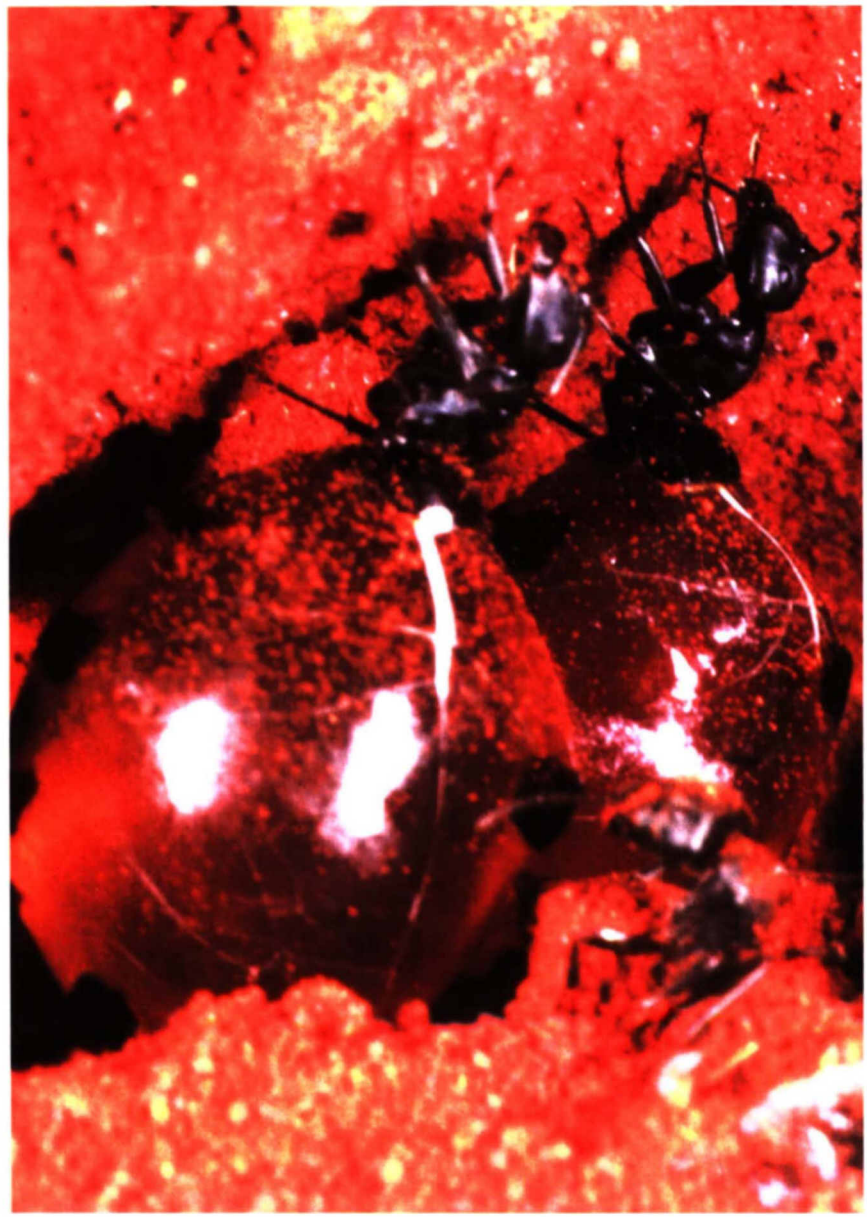
As Earthwatch volunteers sliced open the honey ant nest, they excitedly pointed to a black, wormlike structure protruding from the earth. They had inadvertently exposed the tail of a dormant scorpion (another hazard of our work on the Hamilton Downs cattle station 50 km from Alice Springs in the Northern Territory of Australia) while excavating a colony of honey ants.

