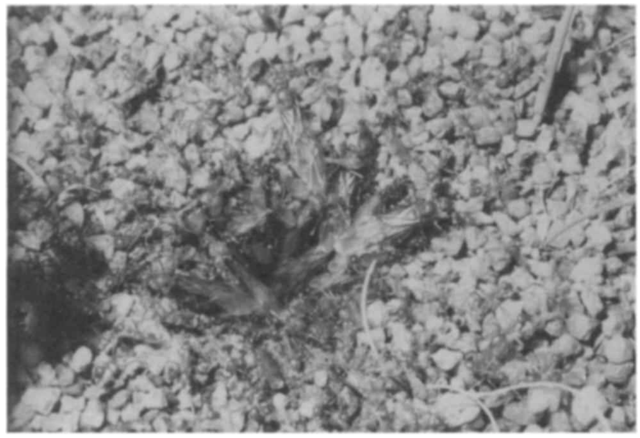

Figure 2. Prenuptial activity at the entrance of a nest of the honey ant, *Myrmecocystus mexicanus,* in Colorado. Note large winged queens and small winged males issuing from the entrance.

Nuptial flights of *M. mexicanus,* occurring in late July or early August in Colorado Springs, seem to follow heavy rains. Pre-nuptial activity begins about dusk when the first few queens peer out the entrance of the nest (Figure 2). The reproductive potential of each colony is high (100-110 males emerging from one nest and 209 queens excavated from another colony). When the queens leave the nest they climb nearby plants or rocks and try to fly. Usually they buzz about the surface unsuccessfully before finally flying away. After mating in the air, the partners drop to the ground. The male dies and the queen tears off her wings, digs a nest chamber (Figure 3), seals it, and begins laying eggs. Usually the queens begin to excavate initial nest chambers within one-half to four hours after the flight, but burrowing may be delayed a day or so. Nest closure begins some two days after the flight (Conway, 1980a).

Founding New Colonies

Initially the founding queen lives off body fat and degenerating wing muscles, and may even consume some of her eggs. The queen cares for the initial worker brood, which subsequently tend the queen and the young, enlarge and open the nest, and go out in search of food. This is called "claustral independent founding," meaning that the queen seals herself in a nest chamber and rears the first brood alone.

Seven dealate *M. mexicanus* queens were captured after their nuptial flights and placed in observation nests. They lived for periods of 181 to 384 days (mean 297.6 days), and during this time larvae were noted eating eggs (Conway 1981). Egg cannibalism (oophagy) is widespread in the social Hymenoptera as queen-laid eggs are sacrificed to feed first-brood larvae (Wilson, 1971).

Figure 3. A *Myrmecocystus mexicanus* queen in the process of excavating and founding a new colony in Colorado after the mating flight. Note that she has removed her wings (dealation).

Adult workers eclosed after 53 to 87 days and the maximum number varied from 5 to 19 depending on the nest. None of the first workers became swollen semi-repletes or repletes (Conway, 1981). Wilson (1971) has noted that first-brood workers are smaller than those of later broods thus favoring more rapid population growth. But in honey ants the smaller workers do not seem to develop into repletes. Workers of *M. mexicanus* began dying 11 to 170 days (mean 67.9 days) after their appearance, indicative of the shorter life span reported for workers of incipient colonies (Wilson 1971).

Bartz and Holldobler (1982) report colony founding in *M. mimicus*, which is quite different from the claustral independent founding in *M. mexicanus*. Nuptial flights of *M. mimicus* near Portal, Arizona were observed after heavy rains in July. Shortly after the nuptial flight, the majority of the nests contained only one queen. But later, when many closed nests were opened, the majority of the nests contained 2-4 queens. The queens were eliminated by workers in each incipient colony until only one remained. Many queens failed to build nest chambers in the vicinity of mature *M. mimicus* colonies because they were killed or driven away by workers of the resident colony.

In laboratory experiments, nests with multiple *M. mimicus* foundresses were considerably more successful in raising workers than solitary queens. Other lab studies showed that the incipient colonies with the largest worker force generally took over the neighboring incipient colonies by raids. One advantage of associating with other queens in colony founding is clear. If females attempt to make the founding effort alone, they cannot produce enough workers quickly enough to engage successfully in inter-colony raiding with mature colonies (Bartz & Holldobler 1982).

