COCOON MIMICRY AND PREDATION BY MYRMECOPHILOUS DIPTERA (DIPTERA: SYRPHIDAE)

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ABSTRACT

Three species of myrmecophilous *Microdon* (Diptera: Syrphidae) *M. albicomatus* Novak, *M. cothurnatus* Bigot, and *M. Piperi* Knab, exhibit aggressive mimicry as immatures. In nests of their host ants (species of *Camponotus* and *Formica*), the 1st and 2nd larval instars resemble the ant cocoons upon which they prey and are transported with the cocoons by workers. Immatures are not attacked by their host ants and appear to possess chemical as well as physical attributes providing integration with their host.

RESUMEN

Tres especies de myrmecophilous *Microdon* (Diptera: Syrphidae) *M. albicomatus* Novak, *M. cothurnatus* Bigot, y *M. piperi* Knab, exhiben mímica agresiva como inmaduros. En los nidos de sus hormigas hospederas (especies de *Camponotus* y *Formica*), el primero y segundo estadío larval se parece al capullo de su presa, los cuales son transportados junto con los capullos por las hormigas trabajadoras. Los inmaduros no son atacados por las hormigas hospederas, y parece que poseen atributos químicos lo mismo que físicos, que proveen una integración con su hospedero.

Ants, despite their elaborate social organization, are plagued by a multitude of other arthropods that live in their nests, from mites to members of their own family. The majority of these myrmecophilous arthropods feed upon ant brood, workers, food brought into the colony, or upon other organisms such as fungi which occur in the nest. In our investigations of the biology of one group of these ant guests, we encountered an unusual form of aggressive mimicry. The younger, immature stages of *Microdon* (Diptera: Syrphidae) closely resemble the ant cocoons upon which they prey and are transported with the brood by the workers.

Most *Microdon* are robust syrphid flies which spend their brief adult life searching for ant nests on which to oviposit. The immatures are unusual in appearance and were originally described as mollusks and scale insects before their true identity was realized. They are found almost exclusively in the nests of ants (Kistner 1982). Typical of the cyclorrhaphous flies (Diptera), *Microdon* exhibits three larval instars, followed by a prepupa and pupa which form inside the hardened integument of the 3rd instar, the puparium. The larvae, when active, creep through galleries or tunnels of ants. Until recently, larvae were assumed to feed upon either fungi, infrabuccal pellets of ants, or even upon tree sap oozing from gallery wood. However, since 1970 there have appeared reports of larvae of *M. baliopterus* Loew and *M. fuscipennis* (Macquart) feeding upon the larval brood of ants (Duffield 1981, Van Pelt & Van Pelt 1972) and of an African species found with *Crematogaster* ants possibly feeding upon pupae (Hocking 1970). It is not surprising that some of these reports also noted aggressive attacks upon larvae by the ants, suggesting that *Microdon* is merely a "persecuted guest" or synechthran in the Wasmannian sense (Wheeler 1901, Wilson 1971).

For most temperate species of *Microdon,* there appears to be only 1 generation a year, with the 3rd instar overwintering. Pupation occurs in the early spring about the time ants become active. The puparium of most species is heavily reticulated with fine anastomosing ridges over a strongly convex dorsal surface. In contrast to larvae, puparia are found most frequently near the drier surface of the nest away from the brood chambers. Presumably this provides the newly emerged adult a better opportunity to escape the nest undetected.

Our investigations involved 3 species of Nearctic *Microdon. Microdon albicomatus* Novak and *M. cothurnatus* Bigot are boreal species found in nests of species of *Formica,* while *M. piperi* Knab is found only in western North America in the nests of species of *Camponotus.*

MATERIALS AND METHODS

Laboratory observations were made of colonies placed in narrow, glass-sided boxes consisting of 2 panes of glass, 40 x 40 cm, held vertically, 2.5 cm apart, by a narrow frame. This provided an excellent view of interactions between host and myrmecophile. To reduce effects of room lighting upon the colony, red cellophane sheets were placed over the panes. Most observations were made using a Nikon stereomicroscope (magnification of 8 to 40X) handheld like a pair of binoculars. Fiber optics illumination was employed to enhance observations while minimizing heat transfer. These observations were based upon 3 colonies of ants, *Camponotus modoc* Wheeler, *Formica subnuda* Emery, and *F. neoclara* Emery, collected from northern Idaho (Latah and Clearwater counties) between July 6 and July 17, 1984. Observations were also made of *Microdon* with other species of ants in the field.

