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**REVIEW OF ADAPTATIONS OF VELVET ANTS
(HYMENOPTERA: MUTILLIDAE)**Mark Deyrup¹**ABSTRACT**

Mutillid wasps are active and conspicuous insects, but their interactions with each other and with other animals are seldom observed. Mostly indirect evidence is used to postulate that an array of traits represents adaptations to exploit ground-nesting, aggressive, often highly dispersed hosts. The massive exoskeleton protects the parasitoid invading nests of biting and stinging hosts; certain unrelated parasitoids attacking the same hosts are similarly armored. Female aptery occurs in mutillids and in many other wasps attacking soil-dwelling hosts. In at least two mutillid lineages, female aptery apparently led to phoretic copulation, which led in turn to selection for large size in males. Hosts are often highly dispersed and vulnerable for only a short time; this mandates prolonged searching in exposed habitats, which may have selected for a long life span and a remarkable defensive repertoire, including a powerful sting, warning squeaking, membership in mimetic complexes of warning coloration, chemical deterrents, and a variety of evasive tactics.

Theft follows thrift; robbers inevitably evolve to exploit savers in natural as well as human communities. Among the insects the paragons of thriftiness are found in the bees and higher wasps, which provide for their young by garnering a large supply of food. The larvae of these good providers are soft-bodied, almost defenseless grubs. Around the nests of these provident wasps and bees prowl other species of wasps and bees. Some of these, the cleptoparasitoids, produce a larva that usurps the food supply and kills the host larva. Others, the parasitoids, produce a larva that feeds on the host larva itself. There must be a continuous and complicated struggle between the producers of resources (in the form of food stores or succulent larvae) and the exploiters that depend on these same resources. Glimpses of the nature of this struggle may be obtained by a review of the apparent adaptations of the species involved.

Of all the species that participate in this lethal contest, none can provide more hours of fascination and frustration than the velvet ants (Mutillidae). The Mutillidae are a family of several thousand species, almost all of which prey on pupae or mature larvae of bees and wasps (Mickel 1928). Velvet ants are fascinating because of their bright colors, sexual dimorphism, longevity, and frequently frantic level of activity. They are frustrating because the evolutionary significance of these traits is not easily demonstrated. Although velvet ants tend to be conspicuous insects, often found in open habitats where they are easily observed, prolonged observations seldom yield any useful information on the interactions between velvet ants and their hosts or natural enemies.

Even the crucial interaction between sexes of the same species remains mysterious. During more than three years of study of velvet ants, I have watched males seeking and actually trailing females on innumerable occasions. Usually the male becomes more and

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more frenzied as he approaches the female, indicating his awareness of her proximity, but the two always seem to miss, frequently because the female goes into hiding at the last moment. The only velvet ant mating I have observed occurred early in the morning, while the female was just emerging from the sand where she had spent the night. The discreet intercourse of mutillids has led to taxonomic problems, as the males are winged and frequently look nothing like the wingless females. Unless they are caught *in flagrante*, there is no easy way to tell which male goes with which female; originally there were many species whose males and females had different scientific names, one of which could be synonymized when a mating pair was observed. Conspicuous and often abundant, velvet ants nevertheless manage to conduct their affairs in secrecy.

The elusive nature of velvet ants presents one with a dilemma that confronts scientists all too frequently. On the one hand, this group of wasps displays a series of striking behavioral and morphological features that I strongly suspect are adaptations for the parasitoid way of life. On the other hand, evidence of the actual function of the apparent adaptations is fragmentary. As in most studies of adaptation, several key features cannot be approached experimentally. There is no way, for example, to attach wings to apterous female velvet ants. In some cases one may apply the scientific method by using unrelated species with similar ecological roles to test hypotheses about apparent adaptations (Jaksic 1981). In other cases there are no appropriate recognized analogs, and hypotheses are, for the moment, supported only by the seductiveness of their logic and whatever bits of evidence are available. Such speculation is useful because it serves to focus inquiry and organize whatever information we have.

In North American velvet ants, there seem to be two major series of adaptations related to the principal mutillid role as parasitoids of ground-nesting Hymenoptera. One series deals with the nature of the hosts, the other may deal with the distribution of hosts in time and space.

One feature of the hosts of velvet ants is that they are formidable opponents, agile and frequently aggressive, well armed with mandibles and sting. A notable characteristic of velvet ants is their extraordinarily massive exoskeleton. Mutillid collectors know this to their sorrow; the thorax can only be penetrated by drilling. When the insect pin finally breaks through, it often plunges on through the sternites and impales the entomologist's finger. The sides and dorsum of the head and body are intensively sculptured with pits and ridges. This sculpturing may serve to strengthen the exoskeleton without contributing excessive weight, but it must also serve to direct attack, as the parts of the mutillid that most easily catch and retain the points of mandibles and stingers are also least vulnerable to penetration. The fragmentary evidence on mutillid-host interactions (summarized by Brothers [1972]) suggests that female mutillids are generally impervious to stings and bites of their hosts. They are easily grasped but not easily hurt. A similar combination of very heavy exoskeletal armor and dense sculpturing occurs in the Chrysididae, an unrelated group of parasitoids that specializes in attacking bees and wasps that nest in holes in dead wood. A great number of slow-moving beetles that inhabit ant-ravaged strata of the soil show a similar combination of heavy exoskeleton and dense surface sculpture on the least vulnerable parts of the body.