Tournaments and Intraspecific Slavery

The discovery of inter-colony raiding during colony foundation helps explain aspects of the phenomenon of intraspecific slavery practiced occasionally by mature *M. mimicus* colonies. *M. mimicus* uses termites as a major food source, but the temporal and spatial distribution of termite galleries is highly unpredictable. Many mature colonies have overlapping foraging grounds and conduct ritualized tournaments in order to defend these spatiotemporal territories (Holldobler & Lumsden 1980).

Opposing *M. mimicus* colonies summon their worker forces to the tournament area using pheromone trails laid by scouts, where hundreds of ants perform stereotyped display fights in which few ants are injured. The largest workers usually perform in the tournaments and the larger workers usually win. Larger workers are produced by more mature colonies. Thus the presence or absence of larger workers on a tournament site can act as a clue to area colony sizes (Lumsden & Holldobler 1983).

Tournaments can last for several days, ceasing only at night when the workers are normally inactive. When one *M. mimicus* colony is stronger and can summon a force of larger workers, the tournaments end quickly and the weaker colony is raided. During these raids, the queen is killed or driven off and the larvae, pupae, callows (newly eclosed workers) and repletes are incorporated into the raiders' nest. This is the first example of intraspecific slavery recorded in ants. Raiding seems to be primarily directed against younger, still-developing colonies in the area. It is hypothesized that tournaments are a mechanism of intercolony communication which opposing colonies use to gauge each other's strength (Holldobler 1976; Holldobler & Lumsden 1980; Lumsden & Holldobler 1983).

Repletes

Whereas honeybees store their nectar in waxen combs, honey ants use living workers, i.e., the repletes. These "honeypots" form when some of the workers hang from the ceilings of specially-constructed domed chambers and are filled by workers with nectar collected each evening from plants. Repletes are some of the largest workers in a *M. mexicanus* colony. When all repletes are removed from a laboratory colony, they are rapidly replaced by the next largest individuals in the colony. By employing the largest individuals in the colony as repletes, the number of workers occupied to provide a given

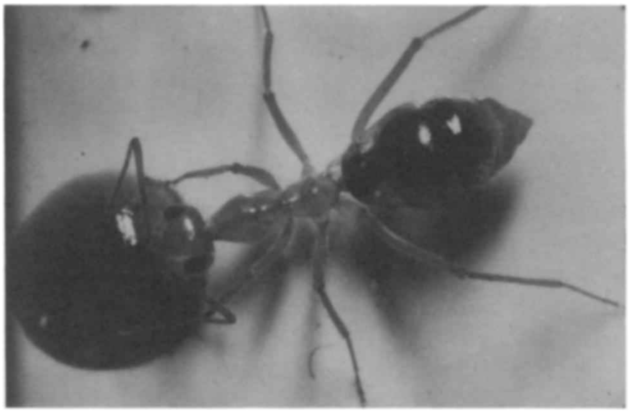

Figure 4. A worker of the honey ant, *Myrmecocystus mexicanus*, drinking colored sugar water in an artificial nest. Note the distension of her abdomen.

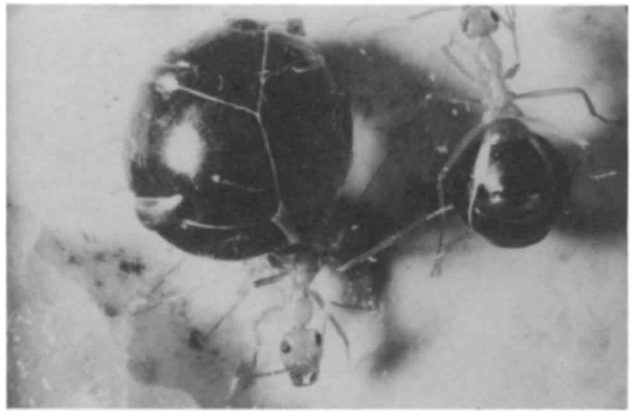

Figure 5. A replete and semi-replete of the honey ant, *Myrmecocystus mexicanus*, produced in an artificial nest given dyed sugar water.

storage volume, and lost from other tasks, can be minimized (Rissing 1984).

As each replete fills, a portion of her digestive tract called the crop, becomes so large that her entire abdomen swells to the size of a small grape, displacing the other abdominal organs. Repletes form within two weeks of emergence. It has been suggested that only young "callow" workers can become repletes since they have more pliable exoskeletons. This is not the case, however, since repletes formed in laboratory colonies lacking callows (Rissing 1984).

To document the role of repletes and the transfer of nectar in the colony, I fed colored sugar water to *M. mexicanus* workers in artificial nests (Figure 4), and watched them develop into blue or red repletes (Figure 5). As repletes are drained of their stores by other members of the colony, they become flaccid depletes, which exhibit twisted abdominal sclerites. Repletes seem to form to store the transient supply of plant nectar produced each summer, thereby guaranteeing a source of carbohydrates to the colony during the winter.

