Notes on the Behavior of Three Species of *Cardiocondyla* in the United States (Hymenoptera: Formicidae)

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Abstract: The behavior, both in the field and in observation nests, of three species of *Cardiocondyla* are described: *C. emeryi* and *C. nuda* were studied in Texas and *C. ectopia* in California. Observations include data on length of immature stages, foraging habits, foods utilized, reactions with other ant species and mating behavior. The data are summarized and compared against observations made by E. O. Wilson on *C. venustula* and *C. emeryi*.

Although the observations presented in this paper are based on a limited number of colonies, we believe that they will substantially augment the habit data now available for three of the five species of *Cardiocondyla* which occur in the United States. When M. R. Smith monographed our representatives of *Cardiocondyla* in 1944, four species were known to occur in the United States, restricted to southern Florida. At that time Dr. Smith opined that subsequent field work would turn up records in other parts of the southern United States. His view has been amply confirmed. The senior author has been able to study colonies of *C. emeryi* Forel and *C. nuda* (Mayr) at La Feria, Texas, and the junior author has studied colonies of *C. ectopia* Snelling at Seal Beach, California. Moreover, the colonies have been favorably placed for continuous observation. It is the lack of continuous observation that has limited previous accounts of the habits of these species. In the many times that *C. emeryi* has been taken in the field, few of these encounters have permitted a protracted study of the colonies. Indeed, in many instances no nest was found and observations were based on the behavior of strays or foragers at food sources. As far as we have been able to determine, no one has attempted to study these tiny ants in observation nests. This is not surprising since they are so small that they are difficult to confine. They can escape through minute apertures and frequently do so. We have been able to study all three species in observation nests. In *emeryi* the observations extended over a period of a year and a half. The observations on the free nests covered a considerably longer period.

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[1] Died 23 July 1973. The sections on *C. emeryi* and *C. nuda* were in unfinished manuscript, completed by the junior author.

Cardiocondyla emeryi Forel

The senior author took stray workers of *emeryi* near La Feria, Texas, as early as 1964, but extensive search failed to reveal the nest. This was particularly frustrating, since it was clear that the nest must be situated in an area that was less than twenty-five feet square. Although this nest was never found, its workers continued to forage for the ensuing three years. At that time the colony either moved to another area or came to an end. Similar difficulties marked the second nest of *emeryi*. In early December of 1970, foragers of *emeryi* were found on a concrete sidewalk in front of the senior author's cottage in La Feria, Texas. The opportunity for observing these foragers could scarcely have been more favorable. They were close at hand and as long as they kept to the sidewalk there was little possibility of losing sight of them. Yet despite daily inspections it was not until nearly two months later that the nest was discovered. The entrance was a tiny, circular opening about one millimeter in diameter in the soil at the edge of the walk. Originally this entrance was completely concealed by a heavy overgrowth of grass. When the nest was excavated, three deälated females and thirty-four workers were secured. These were placed in a small Janet nest for further observation. It later became apparent that only a part of the colony had been taken, for, after a few days, a new nest entrance was opened up and foraging began again. This provided a good opportunity for checking the actions of the captive workers against those of their free nest mates. These observations were continued over a period of eighteen months, for the captive colony proved to be hardy and comparatively easy to handle.

The transfer of the females to the observation nest did not interrupt their egg laying, and subsequent events showed that this proceeds all year long. The egg is a stubby oval, approximately 0.3 mm. long and 0.17 mm. wide. When about to lay an egg, the female turns her abdomen under the thorax until she can touch the tip of it with her mandibles. As a rule the female grasps the egg in her mandibles as it emerges but occasionally the emerging egg will be seized by one of the workers. The eggs, which appear to be unusually sticky, are collected in packets which are often shifted about by the workers.

No attempt was made to maintain the captive colony at a constant temperature, although, for the most part, the temperature ranged between 60°–70°F. The following data are, therefore, mainly useful in showing the relative length of the various stages. Twelve days after the egg is laid the larva emerges. As the larva increases in size, its anterior end becomes more and more bent until finally the mandibles are in close proximity to the swollen ventral body wall. Twenty-three days after the larva has hatched, the meconium is voided and the larva transforms to a pupa four days later. Six days after transformation, the eyes and the mandibular teeth of the pupa begin to show pigmentation, and by the end of two weeks the pigmentation is general. Transformation to the adult occurs a day or two later. As the pigmentation is well advanced by this time, the callow period lasts only a day or two.

