The Ecology and Behavior of a Subsocial Pentatomid Bug and Two Scelionid Wasps: Strategy and Counterstrategy in a Host and Its Parasites

WILLIAM G. EBERHARD

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ABSTRACT

Eberhard, William G. The Ecology and Behavior of a Subsocial Pentatomid Bug and Two Scelionid Wasps: Strategy and Counterstrategy in a Host and Its Parasites. *Smithsonian Contributions to Zoology*, number 205, 39 pages, 13 figures, 24 tables, 1975.—The tropical bug *Antiteuchus tripterus* and two parasites of its eggs, *Trissolcus bodkini* and *Phanuropsis semiflaviventris*, were studied in urban Cali, Colombia. Female bugs guard both their eggs and first instar nymphs. Behavioral observations, combined with analyses of the patterns of parasitism within egg masses of a given form, showed that the details of the bug's defensive behavior and the wasps' attacks strongly influence the survival rates of eggs in different positions in an egg mass.

By removing guarding female bugs from their eggs, it was shown that the net effect of their defense against generalized egg predators is to greatly improve egg survival but that, paradoxically, the net effect against the parasitic wasps is to decrease survival. Although the bugs repel wasps that have found egg masses, the bug's presence over the mass betrays the location of the eggs to hunting wasps. A hypothetical evolutionary history suggests that as the bugs improved their protection of eggs, they produced thinner egg shells, and that they are now trapped into continuing their defense in spite of subsequent advances by the wasps in their hunting behavior. Experimental removal of bugs guarding first instar nymphs and calculations of the cost of guarding in terms of egg production showed that the net effect of this guarding behavior is positive.

Female *P. semiflaviventris* tend to stay and hunt in the tree where they emerge, while *T. bodkini* females tend to disperse. Parasitism rates by *P. semiflaviventris* are strongly influenced by the species of tree where the bug eggs are laid, and both species are influenced by the site of the egg mass (leaf, branch, sucker), but in different ways. Both species also wait near bugs about to oviposit and attack eggs as they are laid, apparently recognizing gravid bugs visually. Parasitism rates of eggs on naturally and experimentally isolated leaves showed that search behavior is accomplished in flight.

Natural selection with respect to oviposition site varies greatly with tree species and the site on a given tree. The balance of selection was evidently different where the bugs evolved than in present-day Cali, where they commonly act against their own best interests.

Both wasp species agree in general with the behavior pattern for Scelionidae, but differ in several characteristics associated with oviposition. *P. semiflaviventris* is consistently farther from the family norm than is *T. bodkini*. The two species of wasp compete at two stages in their life cycle, with neither species consistently dominating. The males fight and exclude each other from egg masses where females will emerge, and multiple ovipositions into single bug eggs produce only single wasps. Both types of competition occur commonly in urban Cali.

Many other aspects of the natural history and ecology of the bugs and wasps are presented.

Contents

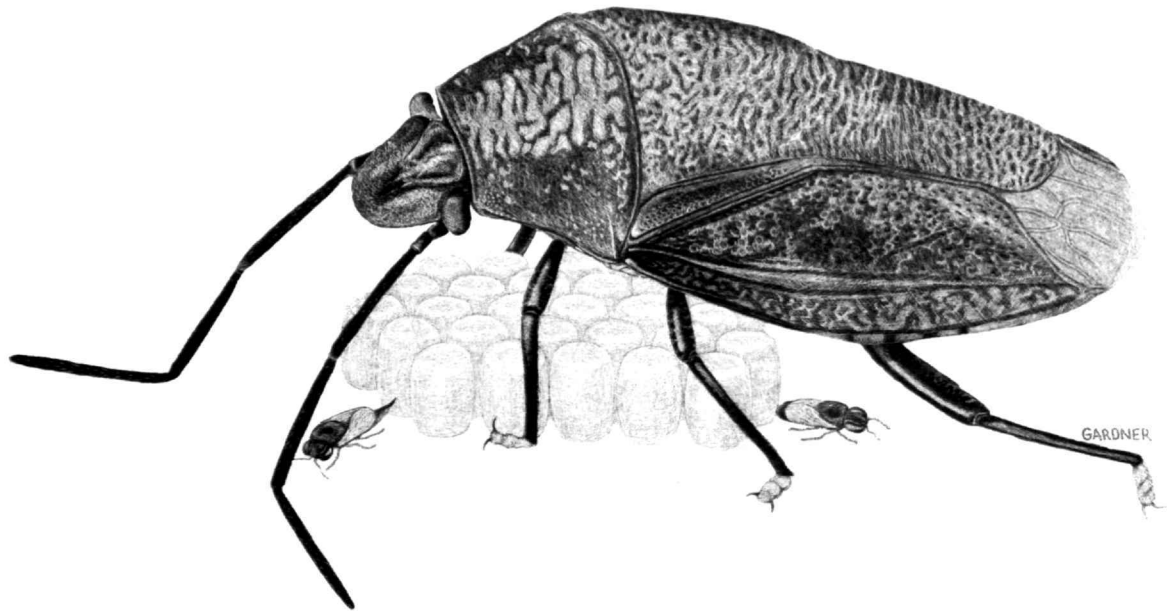FIGURE 1.—Female *A. tripterus* defending her eggs against the scelionid egg parasites *Trissolcus bodkini* (rear edge of egg mass) and *Phanuropsis semiflaviventris* (in front of bug). As the *P. semiflaviventris* female backs in with her abdomen extended, the bug lowers her antennae to the leaf and scrapes the edge of the egg mass with her front foot, and the *T. bodkini* female oviposits in an egg at the poorly guarded rear edge.

The Ecology and Behavior of a Subsocial Pentatomid Bug and Two Scelionid Wasps: Strategy and Counterstrategy in a Host and Its Parasites

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Introduction

This paper describes the natural history of the tropical pentatomid bug *Antiteuchus tripterus limbativentris* Ruckes and two parasitic wasps, *Trissolcus bodkini* and *Phanuropsis semiflaviventris* Girault, which attack the bug's eggs. Female bugs guard their eggs from the wasps and also guard their first instar nymphs. The wasps use special behavior patterns to overcome the female bug's defensive behavior and oviposit in her eggs (Figure 1). The wasp larva kills the bug embryo and consumes the entire contents of the egg; then it pupates and finally emerges as an adult from the egg (generally while the female bug is still standing guard over her nymphs) mates (usually with a sibling), and then leaves to seek out new eggs to parasitize.

The quantitative results of the bug's selection of oviposition site, of her defensive behavior, of competition between the two wasp species, and of the specialized attack behavior of one of the wasps (*P. semiflaviventris*) were measured by analyses of variations in the patterns of parasitism between and within egg masses and by experimental re-

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moval of defending bugs from their eggs and nymphs. Parental protection of the young (subsocial behavior) has evolved many times in the insects (see E. O. Wilson, 1971), and in the Hemiptera is known in 14 species in 12 genera (Bequeart, 1935; Odhiambo, 1959), but this is apparently the first detailed study of the precise effects of parental care in subsocial insects.