Repletes illustrate the degree of elasticity of the "skin" (membranous areas) of this ant. Normally, the sclerites overlap on a worker's abdomen and no membrane is visible. But in repletes the stretching is so great that the sclerites appear as small islands on a membranous sea. The membrane is composed of an outer epicuticle and inner soft endocuticle. This stretching is possibly attributable to the occurrence of resilin in the endocuticle, recently discovered to be a major constituent of certain elastic hinges and tendons in the cuticle of other insects and arthropods (Varman 1981).

Composition of "Honey"

The crop contents of repletes vary in color in each *M. mexicanus* colony from dark amber to almost clear, but the more transparent ones make up only about four percent of the replete population. An analysis of crop contents from dark amber and clear repletes demonstrated that both are acidic, but the dark "honey" contains more dissolved solids and the sugars are mainly glucose and fructose. This mixture has a taste, smell and coloration similar to cane molasses (Conway 1977). Badger and Korytnyk (1956) identified fructose and glucose (59 percent of the total honey solids) in Australian honey ant repletes of the genus *Melophorus*. Repletes of *Myrmecocystus mexicanus* and *M. mimicus* in Arizona were found to contain sugars in the following proportions: fructose 47-49 percent, glucose 42-44 percent, and maltose 7-8 percent, and the crops of a few (ca. 5 percent) repletes of *M. mexicanus* contained two distinct liquid phases, one carbohydrate and the other lipid (Burgett & Young 1974). The protein content of *M. melliger* Forel "honey" was reported to be 9.45 percent (De Conconi & Moreno 1979).

In the clear *M. mexicanus* repletes, sucrose made up the bulk of the sugar content and there were traces of glucose and fructose. Clear repletes may function primarily as water-storage vesicles, an adaptation well-suited to a semi-arid habitat. Indeed, a large semi-replete was produced in a laboratory colony supplied only with water (Conway 1977). Snelling (1976) also recovered some water-filled repletes from *M. mexicanus* colonies in Arizona and from *M. testaceus* Emery in California.

Nest Architecture

M. mexicanus colonies usually nest on the tops of ridges, mesas or bluffs in the foothills of the Rocky Mountains (Colorado Springs) at elevations of 1,700 to 2,200 meters. The ants enlarge and repair the nest by carrying pebbles and earth out of the large symmetrical entrance, which averages 1.2 cm in diameter, and depositing them on the crater which resembles a miniature volcano (Figure 6). The average crater is 2 cm high and 11.6 cm in base diameter. To keep out winter cold and heavy summer rains, the workers may close the entrance partially or completely with fine earth (Conway 1983a).

The entrance leads into a maze of horizontal passages and small chambers that go down about 20 cm and extend asymmetrically out from the entrance for distances up to 61 cm. The subsurface maze probably serves several functions. It may provide a holding area for workers prior to the mass exodus each evening and for reproductives before the nuptial flight. It may also house a few repletes and guests, such as *Cremastocheilus* beetles (Cazier & Mortenson 1965), and provide a favorable area for rearing brood. A single vertical passage continues straight down from the subsurface labyrinth to domed replete chambers below (Figure 7). The first repletes are usually found in chambers 20 to 35 cm below the surface. Replete chambers nearer the surface are smaller, closer together and more numerous than those found deeper in the nest (Conway 1983a).

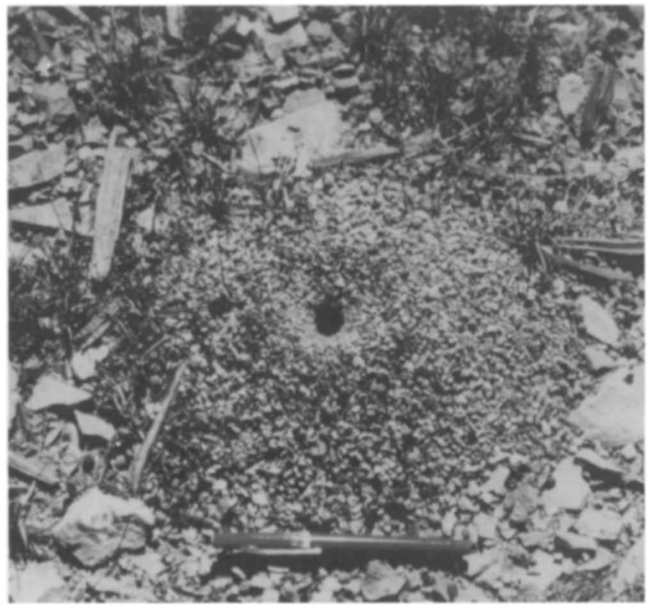

Figure 6. The volcano-like crater around the entrance of a *Myrmecocystus mexicanus* nest in Colorado.