Microdon immatures collected in these same areas or obtained as eggs from laboratory reared and mated females were introduced into the colonies. Because the summer of 1984 in this region was delayed by 4-6 weeks, it was still possible to collect all stages of *Microdon* including adults. The colony of *Formica subnuda* already contained eggs and probably 1st instars of *M. cothurnatus* at time of collection. Although many young as well as mature ant brood were collected from this colony, the queen could not be found.

Field observations were made during 13 collecting trips into northern Idaho between June 19 and August 13. Laboratory colonies remained under surveillance until mid-August, long enough to follow development of newly hatched 1st instars to the late 3rd stage.

RESULTS

During our laboratory studies of larval feeding behavior, we saw *Camponotus modoc, Formica subnuda,* and *F. neoclara* workers transporting 1st and 2nd larval instars of *Microdon* from one brood chamber to another. Surprisingly, some larvae appeared to invite transport by laterally compressing their bodies so that they resembled ant cocoons in both size and shape. Most 2nd instars being carried were 5-8 mm long, while 384 *Camponotus modoc* pupae collected 30 June 1981 averaged 7.10 mm, SD = 1.29. During 3 field observations at partially excavated nests of *Formica subnuda*, *F. neoclara*, and *F. accreta* Francoeur between July 17 and August 1, many 2nd instars were observed undergoing lateral compression within several minutes of exposure to sunlight. They were then picked up by workers and, along with cocoons, were quickly transported into deeper, undisturbed parts of the nest (Fig. 1).

Third instars were never seen exhibiting this behavior or being transported. However, this is not surprising considering their heavy reticulations and bulk. In both laboratory and field nests, workers were observed carrying cocoons with 1 to several 1st or small 2nd instars of *Microdon* attached. In the laboratory, workers were also observed transporting ellipsoid-shaped aggregations of 1st and small 2nd instars. These aggregations appeared in brood chambers during periods of low brood density and consisted of as many as 6 larvae wrapped around each other, their smooth dorsal surfaces exposed. In size and surface texture, aggregations also resembled cocoons. This may increase the chance that larvae will encounter fresh brood in nests with widely separated brood chambers. While the carrying of myrmecophiles by their hosts has been reported by many investigators (Kistner 1982), such "cocoon mimicry" in relation to predation upon ant brood has apparently not.

Our studies clearly indicate that *Microdon albicomatus*, *M. cothurnatus*, and *M. piperi* are obligate predators upon the brood of their host ants. However, during more than 50 hours of observation of all stages of more than 112 larvae of the 3 species, we never observed any feeding upon ant eggs, and with one possible exception, when a 3rd instar was observed on a naked larva, never upon active larvae. Rather, *Microdon* larvae appeared to feed exclusively upon cocoon occupants: larvae, prepupae, or pupae. Both late 1st and all sizes of 2nd instars were observed crawling onto cocoons, cutting slits in the cocoon wall, entering the cocoons, and apparently feeding upon the occupants. Because of the nestbox structure, it was not possible to directly view activity within the cocoons. However, since the occupants were often later cut out of these cocoons by workers, it was possible to observe their shrivelled appearance. During an examination of the contents of 118 cocoons collected in one field nest of *Camponotus herculeanus* (L.) on July 17, 1 1st and 3 2nd instars of *M. piperi* were found on ant larvae/pupae inside the cocoons (Fig. 2). In 2 of these, the *Microdon* larvae had cut into the occupant, causing body fluids to ooze.

Often, when larger 2nd instars entered cocoons, the occupant, the *Microdon*, or both were forced partially out through the original slit or through a tear along a line of weakness in the cocoon wall. Third instars, which were too large to enter cocoons, cut a slit in the wall and inserted the buccal cone (buccal cone as used here refers to the larval head bearing the buccal opening, oral area surrounding the opening, sensory papillae, and antennae) to penetrate the occupant. Feeding as well as entry involved the use of larval mouthhooks. Feeding sessions were sometimes abruptly ended when workers pulled the cocoon away before feeding was completed. The workers were later seen licking the cocoon in the vicinity of the slit. In several instances, it was possible to see a shrunken pupa inside these retrieved cocoons. Larvae were never seen feeding upon booty such as freshly-killed crickets or meat, accepting regurgitated food from workers or brood, or feeding upon infrabuccal pellets, fungi, or tree sap.