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Materials and Methods

Data used in this study were collected intermittently in and near Cali, Colombia, from November 1969 through December 1972 and in Bucaramanga, Colombia, in October of 1972. Voucher specimens of *A. tripterus, T. bodkini, P. semiflaviventris,* and all the species listed in Table 22 have been deposited in the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts 02138; other voucher specimens have been placed in the collection of the Universidad del Valle in Cali, Colombia.

Unless otherwise noted, all tests of significance were Chi². Two statistical procedures used need special explanation. Sometimes, in order to obtain large numbers of data to test hypotheses, it was necessary to sum the data from several trees having different parasitism rates. In these cases, the median was established for each tree and the data from that tree were classified as either above or below this median; finally, the data (above the median, below the median) were summed over several trees.

In comparing total parasitism rates (between trees, for example), it was not possible to use Chi² because host eggs were laid in groups and their probabilities of being parasitized were thus not independent. Instead, all masses in each sample with the usual number of 28 eggs were ordered on the basis of numbers of eggs parasitized, and then the two samples were compared using the Willcoxon Sum of Ranks Test.

The sticky material used to isolate trees and egg masses from walking insects was "Tack Trap," a nonvolatile, relatively inert substance manufactured by Animal Repellents, Inc., Griffin, Georgia, USA.

The reader should keep in mind that all of the observations were made in the highly unnatural environment of urban Cali and that great care must be used in extracting conclusions about the evolutionary interactions between the organisms involved on the basis of this data. For instance, the fact that the bug's oviposition preferences in Cali cause it to place most of its eggs in relatively high- rather than low-risk sites does not imply that natural selection has somehow failed to operate on the bugs; the most likely explanation is that one or several of the many causes of egg mortality is so modified in the urban environment that the relative mortality rates between oviposition sites are changed as compared to those in the environment in which the bug evolved. On the other hand, since many aspects of the behavior of both bugs and wasps are presumably innate and would be performed in the same way in any habitable environment in which the insects found themselves, certain types of evolutionary conclusions *can* be drawn. For instance, the fact that the bug's defense of its eggs, which gives numerous signs of being designed to combat the parasitic wasps, nevertheless increases rather than decreases the chances of parasitism by the wasps implies that the parasitic wasps have in some sense "out-evolved" their hosts. The behaviors involved—defense by the bug, searching and attack by the wasps—very likely are the same in "natural" situations (those in which the animals originally evolved, if such places still exist), and the net result of the bug's defense would thus also be the same.

The Natural History of
Antiteuchus tripterus limbativentris

Antiteuchus tripterus limbativentris Ruckes, a race described from the Cauca Valley of Colombia (Ruckes, 1966) belongs to the principally neotropical subfamily Discocephalinae. This species ranges from Panama to Paraguay. I have found it in Colombia in zones classified by Espinal and Montenegro (1963) as dry tropical forest (Cali and Palmira), humid semitropical forest (Bucaramanga), and humid tropical forest (Buenaventura). In places in Colombia it is an important pest of cultivated cocoa (cacao) and mango trees, and is apparently used as a folk cure for intestinal parasites (Kardonne, 1972). Naundorf (1954) and Sepulveda (1955) showed that the bug can act as a vector of the fungus *Monilia,* which attacks the fruit of cocoa. Lima (1940) notes that *A. amplus* also damages cocoa in Brazil, and Callan (1944b) records *A. piceus* as a minor cocoa pest in Trinidad. Rau (1918), Callan (1944a), and Kirkpatrick (1957) have observed that *A. tripterus* females stand guard over eggs and first instar nymphs, and Callan, Kirkpatrick, and Sepulveda (1955) all deduced from the pattern of parasitism of several egg masses that the bug's defense was at least partially effective against the scelionid egg parasite *Phanu-*

ropsis semiflaviventris. Callan (1944b) recorded maternal care in several additional Antiteuchus species, including A. (A.) piceus, mixtus, and variolus, and A. (Neodine) macraspis.

DISTRIBUTION AND HOST PLANTS OF THE BUGS

The bug A. tripterus is extremely common in trees and bushes in urban Cali, Colombia. The bugs were nonspecific in their host plant selection and were found on the trees Pithecelobium dulce (Combretaceae—an exotic), Canagium odoratum (Anonaceae—also an exotic), Cassia sp. (Cesalpinaceae), Lagerstromia speciosa (Litraceae), Crescentia cujete (Bignoniaceae), cocoa (Theobroma cacao—Sterculiaceae), and mango (Mangifera indica—Anacardiaceae). They also occurred on the shrubs Malvavicus arboreus (Malvaceae), Hibiscus sp. (Malvaceae), Heliconia sp. (Musaceae), and Bouganvilla glabra (Mictaginaceae). In the countryside near Cali the bugs were found on P. dulce, Calliandra sp., Croton sp. (Euphorbiaceae), and Tabebuia chrysantha (Bignoniaceae). Sepulveda (1955) presents a similarly varied host list. Bug populations were generally larger on some species of plants (such as P. dulce, T. catappa, and Cassia sp.) than on others (such as B. glabra, M. indica, and Heliconia sp.), and the majority of my observations were made on the first three species.

Bugs were much more common on plants inside the city than outside. This difference was clear on two species of trees (P. dulce and Calliandra sp.) that occurred commonly in both areas. It also appeared that within the city the bugs tended to be more common where there was heavy pedestrian and/or automobile traffic. For instance, nine small P. dulce trees at the edge of a park near the center of the city (along the Rio Cali), where many people walked, supported heavy bug populations, while other similar trees 10–20 m inside the park had fewer bugs. The reason for these tendencies is unknown.

The size and form of a plant also appeared to influence its attractiveness to A. tripterus. Trees or bushes of a given species having denser growth tended to have more bugs. In the case of P. dulce, many large and small trees were searched, and although the absolute bug populations could not usually be determined, it was certain that the densest populations were in medium and small

trees. The bugs were very common. One particularly densely populated tree was about 2.5 m high at the center and about 7 m in diameter, and had over 200 female bugs guarding eggs or nymphs at one time. Based on surveys in other trees, this represents a total adult population of about 2400 bugs.

The effects of both tree form and location on population size were relatively weak within the city, however, and I was not able to correctly predict how many bugs a given tree would have. Bug populations in individual trees sometimes changed substantially over time.

EGGS

DESCRIPTION.—Eggs were barrel-shaped, 1.47 mm tall and 0.97 mm in diameter, and lacked the spines (chorionic processes) found on the rims of many pentatomid eggs (Esselbaugh, 1947). Their cuticle was smooth and relatively thin and weak compared with those of the eggs of other pentatomids such as Nezara sp., Supputius sp., Podisus cloelia, and Loxa sp. The cap was the strongest part and was reinforced by a fine network of small ridges on its inner surface.