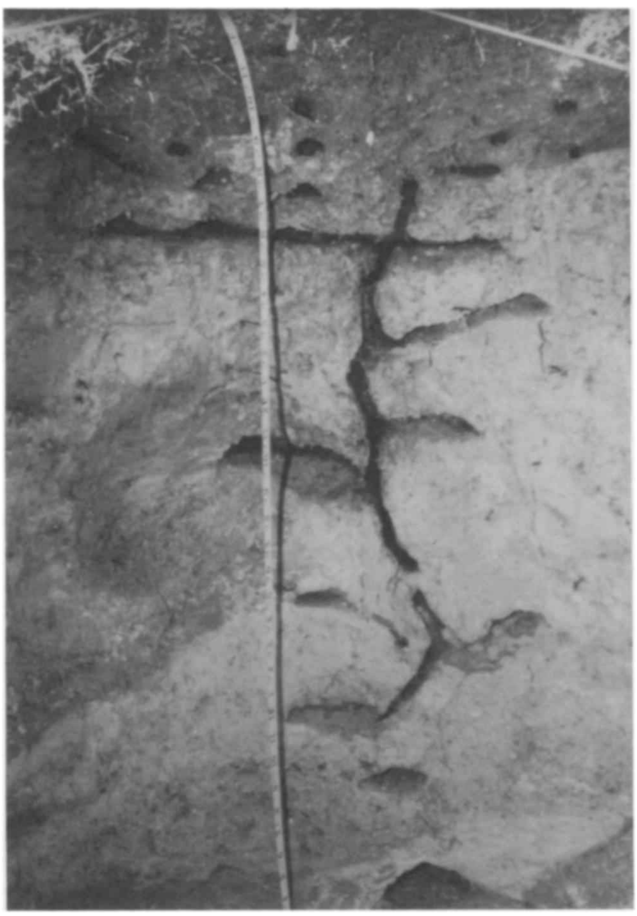

Figure 7. An excavated nest of the honey ant, *Myrmecocystus mexicanus,* showing the subsurface labyrinth of horizontal passages beneath the crater and the single vertical passage leading to the deeper dome-shaped replete chambers.

Chambers are ideally suited for *M. mexicanus* repletes because they provide a rather constant temperature and humidity environment. The chambers are lines with a smooth dark coating that may help keep them intact in loose soil, but the ceilings are arched and left rough, favoring their use for hanging by repletes. Replete chambers vary in size, but may be up to 33 cm long and 5 cm high. The number of chambers containing honeypots in each colony ranges from 7 to 21, and the number of repletes per chamber (n = 40) can vary from one to as many as 348 ($\bar{x}$ = 46). The total number of repletes found in three colonies ranged from 351 to 1,030 ($\bar{x}$ = 729). Two Colorado colonies housed a total of about 5,000 ants, and of these, 22 to 25 percent exhibited some abdominal distension (repletes, semi-repletes and depletes) (Conway 1983a).

M. mexicanus nests in Colorado reach depths of 1 to 1.8 m and are difficult to excavate because the soil contains rocks and layers of caliche (Figure 8) (Conway 1983a). In Arizona, *M. melliger* was reported to have a nest so deep, almost 5 m, that professional grave diggers had to be hired to excavate it (Creighton & Crandall 1954).

Foraging

M. mexicanus is unusual in that it comes out only at night and collects nectar only from yucca plants (*Yucca glauca* Nutt.) (Figure 9) and galls on scrub oaks (*Quercus gambellii* Nutt.). The galls, which are produced by the gall wasp, *Holcaspis perniciosus* (Cynipidae), are found in groups of two or more along the branches of scrub oaks and exude clear sweet droplets (Figure 10), often so abundant that they crystallize to form sugary deposits (Figure 11). The galls and yucca capsules produce droplets only during the summer and eventually dry up and become hard. Occasionally the ants collect "honeydew" by milking aphids feeding on yuccas (Figure 12). After feeding, the workers' abdomens become noticeably distended, and they return to the nest to disgorge their nectar to repletes for storage (Conway 1980b).