Attacks by workers on *Microdon* larvae were extremely rare. The most aggressive action witnessed involved a worker biting and licking the anterior margin of a 3rd instar, forcing it to withdraw from the cocoon it was breaching. The attack lasted less than a minute, and the larva displayed no sign of injury. Workers occasionally licked the rough, dorsal surface of 3rd instars, but no more than they licked other objects within the nest. Obvious acts of aggression did occur when 2nd and 3rd instars of *M. albicomatus* and *M. corthurnatus* were introduced into the nest of an inappropriate host, *Camponotus modoc*. The *M. albicomatus* larvae were bitten and/or sprayed with

Fig. 1. *M. cothurnatus* 2nd instar being carried into nest by worker of *Formica subnuda*. A portion of the fringed marginal band of the larva is visible (arrow). An ant cocoon is under the gaster of the ant.

formic acid by workers, and none survived to molt to 3rd instars. The *M. cothurnatus* larvae were also killed and eaten. These observations suggest that some host records such as *M. cothurnatus* found with *Camponotus* species are incorrect (see Duffield 1981).

DISCUSSION

The lack of aggression by host ants, the existence of cocoon mimicry, and the transporting of larvae suggest that these species of *Microdon* are well integrated into colony life. As larvae, they are not synechthrans, i.e., "persecuted guests," nor synoeketes, i.e., "indifferently tolerated guests," as suggested by several authorities (Wheeler 1901, Wilson 1971), but are rather symphiles that are accepted into the colony.

Most well integrated myrmecophiles or ectosymbionts possess special physical adaptations such as exudatoria, glands or glandular trichomes dispensing appeasement substances, or a myrmecoid body form, and exhibit appropriate behavior such as orientation

Fig. 2. **Second instar of *M. piperi* in cocoon of** *Camponotus herculeanus*. **The** posterior spiracle of the larva is quite distinct (arrow).

to trail pheromones, release of appeasing or narcotizing chemicals, or stimulation of host regurgitation (Kistner 1982, Wilson 1971). These either circumvent the social code, as with appeasement, or take advantage of it, as with stimulating regurgitation by antennation. None of these adaptations are apparently available in *Microdon* despite some reports of ants licking larvae (Lopez and Bonaric 1977). Another way to take advantage of the code would be through acquiring or making the chemicals enabling ants to recognize their brood. For example, in the beetle *Myrmecaphodius excavaticollis* (Blanchard) (Coleoptera: Scarabaeidae), host cuticular hydrocarbons which significantly reduce aggression are acquired apparently by contact as well as by regurgitation (Vander Meer and Wojcik 1982). Also, 3 Staphylinid termitophiles make their own chemicals for mimicry (Howard et al. 1982).

Considering that 1st and 2nd instars of the 3 species of *Microdon* studied are physically similar and yet workers appear species-specific in their aggression, we assume that the aggressive mimicry is chemical as well as physical. If the 1st instar of *Microdon* gains access to a defenseless pupa in cocoon, it will not only find nourishment and protection from attack, but an opportunity to acquire recognition chemicals characteristic of the host. Upon its exit from the cocoon the 1st instar has gained the necessary chemicals to be accepted and even transported as brood. The possible dilution of such chemicals by growth of the larvae is partially compensated by the 2nd instar continuing to attack and enter cocoons.

It is clear that aggressive mimicry, involving chemical and physical characters, enables *Microdon* immatures to gain ready access to host brood. This strategy is very effective as evidenced by the failure of one laboratory colony to produce any adult ants. Heavy predation by *Microdon* eliminated cocoons as rapidly as they formed. In the field, the strategy is enhanced by oviposition occurring in late June-early July, simultaneous with appearance of cocoons in host nests. Indeed, the greatest proportions of 1st and 2nd instars were collected during mid- to late July when mature brood levels were highest. For example, the greatest number of pupae in *C. modoc* colonies occurred in July, 1982-84, (Hansen 1985). *Formica* colonies are similar in brood development. By mid-August, the proportion of these dwindled to less than 10% of the collection, with a concommitant decrease in ant brood. Probably, in early spring of the next year, prior to pupation, overwintering *Microdon* larvae feed upon the late summer-early fall generation of brood that begin to reach maturity in the spring.