Honey Ants

John R. Conway



C. inflatus repletes in nest chambers. Northern Territory, Australia.

Honey ants are similar to honeybees, except they store nectar in swollen workers, called *repletes*, instead of in waxen combs. Repletes form when some workers hang in chambers and are fed nectar collected by other workers.

My work on honey ants began in the 1970s when I studied *Myrmecocystus mexicanus hortideorum* McCook near Colorado Springs, CO. Later, I studied this ant at the Southwestern Research Station near Portal, AZ, and in Australia. Others have also reported on fascinating new aspects of honey ant biology, such as territorial tournaments, intraspecific slavery, and inhibition of honey ant foraging by stone-throwing ants. This article summarizes my work and that of others on these ants.

As stated in my 1991 article, there are several genera of honey ants in the world, but species of the arid lands of Australia (*Camponotus inflatus*) and North America (*Myrmecocystus* spp.) have convergently evolved the largest repletes (Conway 1991). The ability to store nectar may make them less dependent on fluctuating food supplies, especially in arid environments. Repletes store nectar in the crop, a greatly enlarged part of the foregut that fills most of the gaster, and supply other members of the colony during times of scarcity.

There is little information on the biology and ecology of the Australian honey ant C. *inflatus*, first described by Lubbock in 1881. The purpose of the Earthwatch expeditions was to see how closely the evolution of the Australian honey ant had paralleled the American species. In other words, are there similarities in biology, ecology, and morphology of honey ants on the two continents beyond the obvious one of the replete? Also, had there been a convergence in the use of these insects by native peoples in America and Australia? Native Americans of the American Southwest and Mexico considered honey ants a delicacy and would nip off the honey-filled abdomen with their teeth.

Winged queens and winged males leaving *M. mexicanus* nest just before mating flight.

I went to Australia in 1984 to locate honey ants and, after some difficulty, found them with the help of an Aboriginal family near Alice Springs. Although several honey ants are found in Australia, only the large repletes of *C. inflatus* are eaten by Aborigines. In July and August, 1987, I returned with three Earthwatch expeditions to determine nest architecture, density, population size, food sources, foraging patterns, and intra- and interspecific interactions.

One expedition excavated a colony of another honey ant, *Melophorus bagoti* Lubbock, in Alice Springs. This ant is active at high temperatures, but its repletes are only about half as large as those of *C. inflatus* and are more mobile. Aborigines are familiar with this ant, but do not normally eat its repletes. They call it *Ituny ituny.*

Members of another expedition worked with Aboriginal women in Uluru National Park (formerly Ayers Rock) to learn how they locate and excavate nests. An unexpected finding was the discovery of a small nest of a third species of honey ant, *Plagiolepis* sp., adjoining the *C. inflatus* nest we were excavating. The colony was housed in three chambers at depths of 26, 34, and 42 cm, respectively. The population was 246 (114 workers, 96 repletes, 31 semirepletes, and 5 dealated queens). This species has small, turgid repletes whose abdomens are only 2–3.5 mm in diameter.

Honey Ant Habitat

Honey ants on the two continents have different topographical and habitat preferences. *M. mexicanus hortideorum* usually nests on ridge or mesa tops in the foothills of the Colorado Rockies at elevations of 1,677–2,174 m. In Arizona, the nests are at 1,433 m in the foothills of the Chiricahua Mountains. *C. inflatus* nests in Australia were at lower elevations, 683–710 m, on flat plains among mulga trees, *Acacia aneura.* In fact, some nests have entrances 20 cm from mulga trees and passages that extend into the root zones. Mulga seems to be an ideal habitat because the trees provide nectar, insect prey, and shelter from high temperatures and evaporation.

Nest Density

There were 24–26 *C. inflatus* nests in our hectare study site at Hamilton Downs, but the number was difficult to determine with certainty because some were inactive or partially excavated by Aborigines. The minimum distance between active nests was about 5 m.