Other investigators have reported honey ants feeding on other plants. Cazier and Statham (1962) saw *M. mimicus* feeding on or gathering the pollen and nectar from at least two plants, *Parthenium incanum* H.B.K. and *Euphorbia albomarginate* Englm. Snelling (1976) observed *M. mexicanus* taking juices from bruised or broken fruits, such as those of cacti (*Opuntia* spp.) and also nectar from a wide variety of flowers and extrafloral glands. He believes the ants also derive much nourishment from the exudates of aphids and pseudococcids.

M. mexicanus forages at night in Colorado between March and November at temperatures ranging from 0.6° to 27°C, but collects nectar mainly in June, July and August (Conway 1980b). Kay (1974) reported that *M. mexicanus* did not come out of nests near Las Cruces, New Mexico at temperatures lower than 2°C or above 30°C. She concluded that this species can remain active at much lower temperatures than most desert ants and that its low temperature tolerance probably reflects an adaptation to nocturnal foraging.

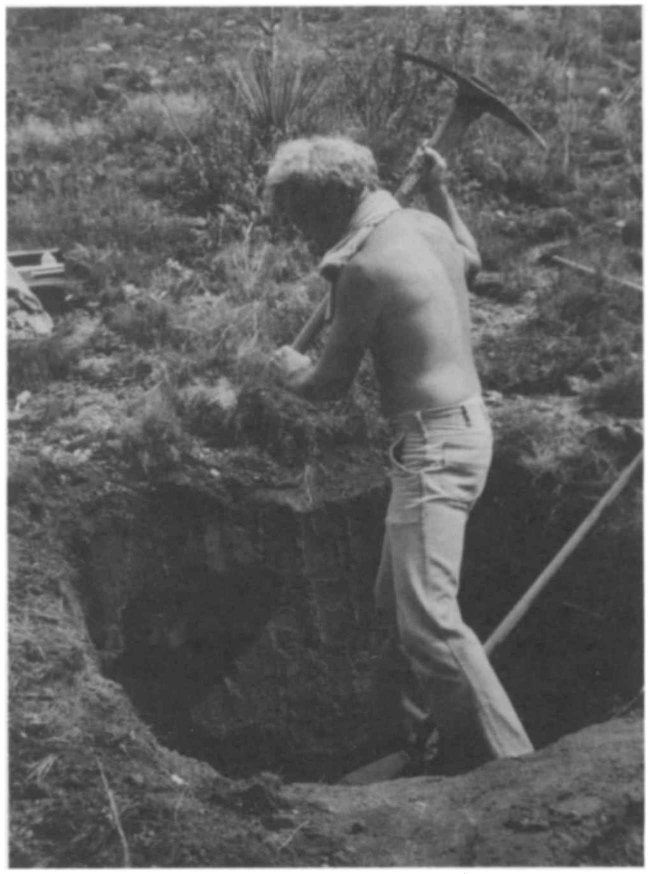

Figure 8. The author excavating a nest of the honey ant, *Myrmecocystus mexicanus*, in Colorado Springs. A pick is necessary due to the caliche and rocks encountered.

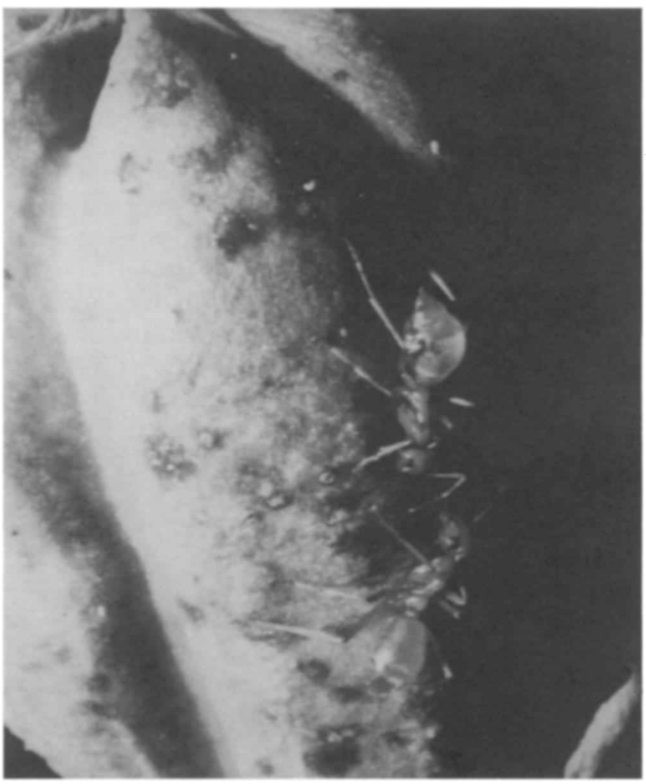

Figure 9. Two *Myrmecocystus mexicanus* workers collecting nectar from yucca capsules (*Yucca glauca* Nutt.) in Colorado. Note their distended abdomens.