The data just presented may be summarized as follows:

Egg to larva	12 days
Larva to pupa	27 days
Pupa to adult	16 days
Egg to adult	55 days

Since the observations on which the above figures are based were made during a period from January 18 to March 15, it is probable that during the warmer months of the year the rate of development of *emeryi* is more rapid.

It was soon apparent that the workers in the captive colony would accept anything edible that was put in the food chamber. Moreover, there was no indication of preference for a particular kind of food. Honey-dew and nectar elicited just as vigorous feeding responses as did the tissues and body fluids of other insects. On the other hand, there were some interesting points in the mechanics of feeding. It is not to be expected that an ant as small as *emeryi* could easily cut to pieces heavily sclerotized insect body wall. But the ants seemed particularly inept at this sort of activity. They often failed to cut up the soft body wall of termites, although they would "mine" termites extensively when the body wall was torn open. They had better success with lightly sclerotized insects such as mosquitoes, crane flies, and may flies and usually managed to cut them apart although the process was a slow one. When this was done, pieces of the dissected victim were sometimes carried into the brood chamber and fed to the larvae, but most of the time the larvae were fed by regurgitation. This also seemed to be true of the free colony. During two years of observation, only a few foragers were seen to carry anything back to the nest. Two of these foragers were relieved of their burdens which, in each case, consisted of a much macerated bit of soft insect body wall.

Most of the insects placed in the food chamber of the captive colony were killed before they were given to the ants, but on three occasions living victims were offered to them. Prudence demanded that these be small insects which would not be able to disrupt the colony. The living victims used were collembola (snow fleas), the small nymphs of the woolly apple aphis, and the first instars of a pentatomid bug. The reaction of the *emeryi* workers was essentially the same for all three. The victims were immobilized either by having the head crushed or by having the appendages bitten off, whereupon their body fluids and softer tissues were cleaned out. While the ants attacked their victims energetically, there was no evidence that any of them were stung. If the captive colony was not liberally supplied with food, the workers would eat the brood. When they did so, it was usually the pupae which were eaten.

To summarize the above, it appears that *emeryi* is omnivorous. It is probably predatory on small, soft-bodied insects and almost certainly scavenges the remains of larger ones. Solid food is rarely brought back to the nest and food transfer in the colony mainly involves regurgitated liquid foods.

Although the captive colony kept the brood chamber fairly clean, it was remarkably slack about the rest of the nest. Dead members of the colony which had been cut to pieces, together with bits of insects which had served as food, would be dropped at random in any part of the nest except the brood chamber. At times so much of this refuse accumulated in the passages that the workers had difficulty in getting through them. This led to a serious mold problem; since the refuse was not concentrated in a kitchen midden, mold easily spread throughout most of the nest. This made frequent cleaning necessary. It was soon found that the best way to do this was to chill the ants to immobility. This was done many times without deleterious results, a rather remarkable response on the part of a species which is regarded as a tropicopolitan tramp.

The foraging activities of the free colony showed a number of puzzling features. About the only clear-cut controlling factor was temperature, for foraging would not occur unless the surface temperature was 70°F (21°C) or higher. Beyond this there was little to indicate what factors were involved in the foraging pattern. The foragers emerged singly from the nest entrance at widely separated intervals. Even under optimum conditions at least fifteen minutes intervened between the emergence of one worker and that of its follower. As a result, there was no concentration of foragers around the nest entrance, since the forager was well away from the nest entrance by the time the next one emerged from it. A secondary result was that no more than a dozen foragers (often less) were outside the nest at once.

