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THE HABITS OF *PHEIDOLE MILITICIDA* WHEELER (HYMENOPTERA: FORMICIDAE)[1]

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During the winter of 1959 the writers were able to study a number of nests of *Pheidole militicida* Wh. These were situated in an area along the eastern base of the Chiricahua Mountains, six to nine miles north of Portal, Arizona. Extended field studies were made on these colonies and samples taken from them were placed in small Janet nests and observed at the Southwestern Research Station. The need for such work will be clear to anyone familiar with W. M. Wheeler's remarkable views on the habits of *militicida*.

Wheeler's initial acquaintance with this ant was made on November 10th, 1910, at Benson, Arizona. A day or two later he found other colonies at Hereford. If Wheeler's hypothesis on the habits of this species is to be appreciated properly, it is important to understand exactly what information he secured from these colonies. Before he excavated them, Wheeler found the remains of numerous majors on some of the chaff piles. The material in the Wheeler Collection indicates that these remains consisted largely of head capsules which lacked all appendages. If Wheeler had found living majors in the nests that he excavated, these disarticulated remains would have received scant attention. Unfortunately, Wheeler did not find living majors in the colonies which he dug out. But it should be remembered that after Wheeler had examined the nests at Benson and Hereford, he knew surprisingly little about the ants that were living in them. He could not even be sure that the majors, whose remains he had discovered on the chaff piles, had come from the nests where he found them. All that Wheeler knew was that he had taken the minor of an undescribed species of *Pheidole* from these nests and that, after considerable digging, he had been unable to secure any accompanying majors.

[1]Contribution from the Southwestern Research Station of the American Museum of Natural History.

The next factual data on *militicida* came to light a year or two later when W. M. Mann excavated nests near Benson in August and found both majors and minors living in them. These majors corresponded to the remains that Wheeler had taken earlier. With both major and minor castes available, Wheeler was in the position to describe *militicida* as a new species, which he did in 1915 (1). If Wheeler had been content to let the matter rest with the description of these two castes his action could have been defended not only as sound but also as conservative, for he had waited until the majors and minors had been certainly associated before presenting his description of them. But Wheeler was not content to limit his efforts to the description of *militicida.* He proceeded to develop a striking hypothesis as to its habits. This was so plausibly presented that one is apt to forget that this highly ingenious account is primarily compounded of supposition. Because Wheeler had found no majors in the Benson and Hereford colonies, he assumed that none were present. Because he had found the remains of majors on the chaff piles of these colonies, Wheeler assumed that all the majors in the colonies had been slaughtered by the minors. Having made these two assumptions Wheeler was forced to make others to support them, for this astonishing behavior on the part of the minor clearly demanded explanation. This Wheeler supplied as follows:

"It appears, therefore, that all the individuals of this caste (the majors) are regularly killed off by the workers on the approach of winter, probably after they have broken open all the hard seeds collected by the workers. Such a slaughter of the members of a large caste during the season when their activities are no longer required, when they would simply be a burden on the colony by consuming stored food and when fresh food cannot be collected, must have great advantages. Although I have never noticed this behavior in any other species of *Pheidole,* I believe that a study of the harvesting species with very large-headed soldiers in the deserts of the southwest may bring other similar cases to light."

It is obvious that the most direct way to test Wheeler's theory would be to examine the nests of *militicida* during the winter months. If such examinations were properly carried out it would be possible to state with certainty whether or not majors are present in the nests at that time. But subsequent observations on *militicida* have all been made during the summer. The writers observed this ant at Safford, Arizona, in July 1950. In August, 1952 A. C. Cole studied colonies at Bayard and Deming, New Mexico, and in August 1956 he found others in the vicinity of Portal, Arizona. The information concerning the exact site of the latter colonies, which Dr. Cole obligingly furnished, was a notable help to this study and we wish to express our thanks for it.

While the observations just cited added to our knowledge of *militicida,* none of them could furnish information on winter conditions in the nests of this species. Thus when Creighton and Gregg reviewed Wheeler's hypothesis in 1955 (2), they could do little more than point out the improbability of his explanation. Although it was clear that a number of southwestern species of *Pheidole,* which have majors with unusually large heads, showed none of the habits predicted by Wheeler, it was still possible that he might have been right in the case of *militicida.* Positive proof that Wheeler's account of the habits of *militicida* is incorrect was secured by the writers in the winter of 1959. During that winter we had fifteen colonies of *militicida* under field observation on all but a few days. Living majors were taken from thirteen of these colonies during the period between January 8th and March 3rd. Our original attempts to secure majors were based upon the obvious method of digging out the colony. This proved to be the worst possible way to get them. Under ordinary conditions only two or three majors stay in the passages near the nest entrance. Since the major of *militicida* is extraordinarily clumsy, it is seldom able to extricate itself if covered with soil. Hence, it is extremely likely to be missed when the nest is dug out, for the major will often remain perfectly quiet if only a thin layer of soil covers it. To be sure that the majors have not been missed, the soil must be sifted as the nest is excavated. With this in mind it is easy to understand why half the nests which Cole excavated in the summer of 1952 (3) appeared to contain no majors. During the first weeks of this study we faced a similar situation. Three of the eight nests excavated had yielded no majors. The remaining five had yielded a total of only fourteen majors, of which the greatest number taken from a single nest was five. Our results were, therefore, inconclusive for in no case had numerous majors been found in any nest.