M. mexicanus forages as far as 20 meters from the nest and its rate of progression varies from 0.28 to 0.94 m/min. Nests are typically spaced and some distance apart, perhaps minimizing intraspecific competition. Foraging workers utilize both diffuse- and trail-foraging patterns. The diffuse pattern involves radiation of workers in many directions from the nest, and seems to be used to locate dead insects and nectar-bearing plants early in the summer. Once the plants are located, trails to them are used night after night. The nectar season ends in late August (Conway 1980b).

M. mexicanus workers are usually not aggressive and are mainly scavengers on dead insects and arthropods, which they bring back to feed the larvae. But they will attack small, soft-bodied insects or insects too close to the nest. The attacking worker seizes the victim with her mandibles (Figure 13) and swings her abdomen forward between her legs to spray formic acid into the wound (Conway 1980b).

Predation on Honey Ants

Although spiders (*Euryopsis spp.*) are sometimes observed carrying dead workers on scrub oaks, Colorado honey ants appear to have few natural enemies. In Colorado Springs, humans are the honey ant's worst enemy, and many colonies that I have studied have now been destroyed during construction of new homes, roads and restaurants. But biologists in other areas report a variety of predators. Parks (1982) stated that coyotes dug into nests of *M. melliger* in southwestern Texas and Snelling (1976) reported one *M. mexicanus* nest in New Mexico that had possibly been dug out by a coyote.

Chew (1979) noted that the frequency of badger digs into nests of *M. mexicanus* is significantly greater than into nests of *M. dipilis* Forel in southeastern Arizona. One reason might be because badgers forage mainly at night and encounter the workers of the nocturnal *M. mexicanus* more often than those of the diurnal *M. depilis*. The digs go only into the upper part of the hard pan (caliche) and usually do not destroy an entire mature colony. The low rates of predation suggest that honey ants are a minor food source for badgers.

Figure 11. A *Myrmecocystus mexicanus* worker feeding on crystallized gall nectar on scrub oak (*Quercus gambellii* Nutt.) branches in Colorado.

The round-tailed horned lizard *Phrynosoma modestum* of New Mexico remains in the shade of large mesquite during midday and preys on *M. mimicus/depilis* foraging in the canopy and moving across the shaded substrate. Examination of fecal pellets showed that honey ants were the main prey of *P. modestum*. The horned lizard is estimated to take 0.5-1 percent of the total available forager population per day and is obviously removing a significant fraction of the annual worker production. This loss probably has little if any adverse effects on the colonies, since foragers are probably the older, most expendable workers in a colony and have a short life span (Shaffer & Whitford 1981).

Interference Competition

Other ants have developed interesting strategies to interfere with and suppress honey ant foraging. The dolichoderine ant *Conomyrma biocolor* prevents foraging by three species of honey ants (*M. mexicanus, M. mimicus* and *M. depilis*) in southeast Arizona by surrounding and dropping stones into the entrances of the nests. Frequencies of 200 stones or more were observed being dropped by groups of workers during a 5-minute interval. *C. bicolor* appears to be diurnal as well as nocturnal, only ceasing activity during the hotter hours of midday.

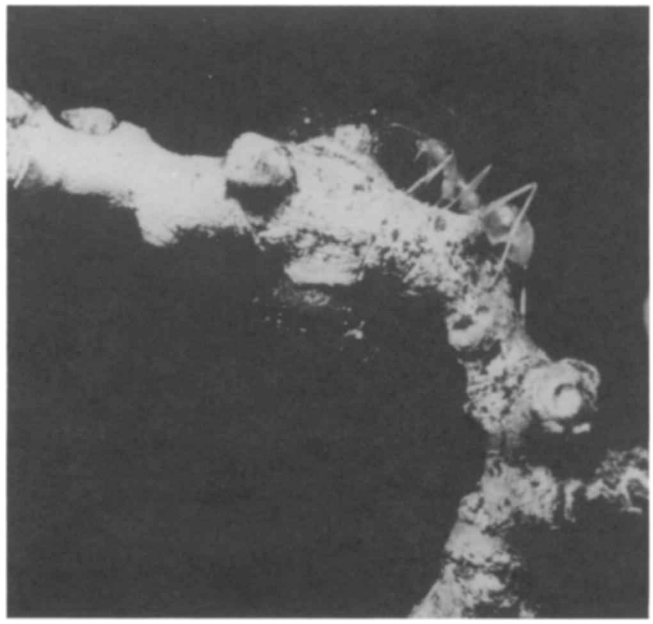

Figure 10. A *Myrmecocystus mexicanus* worker collecting nectar droplets exuding from galls on branches of the scrub oak (*Quercus gambellii* Nutt.) in Colorado.