On leaving the nest the forager might start off in any direction and the course which it followed was extraordinarily crooked. It was exceptional for a forager to move for more than three or four centimeters in a straight line. Moreover, they often doubled back over their previous course. This same random, tortuous course marked the return to the nest and here there was even stronger evidence of lack of orientation, for the returning forager would often overshoot the nest entrance even though it passed close by it. As already noted, few returning foragers carried solid food to the nest, and it seemed possible that the erratic return course to the nest might be an indication that no food had been found. In order to test this, grains of sugar were placed on the sidewalk fifteen centimeters from the nest entrance. The foragers carried the sugar grains back to the nest in their mandibles. But it was exceptional to find that one of these obviously food-burdened foragers returned directly to the nest. Instead they continued on their erratic courses and were equally inept at finding the nest entrance. It may be recalled that when Dr. E. O. Wilson (1959) published his observations on the foraging of *C. venustula*, he reported that the foragers proceeded from nest entrance to food source over a straight course. Moreover, they would stick to this course even when this involved surmounting obstacles which could have been avoided by slight course deviations. Dr. Wilson believed that this behavior was due to the fact that the foragers orient themselves by sight. It is hard to see how such an explanation could apply to the tortuous courses characteristic of *emeryi*. On the other hand, it is equally hard to suggest what, if anything, controls the random foraging of *emeryi*. But it is clear enough that this sort of foraging gives no chance for recruitment by tandem running. Over many months of observation, no tandem running was ever observed in *emeryi*.

The foragers of *emeryi* often met other species of ants on the sidewalk. Most of the dozen or so species which foraged on the sidewalk posed no particular threat to the *emeryi* foragers, but two of them, *Solenopsis geminata* (Fabricius) and *Pheidole dentata* Mayr, are aggressive and carnivorous, and it seemed likely that encounters with these two species would be extremely hazardous for the *emeryi* workers. It was a surprise, therefore, to discover that in such encounters the two larger species exhibited a marked avoidance reaction to *emeryi*. When such encounters occurred, the *emeryi* forager stood still while the other ant scrambled away. This was particularly noticeable in *P. dentata* minors which seemed to go into a near panic in the presence of an *emeryi* forager. Since the size disparity rules out any possibility that the foragers of *geminata* and *dentata* were trying to avoid an attack by the *emeryi* worker, it can only be supposed that despite its small size the worker of *emeryi* possesses a highly effective repellent pheromone. This would also explain how *emeryi* is able to nest in close proximity to flourishing colonies of *S. geminata* and *P. dentata*.

Cardiocondyla nuda (Mayr)

It now seems clear that the senior author was mistaken in treating Forel's variety *minutior* as a subspecies in 1950. At that time there were few long nest series of *nuda* available for study; hence it was not certain how the single nest series which had yielded workers of the typical *nuda* and others of the variety *minutior* ought to be handled. Subsequent studies have shown that the above situation is normally encountered in any long nest series of *nuda*. It follows that *minutior* must be treated as a synonym of *nuda*, as shown by Wilson and Taylor (1967).

In April 1972, several nests of *nuda* were found in a brick sidewalk about seventy-five yards away from the nest of *emeryi* described earlier in this paper. These were built in the thin layers of soil which had pressed up between the bricks. On April 14 one of these colonies was excavated and installed in an observation nest. The colony consisted of two deälated queens and thirty-eight workers. Since *emeryi* had shown itself to be easily adaptable to life in an artificial nest, no difficulty was anticipated in the observation nest of *nuda*. Actually the *nuda* colony proved to be far more difficult to handle.

At first the *nuda* colony seemed to be doing well. Both queens laid eggs and the workers carried out their usual nest activities. But at the end of two weeks, the rate of egg laying declined. Ultimately both queens ceased to produce eggs. By this time some had been in the nest a month, and it might have been expected that larvae would have been present. However, no egg ever hatched. About the end of May, both queens were cut to pieces by the workers and the colony expired.

It seems worth noting that during the brief duration of this *nuda* colony, the observation colony of *emeryi* was bringing much brood to maturity. Since this seems to indicate that nest conditions were satisfactory, considerable effort was made to assure that the *nuda* colony received identical treatment. The two Janet nests were kept in contact to minimize temperature differences. Their humidity was, as far as possible, kept at the same level and the same food was given each. Since the *emeryi* colony survived until the summer of 1972, at which time the last queen died, the obvious conclusion must be that *nuda* requires nest conditions different from those which satisfy *emeryi*.