Then the junior author hit upon a method of using bait to bring the majors out of the nests. The best bait was found to be various sorts of bread or scrambled eggs. Meat seemed decidedly less attractive. The bait was cut into pieces too large for the minors to move and these were placed close to the nest entrance. This baiting seldom failed to produce majors in quantity if continued long enough.

One colony which was baited for five successive days in February yielded a total of seventy-seven majors. Moreover, by using bait majors were secured from nests which had produced none when dug out. For, with one exception, the excavated nests reestablished themselves after a few weeks. This is clear evidence that these nests had not been fully exposed. The character of the *militicida* nest would make complete exposure difficult. All the nests that we have encountered have been built in light, friable soil between large stones. As these stones are removed the soil between them crumbles away and this obliterates any passages that were in it. As a result it is usually impossible to follow the passages to any depth and as excavation proceeds there is not the slightest indication of the direction it should take. In our opinion no nest of *militicida* has yet been completely excavated.

In areas where *militicida* is abundant there are often places where several nest entrances are close together. The distance between the entrances will vary from two to eight feet. It seems impossible at present to state whether each entrance represents a separate nest or whether they all belong to a single elongated nest. The total nest count given in this paper (15) is based upon the latter supposition. The total number of entrances found is five or six times greater. It was soon found that majors and minors from entrances a few feet apart could be mixed together without showing any signs of animosity. At first we accepted this as positive proof that the several entrances all belonged to one nest. But later the disconcerting fact came to light that the same result could be secured with specimens from nests a half a mile or more apart. The only explanation that would seem to fit this surprising behavior is that *militicida* is almost totally devoid of inter-colony animosity. The situation is made even more inexplicable by the strong animosity which *militicida* exhibits toward other species of ants.

We expected *militicida* to forage sporadically during the winter but it was a surprise to discover that it is one of the most consistent winter foragers in the area where it occurs. The only other ant which shows comparable activity is *Myrmecocystus mimicus* Wh. Except for one or two days when rain or snow fell, the minors of *militicida* were out every day during January, February and early March. As a rule the foraging did not begin until 3:00 P. M. By that time the surface temperature had reached 60°F. (16°C.) or better. Full foraging activity developed when the surface temperature reached 90°F. (31°C.). During January the surface temperature drops rapidly towards sundown and foraging in that month ordinarily terminates soon after 5:00 P. M. This brief period of foraging is extended as the days lengthen and by the end of February the foraging lasts about three hours. During the winter months the seeds of two grasses are the principal ones collected. These are the fluff grass, *Tridens pulchellus* Hitch and the spike pappus grass, *Enneapogon desvauxii* Beauv.[2] Both these grasses fail to lose all their seeds at the end of the growing season, but the number of unshed seeds in the heads is low. Counts on five samples (30 cc. each) of fluff grass heads taken within foraging range of five *militicida* colonies gave an average of only 4.6 seeds per cubic centimeter. Nevertheless, these residual seeds furnish a steady, if meager, supply for, as the winter advances, the seeds or the spikelets containing them are gradually blown out of the heads and deposited in a thin layer on the surface of the soil wherever there is a windbreak. In the winter months the *militicida* minors collect their seeds entirely from this layer. During the many days that the foraging minors were observed, not one was seen to ascend a grass stem to get at the seeds. It is difficult to explain this reaction, for the percentage of seeds in the heads is several times as great as that in the layer on the ground. For this layer contains many spikelets that are devoid of seeds and the minors frequently bring these empty envelopes home. On several occasions we took numbers of the spikelets away from the workers as they reached the vicinity of the nest and found that not more than a third of these contained seeds.