Two distinct colors of unparasitized eggs could often be distinguished within the same mass. Usually (perhaps always—some differences were difficult to be sure of) a group of 28 had 14 of one color and 14 of another. Most of the eggs of a given color were usually grouped more or less together. In some cases where the order of oviposition could be deduced (see below), it was clear that the eggs of one color were all laid before any of the others. Dissection of a female killed just after laying the 14th egg of a mass showed that each of her 14 ovarioles had lost one egg and had one left. Thus the differences in color of the eggs seem to be associated with the position (basal or apical) of the eggs in the ovariole.

Almost all embryos in a given group of eggs were usually oriented in the same direction within their eggs (upward with their ventral surfaces all oriented in the same direction), but usually at

TABLE 1.—Sizes of egg masses (N=230)

Number of eggs in the mass:	28	27	26	14
Frequency:	90%	6%	3%	1%

TABLE 2.—*Frequency of masses of 28 eggs that were in the "compact" form (Figure 12) in different tree species*

Location	P. dulce	Cassia sp.	Canagium odoratum	T. catappa
Leaves	32% (N=766)	44% (N=406)	27% (N=189)	42% (N=224)
Branches	32% (N=236)			

least one or two embryos in each group were substantially out of line dorsoventrally with the others. Since the female's bug orientation during oviposition was constant, these eggs must have turned before or as they emerged.

SITES AND ARRANGEMENTS.—As shown in Table 1, there were almost always 28 eggs in each egg mass. The eggs in masses were generally closely packed, and the most common arrangement was the "compact" form pictured in Figure 12, with minor variations on this (such as that in Figure 4) also relatively common. The frequency of the compact arrangement varied with the species of tree, as shown in Table 2; both *T. catappa* and *Cassia* sp. differ significantly (p<0.05) from both *C. odoratum* and *P. dulce*. Since compact egg masses were

TABLE 3.—*Relationship between total number of egg masses in a P. dulce tree and the frequency of oviposition on leaves vs. branches (p <.01)*

Site	Trees with > 20 guarded egg masses	Trees with < 20 guarded egg masses
Leaves	88%	76%
Branches	12%	24%
Number of masses	1308	106
Number of trees	13	9

less heavily parasitized than others (below), these differences may influence parasitism rates on different trees.

As in other pentatomids (Esselbaugh, 1946), the eggs were usually laid on the undersurfaces of leaves or branches. As shown in Table 3, there was a positive correlation on *P. dulce* trees between the relative numbers of masses on leaves vs. branches and the total number of egg masses on the tree (probably an indirect measure of the adult population). This does not necessarily mean that the bugs were reacting directly to the population size on a given tree, as an additional factor or factors could influence both population size and choice of egg sites.

Compact masses of eggs on leaves were usually oriented so that the group's longitudinal axis was parallel to that of the leaf and its pointed end was toward the leaf tip, but this varied somewhat in different species of tree (Table 4). The orientation of masses on *T. catappa* was significantly different from those on the other tree species: it may be that the greater size of its leaves is somehow responsible for the difference (Figure 2). Since the orientation of the defending bug is highly correlated with the orientation of the egg mass, and the orientation of the bug is probably in turn correlated with the hunting behavior of egg parasites (below), the consistent orientation of the egg masses on leaves may be the result of selection pressure exercised by hunting wasps.

Figure 3 shows how oviposition sites varied with leaf size. On leaves from 3–10 cm long, the eggs were nearly always placed near the base. On very small leaves (less than 2 cm long) they tended to be nearer to the tip (p<0.05), while on very large leaves they were distributed randomly. The function of the tendency to place eggs near leaf bases is

TABLE 4.—*Orientation of "compact" egg masses on the leaves of different trees*

Orientation	P. dulce	Cassia sp.	Canagium odoratum	T. catappa
Longitudinal axis more nearly parallel than perpendicular to leaf axis	100%	97%	90%	65%
Those so aligned which had point of group toward leaf tip	95%	95%	98%	69%
Total number of masses observed	163	132	50	87

not certain, but it may serve to protect them from water damage. On observing the undersides of *Cassia* sp. and *P. dulce* leaves just after a rain, I found that the water standing on them was concentrated along the lower edge of the leaf, and in most cases this was the tip of the leaf. Thus eggs at leaf bases are probably less likely to be covered with water during and after rain. Experimental immersal of eggs in water for various lengths of time showed that older eggs were killed more readily and that appreciable reduction in hatching was first seen after between 6 and 9 hours of immersion, when it fell from 70% to 10%.

The apparently random positioning of eggs on large leaves and their placement toward the tips of small leaves do not at first seem to fit this explanation. Observations of large *T. catappa* leaves just after rain indicate, however, that they seldom get wet at all on the underside where the bug eggs are nearly always located; and placement of eggs nearer the bases of leaves less than 2 cm long might be physically difficult for the bug (length about 1 cm) since it lays the eggs nearest the leaf base last, and would thus have to actually climb off the leaf to lay eggs nearer to the leaf base.