Population Size

Information on colony size of the two species is scanty but suggests *M. mexicanus* colonies may be somewhat larger. The populations of two *M. mexicanus* nests were 4,968 and 5,029 individuals. The number of repletes found in the colonies ranged from 692 to 1,223. Two *C. inflatus* colonies housed 1,063 and 4,019 ants including 516 and 1,835 repletes, respectively.

Reproductives and Nuptial Activity

I found six wingless queens in one *C. inflatus* nest, but no males. Much more is known about the reproductives and mating behavior of *M. mexicanus,* which has one wingless queen per colony. Mating flights involving winged reproductives occur in Colorado in late July or early August, often after heavy rains. Prenuptial activity begins about dusk

when queens and males peer out the entrance and lasts about an hour and a half. The reproductive potential of each colony is high; up to 112 males and 209 winged queens were found in the nests. When queens leave the nest, they climb nearby plants or rocks to take wing. Initial flights are usually abortive buzzes across the ground, but after a couple of attempts, flight skills are mastered, and they soar high into the air. The smaller, dark male mates with a queen in the air and dies shortly afterwards. Males have well developed compound eyes and three simple ocelli to locate a queen and a complex copulatory apparatus to inseminate her. Following aerial mating, the queen drops to the ground, tears off her wings, excavates a burrow, and seals the entrance about two days later. She overwinters in the burrow, living off body fat and useless wing muscles, and raises workers who will reopen the nest the following spring to search for food. Other species of *Myrmecocystus* may initially have several queens per colony. Mating flights extend the range of the species and may ensure cross-fertilization because many colonies swarm simultaneously. However, the mortality rate for founding queens is high.

To observe postnuptial behavior, I placed seven newly mated dealate (wingless) *M. mexicanus* queens in observation nests. Some of their eggs developed into larvae that cannibalized other eggs for food (oophagy), a widespread practice in social Hymenoptera. The larvae spun cocoons and became pupae from which the first pale workers (callows) eclosed after 53–87 days. These workers did not develop into repletes and are smaller than workers in subsequent broods, which probably promotes rapid population growth. The first workers began dying 11–170 days (mean = 68) after their appearance, which may be indicative of the shorter life span for workers in incipient colonies.

Guests and Parasites

American honey ants are sometimes plagued by parasites and unwanted guests, but none was found in the *C. inflatus* nests. I observed as many as five uropidine mites on the legs of *M. mexicanus* workers and winged queens, and discovered guests, such as *Cremastocheilus* beetles, a small ant-loving cricket, *Myrmecophilia* sp., and collembolans in nests. The voracious beetles, up to 12 per nest, feed on honey ant larvae.

Repletes

The gasters of repletes expand to the size of a marble. The largest *M. mexicanus* replete weighed 0.98 g and had a gaster 12 mm long. Repletes reach somewhat larger sizes in Australia: 1.4 g and a gaster length of 15 mm for *C. inflatus*.

Repletes can develop from workers two weeks after they emerge from pupae, and for a long time it was believed that only young "callow" workers with pliable exoskeletons could become repletes. However, in 1984, Rissing showed that repletes can also form from mature workers.

Repletes illustrate the extreme elasticity of the intersegmental membrane. The membrane's stretchability is from an elastic substance, resilin, which is also found in the cuticle of other insects and arthropods.

American repletes exhibit a range of coloration that may be caused by the storage of different substances. The many dark amber repletes contain primarily glucose and fructose. In clear repletes, making up 0.2–4% of the replete population, sucrose is the main sugar. Evidence that clear repletes may store water was found in one laboratory colony when a large semireplete developed from a worker supplied only with red-dyed water. Milky-colored repletes, which formed 12.4% of the replete population in one Arizona nest, contain high concentrations of protein and lipids and may store fluids from insect prey.

Nest Architecture

Entrances to American and Australian nests differ in size, shape, and number. The *M. mexicanus* entrance is usually a single

M. mexicanus semireplete that developed form a worker in a laboratory nest supplied only with red-dyed water.

round opening, about 1.2 cm in diameter, surrounded by a crater. The average crater is 2 cm high and 11.6 cm in base diameter. Australian nests lack craters and have either a single entrance or multiple entrances in the thatch under mulga trees.