Despite the short foraging period and the scant seed supply, the *militicida* minors bring in many seeds, for on warm days foraging is very active. Each nest entrance usually has a single foraging column but sometimes two or three columns may leave the same entrance. The columns are seldom more than fifteen feet long, an indication of the easy availability of the seed supply, regardless of its low yield. Since the rate of seed consumption in the captive colonies was very low, it seems probable that winter foraging augments the number of seeds stored in the nests. The *militicida* colony is thus provided with an abundant store of seeds which it can use with the arrival of spring. The spring months are the driest part of the year in the areas where *militicida* occurs. At Portal the total precipitation during April, May and June averages 1.52 inches, approximately 8.2% of the an-

[2]We wish to thank Mr. Joseph Welch, who was working at the Station when this study was made, for his kindness in identifying these and other grasses as well as for helpful suggestions on the terminology of the spikelet.

nual total of 18.40 inches (4). In other stations where *militicida* occurs the percentage of spring precipitation is even lower. As the spring drought begins, the seed supply reaches its lowest ebb, for winter foraging has depleted the meager residue of seeds and no more seeds are likely to be set until after the summer rains. These unfavorable conditions often lead to a suppression of foraging in the spring, but this does not mean that the colony is inactive. For the sexual brood is brought to maturity at this time with the marriage flight following in early July. Thus the heaviest drain on the supply of seeds stored in the nests occurs during the spring months. It is at this time that the stored seeds are broken open and the food in them is made available to the rapidly developing brood.

Before taking up the feeding habits of *militicida* it is advisable to discuss certain features of the grass seeds which they use for food. At maturity a typical grass seed is enclosed in a complicated envelope of bracts. The outermost of these bracts are called glumes, the median ones lemmae and the innermost ones paleae. The lemmae often bear prominent projecting bristles called awns. These parts are attached, close above one another to a much-shortened stem called the rhachilla. Collectively these parts make up a spikelet, which may contain one or more seeds. As a rule when a mature seed is shed, all of the spikelet except the glumes is shed with it. In some grasses this envelope fits the seed tightly, which makes its extraction difficult. In other grasses the envelope is loosely fitted around the seed and its extraction is comparatively easy. The spikelet of *E. desvauxii* shows the first condition, that of *T. pulchellus* the second. Since most of the seeds which the minors of *militicida* bring back to the nests are still in the spikelets, the seeds musts be freed of these envelopes before they can be conveniently stored. Observations on the captive colonies showed that the seeds of *T. pulchellus* offer no particular problem because of their loose envelopes. The minors have little difficulty in pushing the lemmae aside and can often pull out the seeds without detaching the surrounding parts. Perhaps this is why the majors so seldom help when *pulchellus* spikelets are being handled. The spike--lets of *E. desvauxii* are quite another matter. Each of the close-fitting lemmae has nine slender awns at its tip. These radiate outward at an angle of about 45 degrees and form a complete circle of bristles at the upper end of the spikelet. When attempting to free these seeds of the envelope both majors and minors will grasp the awns in their mandibles. When the major does so the awns are usually broken off, but the minor handles them more gently and when two minors grasp the awns at opposite sides of the spikelet and pull in opposite directions they are usually able to break apart the lemmae and thus expose the inner parts of the spikelet. The seed then lies between two paleae but these do not completely enclose it and it is a simple operation for the minors to pick the exposed seed out. When the major extracts the seeds the lower end of the spikelet is grasped in the major's jaws. Pressure from these either breaks the lemmae apart or, if the seed has exactly the right position as the jaws close, it is forced outward between the lemmae and paleae, which spread enough to let the seed squeeze through. The envelope is often left intact when the seed has been extracted by this method. Whether intact or in fragments, the envelope is then ready to be placed on the chaff pile and the seed extracted from it may be cracked open and eaten or stored in one of the seed chambers.

There is abundant evidence that when the seeds are stored they are entire. The minors in our artificial nests spent many hours arranging and rearranging the seeds in groups. We take this to be the equivalent of the packing of the seed chambers in a free nest. No seed in these groups was ever damaged in any way until it was taken out and eaten. Moreover, there were usually a number of partially eaten seeds present in the nests, for the *pulchellus* seeds are seldom entirely consumed. Such opened seeds invariably shriveled after a day or two and usually moulded a few days later. That cracked or damaged seeds could be stored for months in the seed chambers seems thoroughly impossible.