DEVELOPMENT.—No structure was visible within the eggs until 3.5–4 days after oviposition (the times varied somewhat, presumably due to temperature variations), when the embryo's eyes and egg burster became preceptible. They darkened gradually (but did not grow in size) until the nymphs hatched 130–170 hours (about 5.5–7 days) after being laid. Sepulveda (1955), working in nearby Palmira on cocoa (which is grown in the shade and may have been cooler), reports the egg life as 9–13 days. Eclosion times were spread over up to 12 hours in a given egg mass, but no pattern in the sequence of hatching was discernible.
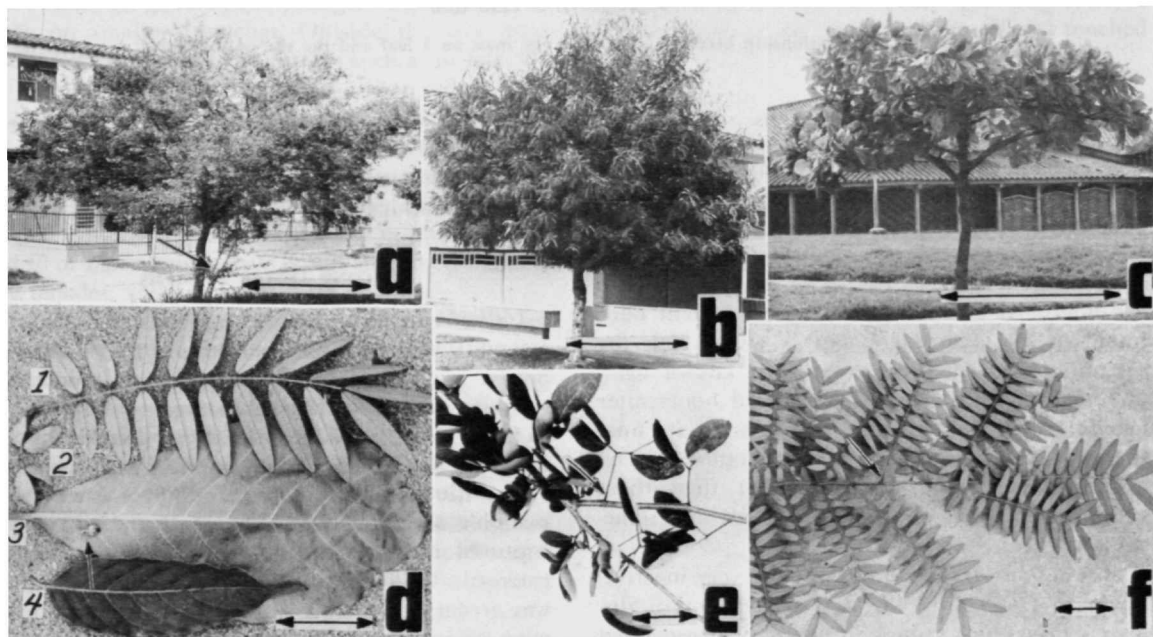
FIGURE 2.—Typical forms of the trees studied most intensively: *a, Pithecelobium dulce* (arrow marks suckers); *b, Cassia* sp.; *c, Terminalia catappa*; *d,* leaves of (1) *Cassia* sp., (2) *P. dulce*, (3) *T. catappa*, and (4) *Canagium odoratum* (arrow marks bug guarding eggs); *e,* pattern of leaf growth in *P. dulce* (arrow marks site where sticky substance was applied in isolation experiments); *f,* pattern of leaf growth in *Cassia* sp. (arrow marks site where sticky substance was applied in isolation experiments). (The scale bars in *a, b,* and *c* are approximately 2 m, those in *d* and *e* are 5 cm, and that in *f* is 10 cm.)
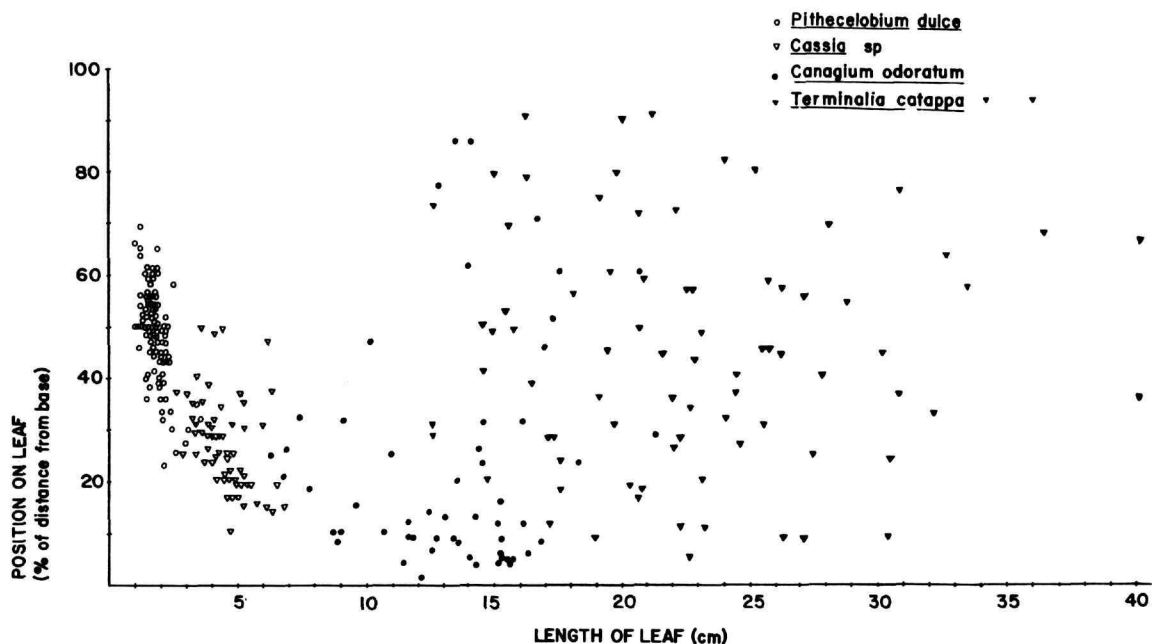
FIGURE 3.—The relationship between position of egg mass on a leaf and the size of the leaf.

FIRST INSTAR NYMPHS

Sepulveda (1955) found five nymphal instars in *A. tripterus*, lasting on the average 7, 12.5, 22.5, 12.5, and 18 days respectively.

Newly emerged nymphs were relatively pale, but acquired their final red-and-black markings within five hours. At first they lacked the repellent odor found in all later stages, but it was found (by squashing and smelling nymphs of known ages) that they began to smell faintly nine hours after hatching, and did not have the odor at its final strength until after more than 10 hours. Young nymphs were rounder and less flat than those which were several days old, and were also somewhat less active when disturbed.

First instar nymphs were generally very inactive, staying very close to the egg mass. Nymphs displaced from their groups in captivity reassembled around hatched and unhatched egg masses and/or other nymphs, but not around adult females. Assembled nymphs always touched either the eggs and/or other nymphs (Figure 5b).

The first instar lasted approximately a week both in nature and captivity, with variations of more than a day. It is probable that the first instar nymphs did not feed, as nymphs raised in plastic vials with water but no food succeeded in moulting to the second instar.

SECOND INSTAR NYMPHS

Individuals from a given egg mass moulted to second instar within a period of up to several hours. Usually a nymph prepared to moult by climbing onto the surface of the eggs and appeared to fix its tarsal claws into the eggs by slowly hooking their surfaces and gently pulling with each leg several times. After about a minute's pause, the nymph's abdomen began to contract, its cuticle ruptured dorsally, and the second instar nymph emerged. This moult (and all subsequent moults) was accompanied by a temporary loss of repellent odor, which remained with the shed skin, and this was probably an especially dangerous time for the bugs (see Table 22). Second instar nymphs reacquired their odor within 35–45 minutes after moulting.

Newly moulted second instar nymphs were nearly white with a few red markings, but they darkened

within a few hours to brown with black markings (see Sepulveda, 1955, for detailed descriptions of all nymphs). They were longer and wider than first instars (3.1 mm long × 2.4 mm wide vs. 2.4 mm × 1.7 mm), but flatter and thinner, and were much more active. They dispersed readily when disturbed and, if not disturbed, left the egg mass two to three days after moulting. The nymphs apparently began to feed in this stage, and were found alone on leaves and twigs far from the nearest egg mass. They showed little or no gregariousness after leaving the vicinity of the egg mass, contrary to the observations of Callan (1944b) on *A. tripterus* and *A. picea.*

Older Nymphs and Adults

Bugs which had left the egg mass were almost always found on branches and trunks rather than leaves, except on the very large leaves of *T. catappa* where nymphs were often seen along the central leaf veins. In general, the younger stages tended to stay on smaller branches. Outside the city most bugs were found in hidden spots such as in crotches and under tufts of lichen, but in urban trees, which had fewer epiphytes and thus fewer hiding places, they showed little tendency to concealment except that they usually stayed on the lower rather than the upper surfaces of branches. In some trees the older nymphs and adults clustered in groups of up to 40 or more; one sample group contained 7 males, 10 females, and 11 penultimate nymphs.