Nests of both species radiate asymmetrically from the entrance, but Australian nests extend farther. Maximum subsurface radiation from a *M. mexicanus* entrance was 63.5 cm, but two *C. inflatus* nests went out 1.8 and 2.4 m. Thus, chambers in Australian nests are scattered over a larger area and radiate from several vertical passages rather than one as in *M. mexicanus*.

The first repletes were encountered at approximately the same depths in both species; namely, 17–61 cm (mean = 40 cm) in *M. mexicanus* and 20–61 cm (mean = 34 cm) in *C. inflatus*. American nests contained 7–21 replete chambers; the two Australian nests had 17 and 66 chambers. American replete chambers are larger, farther apart, and less numerous in the bottom half of the nest.

Profile of *M. mexicanus* nest showing domed replete chambers.

Although the number of repletes per chamber varied greatly in both species, *M. mexicanus* had the largest chambers and the greatest number of repletes per chamber. The number of repletes per chamber varied from 1 to 348 in *M. mexicanus* nests versus from 1 to 191 in *C. inflatus* colonies. The largest *M. mexicanus* chamber was 24 by 24 cm versus 18 by 15 cm for the largest Australian chamber. Maximum chamber heights in both species were about the same, namely 3–5 cm.

Maximum nest depths of the two species are similar. The depths of *M. mexicanus* nests ranged from 1.1–1.8 m (mean = 1.4 m) versus 0.5–1.7 m (mean = 1.1 m) for the Australian nests. Others have reported depths up to 4 m for *M. mexicanus* nests in regions with long, dry summers, and greater depths may be found in Australia as more nests are excavated.

Circadian and Seasonal Activity

The circadian activity of the Australian ant is not clear. We saw honey ants foraging during the day in the winter months of July and August at ground temperatures of 12–30°C, but not at night even though there have been reports of nocturnal activity. Perhaps this ant is diurnal during winter and nocturnal in the hot summer months.

Although there are diurnal and nocturnal American honey ants, *M. mexicanus* is a creature of the night and can remain active at much lower temperatures than most desert ants. In Colorado, *M. mexicanus* forages at temperatures ranging from 0.6–27°C between 17 March and 7 November, but is most active from June to August. Foraging workers use both a diffuse pattern and trails. Workers radiate in many directions from the nest in the diffuse pattern to locate dead insects and nectar-bearing plants early in the summer. Later, semipermanent trails are established to these plants.

Food Sources

Feeding on dead vertebrates is probably uncommon in both species. I once observed Australian honey ants on a Blue tongue lizard (*Tiliqua* sp.) carcass 0.6 m from the nest entrance, and there is one report of *M. mexicanus* feeding on dead rodents in traps in California.

M. mexicanus commonly scours its territory for dead insects and arthropods and occasionally attacks small insects to feed its larvae. Although insectivorous behavior was not observed in the Australian honey ant, Aboriginal women said grubs on mulga leaves, *Muyamuya*, are fed to the larvae. Both species attack intruders or prey in a similar fashion: the worker seizes the victim in her mandibles and swings the gaster forward between her legs to spray formic acid into the wound.

American and Australian species use a variety of nectar sources and may forage on two or more plants simultaneously. I saw Australian ants visiting mulga trees 1.8–9 m from their nests to feed on extrafloral nectaries at the base of the needlelike leaves (phyllodes). Aboriginal women report honey ants also collect nectar from lerp, *Kurku*, black corkwood blossoms, yellow mulga flowers, *Inuntji*, and red *Eremophila latrobei*, *Mintjingka*, flowers. Lerp is produced by a psyllid that secretes a red sugary scale that exudes droplets. Other biologists report honey ants gathering nectar from *Cassia* flowers and Mulga apples (large acacia galls). Foraging is said to be most active after summer rains.