We were surprised to discover that all the seeds opened in the artificial colonies were opened by the minors. The majors never made the slightest efforts to open the seeds and rarely paid any attention to them once their envelopes had been removed. In an effort to force the majors to crack open seeds, several nests containing only majors were set up. These were liberally supplied with seeds of *T. pulchellus*. Some of the majors in these nests lived for several weeks but they never made any attempt to open the seeds and ultimately all of them died, apparently from starvation, in the midst of the seeds which could have supplied them with food. The minors open the seeds of *pulchellus* and *desvauxii* by gnawing at the pointed end of the seed. Sometimes the seed is held by one minor and gnawed open by another, but a more common method involves only one minor, who places the blunt end of the seed on the floor of the nest and, with the seed held in a vertical position gnaws at its pointed end. The seeds of *desvauxii* are entirely consumed but, as noted above, those of *pulchellus* are usually only half eaten. This may be due to the fact that in *pulchellus* the embryo is confined to the half of the seed which the ants eat, whereas in *desvauxii* the embryo extends more than three-quarters the length of the seed.

As will be seen from the previous paragraphs, the major of *militicida* has a very limited part in the harvesting operations and even this small part can be handled equally well by the minors. It seemed unlikely that the major would be limited to so small a share in the activities of the colony. The first hint that they might perform some unique activity essential to the colony was provided by the majors who came out of the nests during baiting. The junior author, who spent much time at this work, noticed that before the major emerged from the nest it would often stand for a considerable period just inside the nest entrance. When it did so it was a thorough nuisance to the minors, who had difficulty in getting past what amounted to a road block. When the major finally emerged from the nest it usually opened its jaws to their fullest extent and made short lunges in the direction of small pebbles and bits of grass as though it were trying to bite them. Later it was found that this same lunging and biting response could be elicited by throwing a small beam of light into the opening before the major left it. It was further clear that the primary reason why the major left the nest was not hunger. They almost never went directly to the bait, but wandered around in their clumsy fashion as though they were looking for something else. It was only after considerable patrol that some of them would go to the bait. These responses suggested that the function of the major might be to guard the nest entrance and, to test this, a nest was constructed which gave them the opportunity to do so.

This nest consisted of two chambers connected by a single, long passage which could be blocked or unblocked in the middle without disturbing the nest. The block consisted of a cotton plug which could be pushed into the connecting passage through a glass tube set at right angles to it. With the plug in place the nest was divided into two separate chambers; with the plug removed the two chambers communicated with each other through the single connecting passage. After the plug was in place majors and minors of *militicida* were placed in one chamber and their prospective intruders in the other. The nest was then set aside until both groups were accustomed to their surroundings. Usually it took no more than twelve hours for each group to become thoroughly tranquil and to demonstrate by this tranquility that it was unaware of the other group's presence nearby.

The ants selected as intruders were *Pogonomyrmex maricopa* Wh. and *Pogonomyrmex californicus* Buck. This choice was made because both species occur in close proximity to *militicida* colonies in the field and the harvesting activities of all three species lead to frequent encounters outside the nests. The results secured from the experimental nest described above were highly interesting. On the removal of the blocking cotton plug both groups would begin to explore the communicating passage. They did so in an entirely different fashion. The *Pogonomyrmex* workers moved slowly into the passage but rapidly backed out of it when they became aware of the advancing *militicida* workers. In most cases the *militicida* minors first entered the passage. Some of them would usually be seized and killed by the *Pogonomyrmex* workers but others returned to the nest and alerted the majors. When these entered the passage they showed precisely the reactions that they had exhibited around their nest entrances. They advanced very cautiously, with the jaws wide open, and made frequent short lunges in the direction of the *Pogonomyrmex*

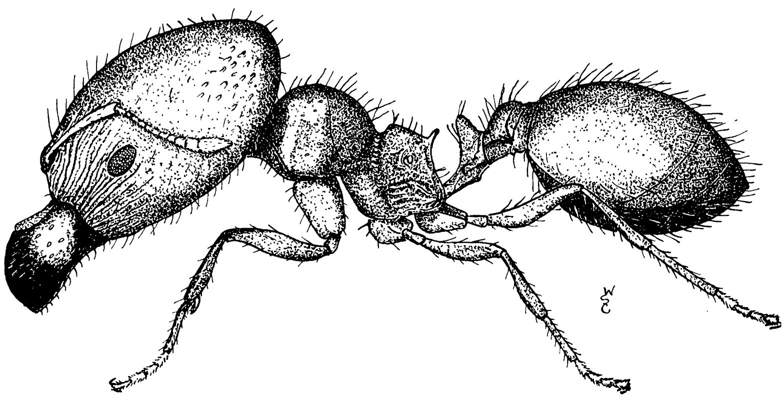

Fig. 1 — Major of *Pheidole militicida* in the defensive posture.