Studies indicate that interference behavior occurs if the nest entrance of *C. bicolor* is less than 1.5 m from a *Myrmecocystus* colony, but if the distance exceeds 3

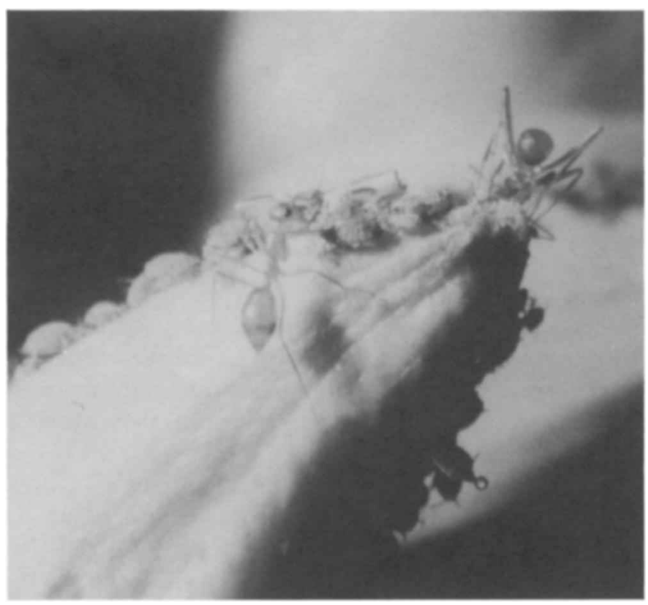

Figure 12. Honey ant workers (*Myrmecocystus mexicanus*) collecting "honeydew" from aphids on yucca capsules in Colorado. Note droplet on the end of the aphid in lower center.