American honey ants also feed on a wide range of nectar–producing plants, but in Colorado they visited green yucca (*Yucca glauca*) capsules and scrub oak (*Quercus gambellii*) galls up to 20 m from the nest. Workers lick exudates off yucca capsules and drink droplets exuding from the red cynipid wasp galls on oak branches. Occasionally they also collect "honeydew" from aphids on yucca capsules.

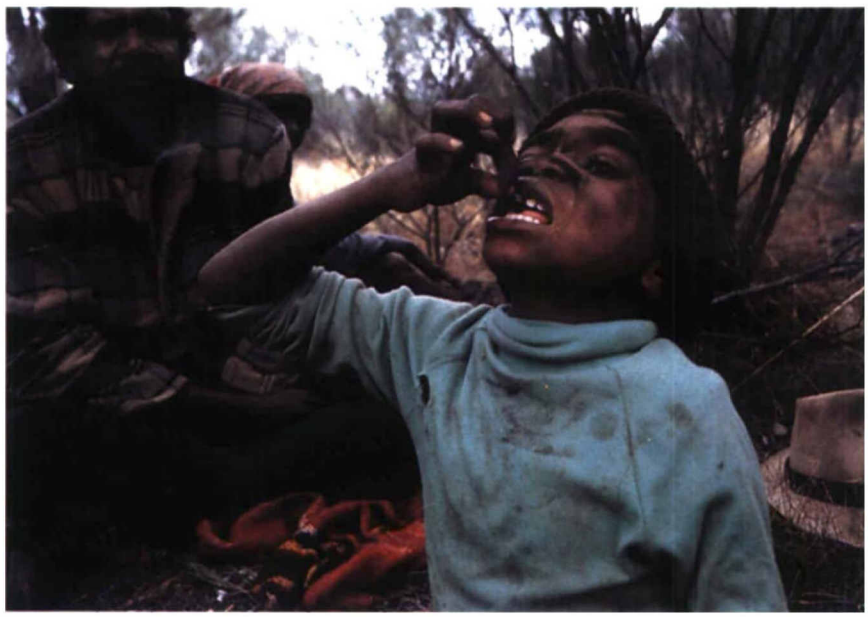
Intraspecific and Interspecific Competition

We observed only one instance of hostility between neighboring *C. inflatus* colonies at Hamilton Downs: a raid from 16 July through 21 July by a large honey ant nest on a smaller one 4.5 m away. The 40 cm square area around the small nest entrance became the scene of frenzied carnage as honey ants and four intruder ant species (two unidentified) fought one another. Formidable large black ants (*Rhytidoponera* sp.) came from nests up to 31 m away to harvest the honey ants. Honey ants also had to fight and spray maurading *Camponotus denticulata* Kirby soldiers from a nest 8.2 m away. They killed some and caused others to lurch away with a drunken–like gait. The raid may have resulted from the establishment of a new honey ant colony in the territory of the larger nest, but since no brood or repletes were removed, it was probably not a slave raid as reported in an American species of honey ant, *M. mimicus* Wheeler. *M. mimicus* feeds on termites, but many colonies have overlapping foraging grounds and conduct ritualized tournaments to defend these territories. When one colony is stronger, the tournament ends and repletes and brood are taken from the weaker colony—the first example of intraspecific slavery in ants.

Both American and Australian honey ants seem to be subordinate competitors in the ant world. Other species chased Australian honey ants away from bee honey placed close to their entrances. *M. mexicanus* is also dominated by other ants, even when the latter are smaller or not as numerous. Sometimes yuccas closest to honey ant nests were monopolized by smaller species, forcing the honey ants to forage on more distant plants. I observed small ants (possibly *Dorymyrmex* sp.) around one Colorado nest on several occasions inhibiting honey ant dispersal. In Arizona, the ant *Conomyrma bicolor* Wheeler prevents *M. mexicanus* from foraging by surrounding the entrance and dropping stones into it. This may be the first example in ants where communication involves an environmental object.