Oviposition.—Most adult bugs were found on twigs and branches, but females with swollen abdomens were not uncommonly found resting quietly on the undersides of leaves. These females were evidently ready to oviposit, as they generally laid eggs within several days without feeding when brought into captivity. In those trees on whose leaves the female usually faced the tip while guarding her eggs (below), the swollen females also usually faced the leaf tip. This immobile stage may represent a period during which the female "monitors" the characteristics of a potential oviposition site before laying her eggs there. Females may change sites several times before finally ovipositing; when I marked the leaves on which five such females were resting (I tried not to disturb the bug as I marked the leaf), all were deserted several days later. These movements may serve as defense against parasitic wasps which have located gravid bugs before they are ready to lay (below).

The act of oviposition was observed on seven occasions, and the movements were relatively constant. Figure 4 shows the sequence of the last 21 eggs laid in one egg mass and illustrates a pattern of placement also seen in other ovipositions. The bug laid a line of three eggs (i.e., numbers 12, 13, and 14) on one side of the group, then two (i.e., 15 and 16) on the other side, and then repeated this sequence. This behavior appears to be designed to produce compact masses like that in Figure 12.

The bug began laying an egg by moving forward until the tip of her abdomen was in line with the front edge of the group of eggs already laid. Then, swinging her abdomen slightly from side to side, she positioned its tip in the groove between two of these eggs. The side-to-side movements probably enabled her to feel the positions of already laid eggs (which she could not see), possibly using the laterotergites of segment nine. The bug lowered her abdomen as she positioned herself and touched
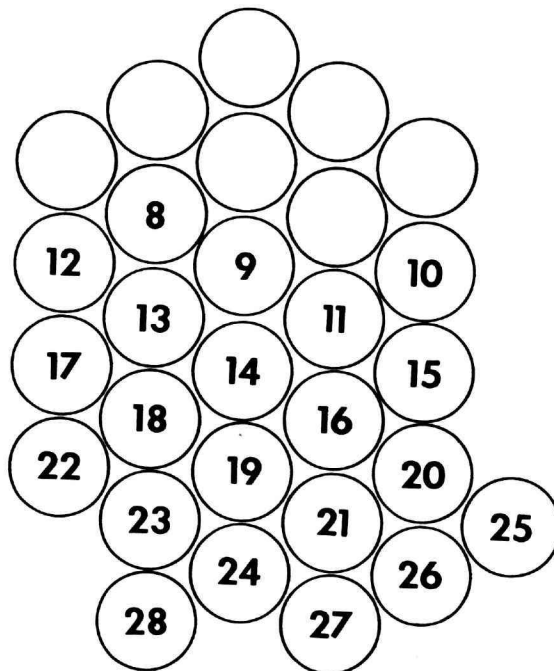
Figure 4.—The sequence of the last 21 eggs laid by a female *A. tripterus.*

the emerging egg to the leaf. Then, moving slightly backward and lifting her abdomen, she drew the egg out and tilted it back against the sides of the eggs already laid.

Females paused from 15 to 60 seconds between ovipositions, some bugs moving backward and more or less covering the egg mass during these pauses, others moving back only slightly. The backward movement may play a part in the defense of the eggs against parasitic wasps (below). Laying females generally faced the base of the leaf, and after completing a mass of eggs, they turned 180° and scraped the sides of the mass several times before settling down—probably another defense against wasps.

The period of time between a female's abandonment of her second instar nymphs and the laying of her next egg mass was determined in the following way. Bugs caught guarding second instar nymphs on *P. dulce* trees (i.e., females no more than a day or two away from deserting their nymphs) were placed in a sleeve cage on another *P. dulce*. The mean time (to the nearest day) to the next oviposition in two such experiments was about 17 days (Table 5). Thus the normal time between ovipositions is probably on the order of 30–35 days (7 days guarding eggs, plus 7 days guarding first instar nymphs, plus 1–2 days guarding second instar nymphs, plus about 17 days of feeding to prepare for the next oviposition).

Since female bugs probably seldom if ever feed while guarding, and since females guarding eggs have more fat than those guarding second instar nymphs (below), it seemed likely that females found guarding new eggs would be able to reovi-

TABLE 5.—*Number of days required by female bugs to reoviposit*

Treatment	Average	Range	Number of bugs
Females removed from groups of second instar nymphs			
Experiment 1	16.6	12–21	13
Experiment 2	17.2	13–25	35
Females removed from newly laid eggs			
Experiment 1	20	16–25	21
Females removed from groups of newly hatched first instars			
Experiment 2	19	14–24	22

posit sooner when removed from their eggs than those removed from second instar nymphs. Just the opposite was true, however, as 21 females which were found on new eggs and placed in the same sleeve cage, on the same day, with the females removed from second instar nymphs in the first experiment described above averaged 20 days to the next oviposition, requiring significantly longer (p<0.002, Willcoxon Sum of Ranks Test) than the others (Table 5). A similar experiment, during somewhat cooler weather and involving females taken from newly hatched first instar nymphs and others taken from second instar nymphs, gave median reoviposition time of 19 and 17 days respectively (Table 5), the females from second instar nymphs again laying eggs in significantly shorter time (p<0.01, Willcoxon Sum of Ranks Test). These data suggest that the female undergoes some sort of hormonal cycle controlling fat and/or egg synthesis even when out of contact with her eggs and nymphs.

These data should perhaps be treated with caution, at least concerning the absolute lengths of interoviposition periods, since of 35 masses laid by females removed from second instar nymphs in the second experiment 8 had only 14 eggs (differs from Table 1, (p<0.01). Only females taken from second instars showed this behavior, as none of 22 masses laid during the same time by females from first instar nymphs had 14 eggs (p<0.05). However, dissections of bugs found guarding newly laid masses with less than 28 eggs showed that females probably usually do have a full complement of 28 eggs ready to lay, but may fail to lay some of them. Each of four females on masses of 14 eggs had 14 more eggs of nearly identical size inside her abdomen and a fifth female on a mass of 15 had 11 more eggs inside.

MIGRATION.—The great majority of nymphs and adults on one *P. dulce* tree were removed by hand on 11–13 September 1972, and the tree was then revisited and again cleaned of adults and larger nymphs 16 and 25 days later. These repeat visits revealed a substantial rate of immigration; 214 females and 213 males were found during the first re-collection and 71 and 79 during the second, giving a combined rate of 11.5 females and 11.7 males arriving at the tree per day. This figure may be slightly high as a few adults were undoubtedly missed during the first collection. The study tree

was not isolated, being part of a row of *P. dulce* and only about 2 m and 8 m from its nearest neighbors (trunk-to-trunk distances), both of which had substantial bug populations. Nevertheless, this high rate of movement between trees was unexpected because (1) *A. tripterus* is not an especially good flier and even dislodged bugs usually simply circled and flew back upwind to land on the tree where they had been, and (2) bugs were seldom seen flying, even in densely populated areas.