Better results were secured from observation on the free colonies of *nuda*. The foragers leave the nest singly but as they emerge more frequently than do those of *emeryi* there are usually more of them outside the nest. They forage somewhat more rapidly than do the workers of *emeryi* and the courses they follow, while by no means straight, are far less tortuous than those of *emeryi*. It is rare for a forager of *nuda* to double back on its own course. The result is that their progress between nest entrance and food source is more direct. They also seem to have less difficulty finding the nest entrance on their return.

Cardiocondyla ectopia Snelling

A single polydomous colony was found in the junior author's front yard in mid-July 1972. The subcolonies from northeast to southwest were designated A, B, C. Subcolony B was situated 2.6 m. SW of A; C was about 3 m. S of B. The entrances of A and B, both between bricks set into the soil, were fully exposed and marked by piles of debris. That of C, although similarly marked by debris, was more difficult to discover because it was partially concealed by a dense mat of *Euphorbia serpens*.[2]

Foraging activities of this species have been observed intermittently for about one year. Other than modifications of diurnal activity, which seem directly related to temperature, activity appears to be uniform. During the cooler months, November to March, there is little surface activity. Daytime temperatures often are not sufficiently high to prompt activity, or the duration of suitable temperature levels is too short.

During July 1972 the colonies were watched whenever circumstances permitted. At five-minute intervals during observation periods, two temperature readings

[2] Determined by R. Gustafson, Natural History Museum of Los Angeles County.

were made—one of the ambient temperature at a level of six feet, the other of the surface of the asphalt driveway. At this time of the year, worker ants emerge from the nest and begin foraging when the ambient temperature is at 19°–20°C; the asphalt surface, in full sun, is at about 24°C. On one date in July, the ambient reading at 1100 hrs. was 26°C and workers were no longer moving onto the exposed surfaces. For workers from colonies A and B, access to food resource areas was across a distance of about 0.3 m. When surface temperatures reached as high as 42°C at 1100 hrs., there was no foraging activity by individuals from these colonies. Workers from C continued to forage, though at a greatly reduced density, since they had direct access to the patch of *Euphorbia*.

On another day, however, by 1100 hrs. the ambient temperature was at 23°C, the surface at 36°C. Because of cloud cover, the surface temperature had been at that level for nearly an hour. From 1000–1045 hrs., ants were active on the paved surfaces, but at about 1045 began to abandon these surfaces. On other days, when surface temperatures never exceeded 35°C, there was a noticeable lessening of activity after 1100 hrs., so it would appear that time of day is, at least partially, a controlling factor in the foraging pattern of this species. However, notes by the junior author record some surface activity as late as 1925 hrs.

Foragers traveled at least 6 m. from the nest in search of food. The small size of the ants made observation difficult once the workers reached food source areas amid the plants in the yard. Attempts to determine foraging distances were frustrated by two factors: the reluctance of the ants to accept bait of any sort and the competition of the much larger Argentine ant *Iridomyrmex humilis* (Mayr). The latter species quickly discovered and monopolized baits.

Individuals which foraged in the mats of *Euphorbia* were observed with some success. Many proceeded directly to the flowers and took nectar. Several seconds (3–21, average 7.4) were spent at each blossom. After a period of up to 35 min. the forager returned to the nest with distended gaster. Other workers wandered about, picking up bits of soil, fragments of plant fiber, and pieces of dead arthropods. Once an acceptable item was discovered, it was transported back to the nest. Fragments collected were so small that no attempt was made at specific identification.

From the onset of foraging until about 1030 hrs., the *Cardiocondyla* workers foraged throughout the area, even though *I. humilis* frequently utilized the same areas. After about 1030, however, most areas were abandoned by the smaller species. An exception was the patch of *Euphorbia* adjacent to nest C. This resource was worked until about 1300 hrs., after which time only Argentine ants were to be found on it. Since this pattern was consistent, it seems safe to assume that the foraging period of the *Cardiocondyla* regularly ends in early afternoon. Occasional encounters between the two species were uncommon. As a rule, both species retreated from the point of encounter. Often, however, the *Cardiocondyla* would continue along its original course or was but slightly diverted. The *Iridomyrmex* behaved in a very erratic fashion, and usually left the point of encounter rapidly, and at a course highly divergent from its original course. Less often, the *Cardiocondyla* worker would stop with gaster slightly elevated, head lifted and directed forward, with spread mandibles.