Another mutillid adaptation associated with the nature of the hosts is the absence of wings in females (apterygyny). Mutillids appear primitively to be parasitoids of ground-nesting Hymenoptera, as the great majority are today (Brothers 1975). Apterygyny has also arisen independently in several different groups of Bethyidae and Tiphidae (Evans 1969), which are parasitoid wasps that seek out soil-dwelling hosts and parasitize them in situ. Workers of the entire family Formicidae (ants), another family whose members forage in the soil and leaf litter, are also wingless. Species that spend much of their time burrowing through the soil run the risk of having their wings abraded to uselessness or tattered by encounters with other insects, and wings are also likely to impede progress through the soil.

One consequence of apterygyny is that it hampers passage across barriers, such as streams and swamps. At least three lineages of mutillids, as well as various groups of bethylid and tiphid wasps, have independently evolved phoretic copulation, thereby

increasing dispersal ability (Evans 1969). Phoretic copulation appears to have led to adaptive changes in the morphology of male mutillids, particularly the clypeus, which cradles the head of the female during flight (Sheldon 1970). Another more complex adaptation seems to have occurred in these groups of mutillids; large males are presumably better able to carry females during copulation, and males of species of phoretically copulating mutillids are notably larger than the females (Deyrup and Manley 1986). This in turn implies that females are laying male eggs on large hosts and female eggs on smaller hosts. This choice is possible because of a combination of three factors: (1) haplodiploid sex determination allows aculeates to determine the sex of their offspring, (2) since mutillids are generally flexible in their host relationships (Mickel 1928), they are able to utilize host species of different sizes, and (3) since ground-nesting bees and wasps of different sizes usually occur in the same area, an excessively skewed sex ratio will not necessarily result from determination of sex of offspring on the basis of the size of the host. One would not expect to see a close relationship between sex and size in species that tend to attack hosts that form large aggregations. This is borne out by a study of the size relationships of one such species (Deyrup and Manley 1986). Utilization of non-aggregating hosts of various size classes may therefore be a preadaptation for phoretic copulation.

A more general series of adaptations in velvet ants is combined into a remarkable defensive repertoire (Schmidt and Blum 1977). The heavy exoskeleton, resistant to both crushing and piercing, was mentioned above as a defense against hosts, but it should also serve as a defense against potential predators. In addition, females possess a notoriously effective sting, which is probably not normally used against the adult host (Brothers 1972). The deterrent effect of the sting is reinforced by a warning squeaking produced by stridulatory plates on the abdominal tergites (Masters 1979, 1980). At least some species have repellent mandibular glands (Fales et al. 1980), and the second gastral segment also has a major series of glands, the "felt lines" (DeBolt 1973), though the function of these is unknown. The effectiveness of these defenses is enhanced by aposematic coloring, often orange, black, and silver, and participation in elaborate Müllerian mimetic complexes. These defenses do not seem to breed overconfidence, as mutillids in the field are particularly wary insects. An individual that has been proceeding steadily over the ground is spurred by alarm into a very fast erratic dash, which often ends in concealment under leaf litter, where the mutillid remains motionless for some minutes before emerging. This can be easily observed in the common genera *Dasymutilla*, *Timulla*, *Pseudomethoca*, and *Ephuta*. At least some species in these genera and in the genus *Photomorphus* feign death, curling up motionless when the sand or litter is sifted.

Among the lower animals an obsessive buildup of arms and defenses is not usually coupled with paranoia. Except for the defending hosts of velvet ants, no habitual attackers of velvet ants are known (Manley 1984, Schmidt and Blum 1977). I have never seen any arthropod or vertebrate attack a female velvet ant. The complex of defensive and evasive behavior seems designed to deal with very rare predation events. Over time, however, rare events increase in probability, and female mutillids appear to be long-lived insects (Schmidt 1978; Donald Manley, Clemson Univ., pers. comm.). A very strong selective pressure for high investment in defense and adult longevity is understandable if reproductive opportunities tend to be rare and unpredictable. This is almost certainly true for mutillids in many environments where hosts are not aggregated. In central Florida, for example, ground-nesting aculeate Hymenoptera are usually distributed over great expanses of uniform sandy soil, and the nests are concealed in various ways. The mutillid must find the burrow of a species within a certain size range; it must either dig its way into the closed nest or overcome the active defenses of an adult host; it must find within the nest host larvae that are both accessible and of the right developmental stage. After watching many velvet ants for hours without ever seeing one even find a burrow (except in situations where hosts form aggregations), I am convinced that many hours or days of good searching weather are probably needed to find adequate numbers of hosts. If this is true, one would predict that non-aggregating ground-nesting bees and wasps might lose their mutillid parasitoids in northern parts of their ranges.

Research on mutillid biology is not likely to proceed rapidly. Inherent in the life-style of the velvet ants are factors that allow the field researcher to spend a long time without making a single observation of major biological significance. Many of the most interesting activities of velvet ants must take place in the depths of an underground burrow. Perhaps those of us who work with these insects are subliminally attracted to them because they share the pattern of a scientist's life of ceaseless, rather obsessive activity, with rare breakthroughs taking place in some obscure gallery where nobody notices them. Extreme persistence, and a research life prolonged by all possible means, must be our strategy.

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