Predators

There seem to be few honey ant predators. *Rhytidoponera* sp. carried off workers from Australian nests. Spiders (*Euryopsis* sp.) occasionally caught *M. mexicanus* workers on scrub oaks in Colorado, and two nests were breached by an animal, probably a badger, *Taxidea taxus* (Schreber), in Arizona. Others have reported predation on *Myrmecocystus* spp. by lizards in New Mexico and California and a nest possibly excavated in New Mexico by a coyote. In Colorado Springs, civilization seems to be the honey ant's worst enemy. Many of the colonies I studied have now been destroyed by new roads and buildings.



Aboriginal boy, eating a *C. inflatus* replete.

Significance of Honey Ants in Aboriginal Culture

Aboriginal women usually locate and dig honey ants, a skill taught to young girls by senior women. Although several Aboriginal uses of repletes have been reported, they are usually eaten singly as a sweet snack.

C. inflatus has a widespread, patchy distribution in Australia and occurs in areas occupied by tribal groups who have several names for this honey ant. *Yerrampe,* the Aranda name, is probably the most common. Aboriginal women at Uluru National Park seemed aware of the castes and life cyle of this ant. They call the workers *Purara* and repletes *Tjala. Panganypa* means little active *Tjala* and probably refers to semirepletes. *Kantilykantilypa* are the babies of workers, possibly the eggs, and *Panganpa* may refer to the pupa.

Aboriginal knowledge of honey ant biology is probably quite accurate in some respects, but not in others. For example, Aborigines seem to know how to find nests and where the ants get nectar, but they seem unclear about how repletes develop, how workers get honey from repletes, and the role of the queen.

Aborigines expend much time and effort digging honey ants. In a one-year study of a group of 22 Aborigines, one investigator estimated 76 excavations involving 80 hours of digging. Quantities of honey retrieved per dig ranged from 45 to 250 g.

We found 26 Aboriginal excavation pits in one hectare at Hamilton Downs. One to three pits were associated with each nest. The pits were 0.09–5.72 m^2 (mean = 1.1) in area and reached depths up to 1 m. Others report digs as deep as 1.8 m and several meters in diameter.

Aborigines have many beliefs associated with honey ants. For example, people are warned to talk softly and avoid whistling when searching for or digging nests because the ants are timid and move away from noise. Some believe the nest extends to the heart of the Earth. Others are afraid to dig too deeply because they believe the queen is a snake at the bottom of the nest. Some Aborigines break a replete against the forehead during excavation to ensure finding many repletes. The bursting action is called *Tjalantananyi.*

Honey ants are important in Aboriginal mythology, or the Dreamtime, and elaborate ceremonies are performed by some tribes to ensure an abundance of honey ants in the future. There are several accounts of honey ant people in central Australia: the Yarumpa, people northwest of Alice Springs; *Purara,* a Pitjantjatjara clan totem in the Western Musgraves; and *Jiramba,* the Aranda honey ant totem at Ljaba. Verses from a Ljaba honey ant song describing the ants in chambers under mulga roots have even been recorded.

Aborigines have depicted honey ants for thousands of years in ground mosaics, cave paintings, and body paintings. Today they are painted on canvas. Most of the art is abstract and geometric with circles, arcs, lines, dots, and animal tracks predominant. Although symbols may have many meanings, those for certain ancestors, such as the honey ant, are widely recognized. One investigator, who studied the art of the Walbiri people at Yuendumu, identified designs depicting parts of the honey ant nest and seated women with digging sticks excavating nests. Today, tourists can buy Aboriginal paintings, T-shirts, and postcards depicting honey ant dreaming. A treasured remembrance of the Australian study is an Aboriginal honey ant painting given to me by Earthwatch volunteers.

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