Workers departing from the nests were observed often. Most proceeded singly in a very irregular but basically unidirectional mode. There were many turns and divergences for no apparent reason. Return from the foraging area did not always reverse the outward course. In fact, seldom was this so, for often the ant would head back to the nest from a point in the foraging area fully a meter from where she entered it. The return was frequently much less direct than the departure, involving more divergences from the straight line and much back-tracking. Once within 0.2 m. of the nest the ant seemed more certain of her direction and would head more or less directly toward the nest entrance. Even so, misses were frequent and some search was necessary.

From the above we may perhaps deduce that orientation is partially solar-directional and partially a matter of visual recognition within a limited area. There may also be a distance recognition factor, as suggested by a series of tests. An individual which discovered a bait placed in the driveway was marked on the gaster. After feeding, it returned to the nest, 1 m. distant. A period of almost 15 min. elapsed before the marked ant appeared, heading toward the bait. The path between the ant and the bait was washed with ethyl alcohol and the bait displaced 5 cm. to one side. The worker proceeded across the washed area with only momentary hesitation. She stopped when she reached a point about 1.5 cm. from where the bait had been and began searching for several centimeters in all directions. Ultimately the new location was discovered. This experiment was repeated, with similar results, several times with different individuals. When the bait was displaced as much as 15 cm., it usually was not relocated for the ants would not search so far from the known locus.

Although most foragers depart singly from the nest, tandem running is frequent in this species. Tandems almost invariably consist of a pair of ants, rarely three. The pattern is as described by Wilson (1959) for *venustula*. By working with marked individuals in an observation colony, it was possible to discover that the leader of the tandem pair was guiding the follower to a previously discovered food source and that the follower was recruited. The follower, in turn, would recruit another individual once she returned to the nest. When the lead ant arrived at the bait, she would immediately begin feeding. The follower, after searching for a few seconds, would discover the bait and also begin to feed.

On 23 July 1972 colony A was excavated and placed in a Janet nest. The colony consisted of eight deälate females, two alate females, about 75 workers, and two males. Brood was not counted but estimated at 55 larvae and 15 pupae. About five hours after removal to the artificial nest, mating between one of the males and one of the alate females was observed. The female was motionless, antennae slightly extended, head vertical, mandibles slightly open. The male mounted the female, parallel with her body, and began to nip at the top of the head of the female, then rapidly jerked his head up and down along the front of the female's, apparently effecting contact with her mouthparts. The jerking movement of the male was excited and rapid, appearing almost violent, and lasted about 15 sec. After this, he backed along the dorsum of her body, curled the gastric tip under that of the female, establishing genital contact. Genitalic contact lasted about five sec., after which the male returned to the forward position, cleaned the gastric apex, followed by renewal of the entire procedure. The entire sequence of activities was repeated three times within a five-min. period. After the last repetition, the male completed his cleaning procedure, then remained motionless. At this time the female began to walk about and the male eventually fell off. At some time during the following day this female shed her wings and became indistinguishable from the others. The other female was not observed to mate; on 17 August she was not to be found among the colony residents.

Santschi (1907) stated that males of *nuda* "var. *mauritanica*" assisted in moving brood. We have no observations to indicate that the male of *ectopia* practices such remarkable behavior.

Males of this species are ergatoid, hence wingless, so mating flights do not take place. Mating, of necessity, occurs within the nest. But, does the mating take place between individuals born within the same colony, hence potentially brother and sister? If so, does the female always, or only occasionally, shed her wings and remain with her colony? Or does she shed her wings and migrate with part of the worker force to establish a new colony by budding? Does she sometimes fly after mating either to (a) found a new colony or (b) become adopted into a neighboring nest? Or does she fly forth from her parent nest still virgin, become adopted into a neighboring colony, and mate with a male there?