workers. As the *militicida* majors wedged themselves tightly into the passage, three or four ranks deep, the passage was completely blocked and the front face of this block was a highly dangerous area for the *Pogonomyrmex* workers for it consisted of the closely approximated heads and wide open jaws of the *militicida* majors. As to what happened next depended on the *Pogonomyrmex* workers, who would charge up to the barrier and slash at the *militicida* majors with their mandibles. These attacks were usually futile, for the only exposed parts of the *militicida* major which could be damaged were the antennae and these were held so closely against the head that the *Pogonomyrmex* workers were seldom able to grasp them. If these attacks were vigorously pressed the *militicida* major usually stood perfectly still and waited until the mandibles of its opponent were near its own. It then lunged forward, closed its jaws on the mandible of the *Pogonomyrmex* worker and attempted to break off the crushed mandible. The majors did not always succeed in doing so, particularly in the case of *maricopa,* whose heavy mandibles are hard to break, but they seldom failed to mangle the mandible so badly that it was useless. It may be added that this attack on the mandible is deliberate, for the *militicida* major will rarely strike at other parts when these are presented. We have repeatedly seen the *Pogonomyrmex* workers thrust their antennae or legs between the open jaws of the *militicida* major without causing the major to strike. They do not do so until there is a good chance that the mandible can be grasped and they rarely miss their target. After a number of *Pogonomyrmex* workers had been put out of action with useless mandibles, or sooner if the *Pogonomyrmex* workers did not press the attack vigorously, the *militicida* majors emerged from the passage and began a different sort of action. They no longer faced their opponents and struck at their mandibles but approached them from the rear and struck at the thorax or the petiolar nodes. As a result, most of the *Pogonomyrmex* workers were ultimately cut in two, either at the petiole or behind the pronotum. In this more open fighting it was also obvious that the petiolar nodes and the mesothoracic area were the principal targets. An examination of the *Pogonomyrmex* workers at the end of an engagement always showed much damage to mandibles, thorax and petiolar nodes and surprisingly little damage to legs and antennae. In short, there is nothing haphazard about the way in which the *militicida* majors deal with their opponents; they only strike at parts which will put their opponents out of action or kill them. It is clear that their method is highly effective for it was only occasionally that the *Pogonomyrmex* workers got the better of the engagement. Even when they outnumbered the *militicida* majors they often failed to kill a single one of them and when they did so it was usually a result of the *militicida* major having been stung. This incapacitates them but does not immediatelv kill them.

It should be clear that the activities just described are considerably more methodical that the ordinary scrimmages between fighting ants. In these activities the *militicida* major shows an efficiency that is completely unlike its bumbling efforts elsewhere. This, plus the fact that these responses are repeated with surprising exactness time after time, and by majors from different nests, leads us to conclude that they are the normal guarding responses of the *militicida* major. If this is true the major of *militicida* is best regarded as a soldier. Its role in the harvesting activities of the colony is slight and it is not primarily a seed-crusher, as has been mistakenly supposed.

The defensive activities of the *militicida* major probably account for the mutilated remains which Wheeler found when he discovered this species, for the defending majors do not always dispatch the intruders without loss to themselves. This seems a more probable explanation than that proposed by Creighton and Gregg in 1955 (2), who suggested that the accumulation of dead majors discovered by Wheeler might have been a result of the high death rate of that caste during the peak of the harvest season. This now seems unlikely, for the death rate of the majors during the winter months has proved to be extremely low. Most of the fifteen colonies that we studied discarded no dead majors during the three months that they were under observation. Only four dead majors were placed on the chaff piles during this period. Each of these was carefully examined under a binocular microscope for signs of mutilation and each was found to be completely undamaged with not even a tarsal claw missing. This disposes of the last bit of evidence on which Wheeler based his hypothesis, for it is now clear that the minors of *militicida* neither kill the majors nor cut them to pieces after they have died. Thus Wheeler's views of the habits of *militicida* have proved to be at total variance with what these habits actually are.

In conclusion, it may be noted that *militicida* is a very difficult subject for investigations in artificial nests. This species is unusually sensitive both to temperature and humidity. Temperatures below freezing invariably kill the ants and they are almost as seriously affected by a heavy condensation of water on the glass of the nests. They seem unable to keep out of the water droplets and many of the minors die in them. They also die if the nest is too dry. This sensitivity made it difficult to maintain the captive colonies for any length of time. At the suggestion of Dr. Robert Chew, of the Department of Biology of the University of Southern California, the artificial nests were placed on a rack, in a covered aquarium, above a saturated solution of sodium chloride. In a closed system this should maintain a constant humidity of 78% of saturation regardless of temperature. The arrangement proved eminently satisfactory. It not only reduced condensation but also largely eliminated the need for adding water to the individual nests. We wish to thank Dr. Chew for suggesting a method which not only benefited this study but which should be of value to anyone faced with the maintainance of a "fussy" species in the laboratory.

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