The original collection of adults from this tree had 518 males and 696 females or a ratio of 0.74 male:female. Assuming that the male:female ratio in the trees from which the immigrants came was the same, the relatively large number of males which actually arrived suggests that males are more mobile than females (p<0.01). This is perhaps not surprising since females are immobile approximately two weeks while guarding the eggs and nymphs of each brood. Since they live approximately 80 days as adults (Sepulveda, 1955) and probably lay 2–3 batches of eggs, this would amount to 35%–50% of their life spent immobile. In fact, assuming conservatively that females spend only 35% of their time guarding, that both sexes migrate equally, and that the total sex ratio in the population is 0.74:1 male:female, the expected numbers of arriving males and females would be 306 and 269, not significantly different from the observed 292 and 285.

Migrating females were apparently more likely to lay eggs than others. Thus 22.2% of the 696 females in the first collection were guarding eggs or nymphs; assuming a steady immigration rate (11.5 females/day) and the frequency of oviposition calculated from the first collection (0.017 mass/female/day), only 33 of the immigrant females should have been guarding offspring rather than the observed 58 (p<0.01).

The relative numbers of nymphs and adults found in this tree suggest the additional conclusion that, despite the high rate of arrivals, even more bugs left the tree than arrived. Relatively careful counts of the numbers of unhatched eggs present 16, 9, and 1 week(s) before the first collection indicated that the adult female population was approximately constant during this period. Since the total time from egg to adult is about 10 weeks (Sepulveda, 1955), relatively constant numbers of adults were being produced from nymphs

during at least the last 6 weeks before the first collection was made. The total number of last (5th) instar nymphs found on the tree in the first collection was 1108, or approximately 90% of the total number of adults. Since substantial movements between trees by nymphs are unlikely, and since the duration of the 5th instar is only about 20% that of the adult, it appears that a large portion of the bugs which grew up on the tree left after reaching maturity.

Several isolated observations indicated that adult bugs of both sexes leave in especially large numbers when trees shed their leaves. The best studied case was in one *P. dulce*, which had had weekly counts of 60–75 masses of unhatched bug eggs for five weeks; within three weeks during which the tree was shedding, the count fell to 5 masses. Observations of the trunk and branches showed that the entire adult population in this tree had dropped dramatically.

Other more casual observations also associated shedding with bug desertion in both *P. dulce* and *T. catappa* trees. None of the four tree species which were observed most intensively seemed to have an established season for shedding and, with the exception of some individuals of *T. catappa*, these trees were never completely without leaves, new ones emerging before the last of the old ones fell. I saw no dramatic fluctuations in bug populations during the erratic dry and wet seasons in Cali, but did not make careful long-range counts. Eggs were found at all times of the year.

OTHER BEHAVIOR.—Mating, feeding, and defecation were seen on trunks and branches. I found six mating pairs, each with the two bugs facing away from each other. Feeding bugs often held the tips of their abdomens lifted away from the branch, and sometimes appeared to have difficulty withdrawing their prosboces from the wood when disturbed. Although ants such as *Ectatomma ruidum* and *Campanotus* sp. often tended membracids and coccids in trees harboring *A. tripterus*, I never saw an ant show any sign of interest in a bug. The bugs lifted their abdomens when they defecated a clear, tasteless (to me) liquid, several drops at a time.

Both adults and nymphs gave characteristic responses when they were disturbed by bugs or other objects which approached them. The most common responses were to antennate toward the object, to give a brief "shudder" of the entire body,

and to walk away. Upon more intense disturbance (pinching a foot, for example), both nymphs and adults kicked at the offending object with the middle or hind legs and/or gave off an unpleasant odor. In favorable lighting one could sometimes see the adults squirt the substance several centimeters laterally. Usually they buzzed their wings for several seconds a minute or so later, perhaps to rid themselves of any liquid still clinging to their bodies. This behavior is probably what Callan (1944b) took to be part of the defensive behavior of females guarding eggs.

The repellent substance was poisonous and both bugs and their eggs were killed by being placed in a jar where adults had recently given off odor. On two occasions I saw a first instar nymph die within a minute after being hit directly by a spray (I had pushed the female partway off her group of nymphs). The substance was painful when placed on soft areas of my skin or near my eyes and also apparently corroded the plastic of a pen which I used to nudge females off their groups of eggs and nymphs.

Both males and females had bright orange bands along the lateral edges of the ventral surface of their abdomens. When adult bugs were disturbed by the wasp *Bicyrtes variegata* (a predator on large nymphs—see Eberhard, in press), or by other stimuli approaching them more or less dorsally, they sometimes tilted their bodies laterally, a movement probably designed to facilitate spraying the offending object with repellent fluid (which was ejected from openings near the bases of the legs). The orange flanks of the bugs were also exposed by this tilting of the body and the coloration may thus be aposematic in function.

Adult males were usually darker (dark brown) dorsally than females (tan to brown). I was able to correctly guess the sex of 71 of 75 bugs in the field solely on the basis of their dorsal coloration, missing two males and two females.

Bugs resting on the undersides of *T. catappa* leaves in bright sunlight extended their legs to lift their bodies away from the leaf surface, a movement probably serving in temperature regulation. Bugs in raised positions lowered themselves within a few minutes when their leaves were shaded, and rose up again when the shade was removed. Both bugs guarding eggs and others raised themselves in this way, but guarding bugs immediately

lowered themselves when disturbed by an approaching object or shadow.

BEHAVIOR OF FEMALES GUARDING EGGS AND NYMPHS

Female *A. tripterus* stood over their eggs and nymphs both night and day and responded to various types of disturbances. They kept the eggs under the front part of their bodies (Figure 5) and were not easily displaced by pushing or pulling. Their defensive movements included: tilting the body toward the disturbance (thus forming a shield between it and the eggs or nymphs); waving one or both antennae toward it; shaking the entire body with quick shuddering movements; scraping the edge of the egg mass with the front legs (usually done alternately, with the bug swinging her body laterally so that she scraped along most or all of the entire front and lateral edge of the mass, although occasionally they also scraped with their middle legs); and kicking backward with the hind and middle legs. Antennal and, to a lesser extent, leg movements were directed toward the disturbing stimulus. First instar nymphs clustered below the female did not generally respond to her defensive movements, but second instars often dispersed.

When female defensive responses were tested by presenting the bugs with a model parasitic wasp, females guarding eggs gave somewhat different responses than those guarding nymphs. The model consisted of a small bit of black paper about the size of a parasitic wasp glued to the end of a 15 mm clear nylon thread that was fixed to the end of a 25 cm glass tube. The stimulus was moved near the bug in approximately the pattern shown in Figure 6. Visual stimuli from my hand may have also stimulated the bug and, since she usually moved her antennae toward the model as it approached, presentations often involved tactile stimulation as well. It was clear from these tests and from observations of wasp-bug interactions, however, that the sight alone of a wasplike object would release the bug's defensive behavior.