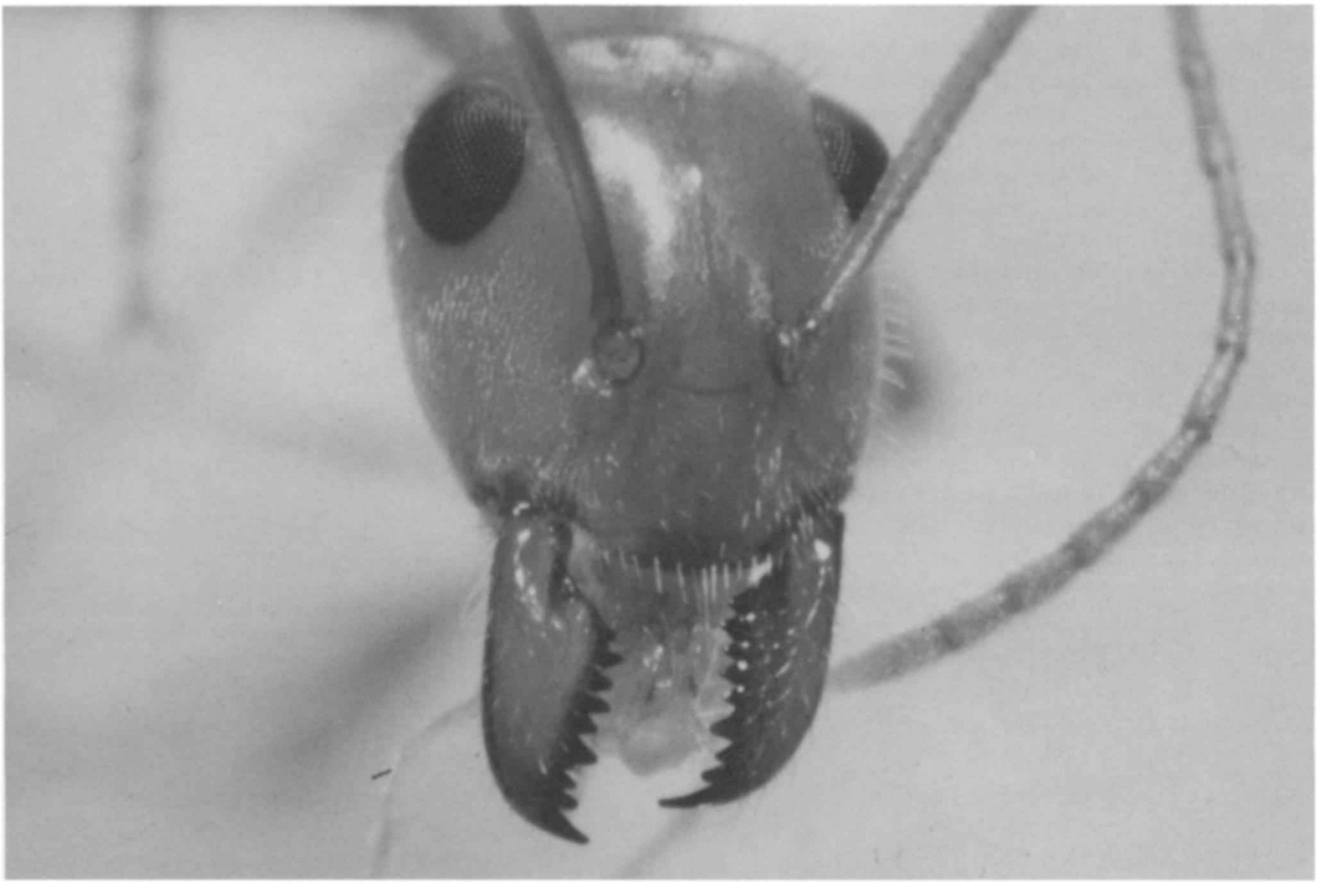

Figure 13. Head of a honey ant worker, *Myrmecocystus mexicanus*, showing the nine-toothed mandibles characteristic of the species.

m, no stone dropping occurs. Besides an overlap in foraging times and nesting areas, *C. bicolor* and honey ants also use the same food sources. Interference competition reduces the foraging of *M. mexicanus* to approximately ⅛ of normal activity. One hypothesis is that stone dropping serves as a signal to reduce the necessity of chemical display and the number of workers needed. If true, then this is the first recognized example in ants where communication signals are produced using an object in the environment, rather than mechanical, acoustical or chemical signals generated by the ant (Moglich & Alpert 1979).

Workers of another dolichoderine, *Iridomyrmex pruinosum* (Roger), perform interference behavior at the nest entrances of *M. mimicus* and *M. depilis* by displaying their raised gasters to the resident ants and discharging a strong-smelling repellant from the pygidial (anal) gland. Surprisingly this strategy works in spite of the fact that a worker of *I. pruinosum* is about four times smaller than a forager of *Myrmecocystus*. The interference at a *Myrmecocystus* nest is most likely to occur if the *I. pruinosum* colony is less than 7 m away. There is a niche overlap between *I. pruinosum* and the honey ants as they are both diurnal and utilize many of the same food resources.

Conclusion

My interests in the comparative biology of these insects has taken me farther afield in recent years. Studies of closely related species of *Myrmecocystus* were begun at the Southwestern Research Station of the American Museum of Natural History in the Chiricahua Mountains of Arizona a couple of years ago and continued when I co-led a Cincinnati Zoo Expedition back to the Station last summer. The primary objective of our expedition was to excavate a living honey ant colony to put on permanent exhibit in the Insectarium at the Cincinnati Zoo. To my knowledge, this will be the first honey ant colony on public display.

In 1984, I traveled to the Outback of Australia to try to locate two species of honey ants, *Camponotus inflatus* and *Melophorus bagoti*. These species have large repletes and represent a striking example of convergent evolution, that is, organisms of different ancestry independently evolving the same solution (repletes) to a common problem (aridity). Some honey ants in Australia are associated with mulga trees (*Acacia aneura*) and are said to get honey either from flower nectaries or the red scale insects that cover the mulgas in spring (Conway 1985).

When I arrived in the Outback I discovered that the only people able to find honey ants were aborigines. So I arranged to camp in the bush near Alice Springs with an aboriginal family. Honey ants are still eaten by the aborigines and are considered sacred in the Dreamtime mythology of some tribes. I was told that aborigines partially dig up a honey ant nest and eat up to 50 repletes at a time before moving on to another nest. In this way they behave like North American predators, by not destroying the colonies and thus conserving a valuable resourse (Conway 1985).

The new findings on honey ants in the United States have contributed greatly to our knowledge of the biology of this group and of ants in general. The paucity of information on Australian honey ants suggests that equally interesting findings await discovery on that continent.

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