Unfortunately, no answer as yet can be given to the above questions. We incline to the last-mentioned alternative, however. Adoption into another colony seems to be a very simple matter. Workers and females from different nests have been introduced into the observation colony without evidence of animosity; the new ants acted as if they were a part of the colony. One alate female in colony A at the time of its capture was not observed to mate, nor did she shed her wings. On 17 August she disappeared. No remains were found in the midden. From this we assume she escaped by flight. It is assumed that she attempted to locate another colony.

In our view the pre-mating flight–adoption–mating alternative seems most logical, even though there is no firm evidence for it. A mated female represents a considerable reproductive potential, far more than does an unmated female. Furthermore, mating with a male from a different colony is genetically more sound.

Females do not emerge en masse for flight. Rather, they emerge singly and take flight over a period of an hour or more. On 17 July 1972 females flew from colony C as follows: 0905—1♀; 0906—1♀; 0907—1♀; 0908—2♀♀; 0910—1♀; 0915—1♀; 1018—1♀; 1023—1♀. On 23 July 1972: 1010—1♀; 1012—1♀; 1015—1♀; 1018—1♀; 1035—1♀. On 7 August 1972 one female emerged from C at 0930. On 19 February 1973 a single female flew from C at 1400, air temperature about 23°C, as was true for all of these (observed range: 22.7°-24.1°C).

DISCUSSION

Wilson (1955) summarized the natural history of *venustula* as he observed it in Puerto Rico. He found that the colonies were polydomous and that the populations were low, probably not in excess of two hundred workers. Nest entrances were small and surrounded by debris. Foraging occurred mostly during the middle part of the day. Tandem running was observed and presumed to be a highly evolved form of recruitment. Tandem running was also noted to occur in *emeryi* in Puerto Rico.

Our observations, based on *emeryi*, *nuda*, and *ectopia*, tend to corroborate Wilson's conclusions. The siting of nests seems to be very similar for all four species, and the entrances are concealed by miscellaneous debris. Foraging of the three species which we studied takes place mostly during the midmorning to midafternoon period, at temperatures above 19°C, and ceases when the ambient temperature reaches 26°C.

Colonies of *ectopia* appear to be polydomous, as in *venustula*, with the components up to six meters apart. Multiple queens seem to be normal in all species. Males of *ectopia* are wingless and mating takes place within the nest. Alate females emerge singly and fly quickly. Mating possibly occurs before emergence or it may be that the females seek adoption in a neighboring nest and mate there.

Curiously, although Wilson reported tandem running of *emeryi*, the senior author found no examples of such behavior in this species at La Feria, Texas. The foraging pattern of this ant is highly erratic and it may be that tandem recruitment is not common in this species. This recruitment technique was not observed in *nuda*. The two species should be more thoroughly studied.

Better results were obtained for *ectopia*. Departing workers pursue an erratic pattern when searching for food; but once a large source, requiring more ants, is located, the foragers return more or less directly to the nest. Here, another worker is recruited and led back to the food source, again more or less directly. Additional ants are recruited in the same manner, if necessary.

Wilson described his experiments with tandem pairs of *venustula*. Similar experiments with *ectopia* produced similar results. From these data it seems clear that chemical trails are not laid down and orientation to a food source is probably based on solar position and distance. Since there is no chemical trail to indicate direction, it follows that the discoverer must lead its nestmates to the food source. The leader of the tandem pair evidently releases an excitant pheromone by which the follower is led. It seems possible that this chemical is so volatile it functions for only a short distance and that only a single individual can follow it. Hence tandems consist only of a single pair.

The ants are small and can carry only small arthropods or fragments of larger ones. Relatively large items, such as can be exploited only by large numbers, probably are seldom available. These are likely effectively taken over by larger ants (*Pheidole, Solenopsis, Iridomyrmex*, etc.) or by those which recruit in large numbers (*Monomorium, Wasmannia, Iridomyrmex*, etc.). While individuals of *Cardiocondyla* can apparently repel individuals of *Iridomyrmex*, it is unlikely that the colonies can effectively compete against such numerically superior species at more bountiful food sources. Further studies of these and other *Cardiocondyla* should investigate food resource utilization as compared to other ants in the same foraging area.

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