The efficiency of the predation by *Microdon* immatures is perhaps offset by high mortality among 1st instars and adults, resulting in a peculiar bimodal mortality curve. Although we did not attempt to determine 1st instar mortality, 90% has been reported for one species of *Microdon* (Duffield 1981). In the laboratory, workers apparently do not hesitate to attack and kill adults shortly after their emergence (Wheeler 1908, Akre et al. 1973). However, 2 factors may reduce adult mortality in nature. Our field collections suggest that late 3rd instars move away from the brood and areas of intense worker activity toward the surface of the nest, probably in the spring. Also, most adults emerge in early morning, a time when ants are least active. Therefore, although *Microdon* immatures are efficient predators, high mortality in other stages suggest that these flies are not important regulators of *Camponotus* or *Formica* populations.

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REFERENCES CITED

AKRE, R. D., G. ALPERT, AND T. ALPERT. 1973. Life cycle and behavior of *Microdon cothurnatus* in Washington (Diptera: Syrphidae). J. Kansas Ent. Soc. 46: 327-338.

DUFFIELD, R. M. 1981. Biology of *Microdon fuscipennis* (Diptera: Syrphidae), with interpretations of the reproductive strategies of *Microdon* species found north of Mexico. Proc. Ent. Soc. Wash. 83: 716-724.

HANSEN, L. D. 1985. The biology of carpenter ants in Washington, Ph.D. dissertation. Department of Entomology, Washington State University. 131 p.

HOCKING, B. 1970. Insect associations with the swollen thorn acacias. Trans. R. Ent. Soc. London 122: 211-255.

HOWARD, R. W., C. A. MCDANIEL, AND G. J. BLOMQUIST. 1982. Chemical mimicry as an integrating mechanism for three termitophiles associated with *Reticulitermes virginicus (Banks). Psyche 89: 157-167.*

KISTNER, D. 1982. The Social Insects' Bestiary. Chapt. 1, pp. 1-244. *In* H. R. Hermann (ed.), Social Insects. Vol. III. Academic: New York. 459 p.

LOPEZ, A., AND J.-C. BONARIC.. 1977. Notes sur une numphe myrmécophile du genre *Microdon* (Diptera, Syrphidae): Éthologie et structure tégumentaire. Ann. Soc. Ent. Fr. (N.S.) 13: 131-137.

VANDER MEER, R. K., AND D. P. WOJCIK. 1982. Chemical mimicry in the myrmecophilous beetle *Myrmecaphodius excavaticollis.* Science 218: 806-808.

VAN PELT, A. F., AND S. A. VAN PELT. 1972. *Microdon* (Diptera: Syrphidae) in nests of *Monomorium* (Hymenoptera: Formicidae) in Texas. Ann. Ent. Soc. Am. 65: 977-978.

WHEELER, W. M. 1901. *Microdon* larvae in *Pseudomyrma* nests. Psyche 10: 222-224.

———. 1908. Studies on the Myrmecophiles. III. *Microdon.* J. New York Ent. Soc. 16: 202-213.

WILSON, E. O. 1971. The Insect Societies. Harvard/Belknap Press: Cambridge, Mass. 548 p.

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SEASONAL PATTERNS OF REPRODUCTION IN TWO SPECIES OF DESERT BEETLES (COLEOPTERA: TENEBRIONIDAE)

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ABSTRACT

Current literature on desert beetle activity infers that seasonality of beetle activity is temperature and rainfall dependent, reflecting reproductive activity. In this study 2 desert tenebrionid beetles were compared. *Eleodes hispilabris* Say fits the expectations for reproduction, gaving 1 reproductive bout coincident with rainfall. *Eusattus muricatus* LeConte, however, has at least 3 reproductive bouts during the activity period, only 1 of which coincides with rainfall.

E. muricatus, although smaller, lays larger eggs than does *E. hispilabris*. Larger eggs may increase egg survivorship during suboptimal timing of oviposition by decreasing egg surface to volume ratios and thus minimizing desiccation. Larger nutrient reserves may increase survivorship of newly hatched juveniles.

Gonadal effort by *E. hispilabris* was typical, i.e., females expended greater amounts of energy than did males. In *E. muricatus,* however, male gonadal effort exceeded that of females. This is discussed with respect to reproductive effort theory.

RESUMEN

La literatura actual sobre las actividades de escarabajos del desierto, infieren que la actividad estacional de los escarabajos depende de la temperatura y precipitación, reflejando la actividad reproductiva. Se compararon en este ensayo 2 escarabajos tenbriónidos del desierto. *Eleodes hispilabris* (Say) se ajusta a las expectaciones de reproducción, teniendo un turno reproductivo coincidente con la precipitación. Sin embargo, *Eusattus muricatus* LeConte, ha tenido por lo menos 3 turnos reproductivos durante el período de actividad, de los cuales solo uno coincide con la precipitación.