The frequencies of the various defensive responses are presented in Table 6. Scraping behavior diminished significantly when the bugs were guarding nymphs, but shuddering increased. It is reasonable that scraping should decrease since (1) the female might damage her nymphs or knock them off the leaf, and (2) there is no longer any

danger of parasitism by the wasps against which this movement is particularly effective. The significance of the change in shuddering behavior is not known.

Only very seldom, and only in moments of great duress, did bugs battling wasps give off enough odor for me to sense it. I also had the strong impression that bugs guarding eggs were much less likely to discharge the poisonous repellent odor when I disturbed them than were bugs over nymphs or nonguarding bugs.

Female bugs showed no sign of being able to distinguish their own eggs from those of others and it was possible to transfer females to new egg masses if the bug was moved directly from one to the other. The longer the bug was out of contact with eggs, however, the less likely she was to accept the new group (even if she was placed back on her original mass). On several occasions I saw a female which had apparently changed groups spontaneously, leaving a group of new eggs unguarded as she stood over a nearby group of old, empty eggs.

Females guarding nymphs were apparently more attracted by the nymphs than by the mass of empty eggs, as several females whose nymphs had clustered a centimeter or so from the egg mass were standing over the nymphs rather than the eggs. Females did not show any response to stray nymphs, however.

Female bugs probably seldom if ever fed while guarding eggs or nymphs, since I never saw a guarding female feed and since adults were seen feeding only on trunks and branches, never on leaves where most eggs were located. The defensive behavior of a female with her proboscis stuck in the plant would probably be less effective since she would be less mobile, and this may explain the female's abstinence. Sepulveda (1955) noted puncture marks near egg masses on the stems of cocoa pods and speculated that defending females may feed. The evidence is weak, however, since stems are a preferred feeding site for eggless bugs (Naundorf, 1954). Dissections of ten females collected guarding newly laid eggs and of ten others collected guarding second instar nymphs also indicated that defending females fed little, if at all. The females from new eggs all had moderate to large fat bodies, while the others, which had been
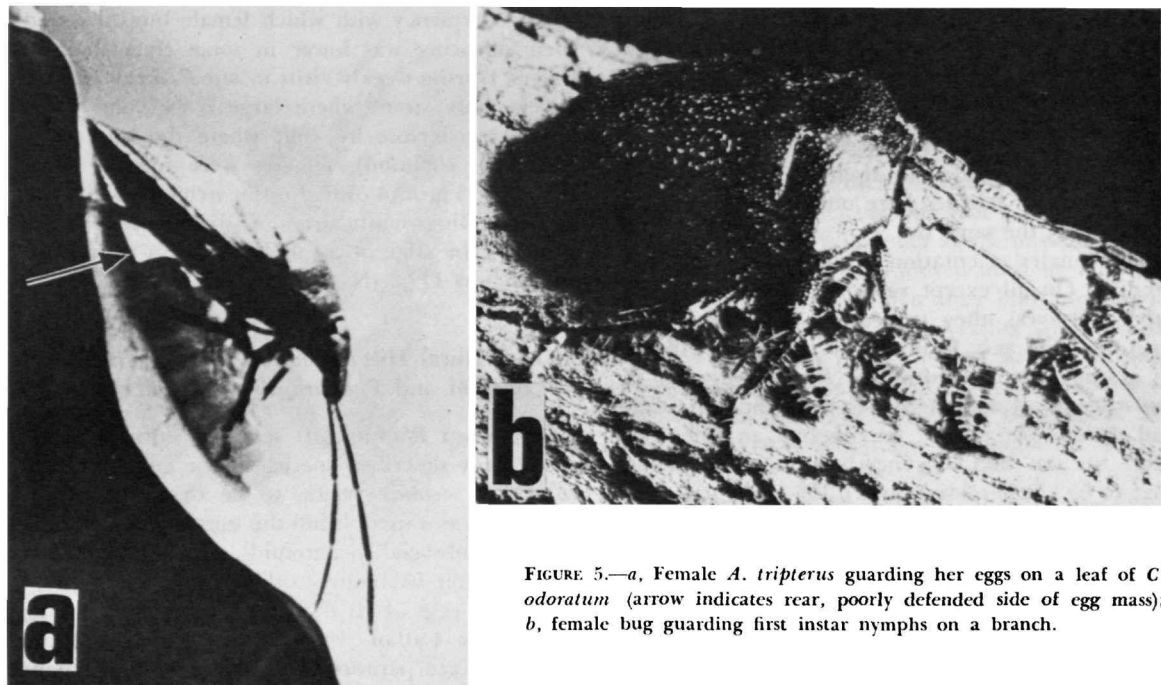

FIGURE 5.—a, Female A. tripterus guarding her eggs on a leaf of C. odoratum (arrow indicates rear, poorly defended side of egg mass); b, female bug guarding first instar nymphs on a branch.
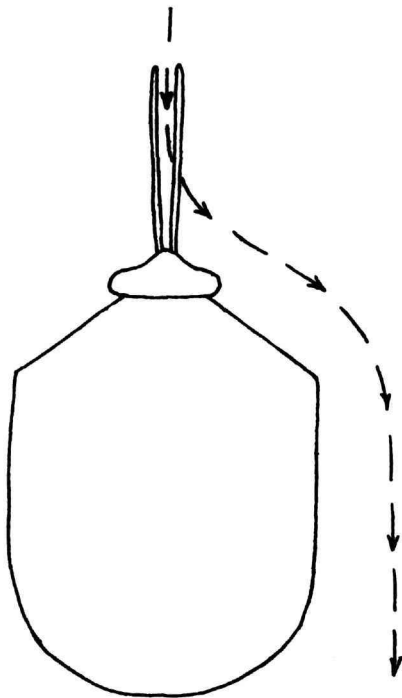
FIGURE 6.—Pattern of presentation of model wasp to defending female bug.

TABLE 6.—*Responses of defending female bugs to artificial "wasp" stimuli*

Bug's response	Bug guarding eggs (43 trials)	Bug guarding nymphs (42 trials)
Move antenna toward stimulus	43	42
Lean toward stimulus	42	41
Move toward stimulus	38	41
Shudder	17*	36*
Scrape	28*	8*
Kick	16	24

*Differ significantly ($p < .05$).

guarding for about two weeks, had small or at most moderate fat bodies. Most of the fat was probably used to maintain the bug itself, as the ovaries in both groups of females were undeveloped and approximately the same size.

The females' orientation as they guarded was not random. On all except very large leaves (i.e., *T. catappa* leaves), they tended to align themselves with the leaf's axis, facing either its base or its tip. In a study of the position of female bugs on *P. dulce* leaves, it appeared that both the leaf itself and, to a lesser extent, gravity had an orienting effect on the bug. On nearly horizontal leaves, 83% of 69 females faced toward the tip rather than the base; on leaves with their bases below their tips, this percentage was 73% ($N = 66$); and on leaves with their tips below their bases, it was 94% ($N = 522$) (the last two figures differ significantly, $p < 0.01$). This orientation, which would seem to make the bug less able to sense dangers arriving at its leaf by walking along the stem, may be a result of the parasitic wasp's tendency to hunt in flight.

The orientation of females when guarding compact egg masses like that in Figure 12 was also far from random, even on *T. catappa* leaves where the egg mass itself was often not aligned with the leaf's axis (Table 4). Of 94 females found on such groups in *T. catappa*, 92% faced so their heads were over the pointed end of the group (the top of the group in Figure 12). This consistency probably aids in the defense of the group by bringing the bug's front legs to bear on the smooth sides of the mass where their scraping will be most effective.

The frequency with which female bugs deserted their offspring was lower in some trees than in others. During weekly visits to one *P. dulce* tree on a very busy street where large trucks and buses often passed close by (but where the bugs were extremely common), females were missing from 27% of 195 groups of first instar nymphs, while the corresponding figure from a slightly smaller *P. dulce* at the edge of a small park in a residential section was 11% ($N = 82$) ($p < 0.05$).

The Natural History of the Wasps *Trissolcus bodkini* and *Phanuropsis semiflaviventris*

The wasp *Phanuropsis semiflaviventris* Girault is the only described species in the genus *Phanuropsis* (a second species, to be described by L. Masner, was raised from the eggs of *Edessa* sp., another subsocial pentatomid), and there is no literature on its biology other than that it parasitizes the eggs of *A. tripterus* and *A. picea* (Girault, 1916; Callan, 1944a). Wasps of the genus *Trissolcus* are parasites of pentatomid eggs (Ashmead, 1893). Vaukassevitch (1925; cited in F. Wilson, 1961) describes several aspects of the ovi-

position behavior of *T. simoni* which conform to the general pattern for the family Scelionidae. Both *P. semiflaviventris* and *T. bodkini* were found in *A. tripterus* eggs in Cali and Buenaventura, Colombia, while only *P. semiflaviventris* was present in Bucaramanga, Colombia, and apparently in Trinidad (Callan, 1944a); *T. bodkini* was the only species in a small sample of four parasitized masses collected in Guapi, Colombia.

HUNTING BEHAVIOR

GRAVID BUGS.—Females of both species of wasp were not infrequently found on leaves waiting near swollen female bugs that were apparently about to oviposit (Figure 7), and on several occasions they were observed parasitizing eggs as the bug oviposited (female wasps were distinguished in the field by their more pointed abdomens and more clubbed antennae). Several females were also seen waiting near mature male bugs and penulti-
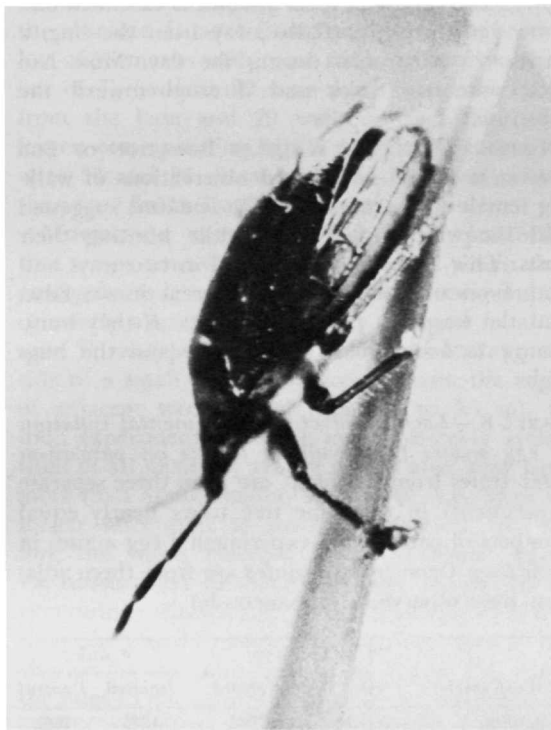
FIGURE 7.—Female *T. bodkini* wasp waiting near a gravid female bug.

mate nymphs which were resting immobile on leaves, suggesting that the important cues used to recognize gravid females were visual—their general size and the unusual sites (leaves) where they rested. An experiment designed to test this, however, indicated that additional factors were also involved.

About 40 mature bugs of both sexes were killed in alcohol, dried, and mounted with their legs removed on short insect pins. The bugs were then stuck on the undersides of the leaves of a *Cassia* sp. tree, which had substantial populations of bugs and both species of wasp. When I returned the next day, only one of the dead bugs had a female wasp waiting near it; the behavior of this female (a *P. semiflaviventris*) suggested why wasps had not congregated around the models. She walked by the base of the leaf with the model on it seven times within about 15 minutes, each time starting out toward the bug only to turn back before reaching it. This suggests that the sight of the bug was attractive to the wasp, but that the presence or absence of some other cue(s) counteracted this attraction. The wasp eventually flew away.

Gravid bugs probably change leaves from time to time before laying, but *T. bodkini* wasps which were waiting nearby did not seem able to follow them. When a gravid bug and two female *T. bodkini*, which were found waiting at her side, were placed in a large glass jar along with the branch of *C. odoratum* on which they were found, the bug moved periodically from one leaf to another, but the wasps did not follow her as she moved. In one typical case neither wasp moved until the bug was 1.5–2.5 cm away, and then they both walked in apparently random directions rather than toward the retreating bug. Nevertheless, within 30 minutes the bug was quiet again and both wasps were waiting near her. The bug's only response to the wasps in this situation was to antennate toward them when they approached her. These observations suggest that the immobility of the bug is an important cue for the wasp, and that once the bug moves it is no longer attractive until it stops again.

EGG MASSES.—Female wasps of both species behaved as if they used the sight of female bugs to locate egg masses as well as gravid females. Females of *P. semiflaviventris* demonstrated this most dramatically. When a guarding female bug was displaced several centimeters to the side of her group

TABLE 7.—*Variations in numbers of wasps seen attacking bugs defending eggs*
<4 days old in 6 T. catappa trees during one day

Time	Number of wasps seen attacking	Number of bugs being attacked	Total number of bugs seen guarding eggs
P. semiflaviventris			
7:00–9:00 AM	30	24	87
1:45–3:00 PM	67	32	56
9:00–9:30 PM	12	11	23
T. bodkini			
7:00–9:00 AM	4	4	87
1:45–3:00 PM	8	8	56
9:00–9:30 PM	1	1	23

of eggs, *P. semiflaviventris* females which had been nearby preparatory to attacking (Figure 10a) would often ignore the undefended eggs and move so as to realign themselves with the bug's new position, sometimes passing very near the now unguarded eggs (other times the wasps turned and began to oviposit in the unguarded eggs or moved away). On one occasion a female wasp was seen attempting to oviposit (backing in with abdomen extended) below an adult female bug which did not have any eggs but nevertheless scraped actively in defense against the wasp.

Female *T. bodkini* also behaved as if they used the bug's presence to locate egg masses. On five different occasions I saw a female walking on a trunk where there were large numbers of bugs and each wasp turned to move toward motionless bugs (both males and females), approached to within about 1 cm and paused for a moment. Then, sometimes after moving away and approaching again from another angle, the wasp moved on. The bugs usually remained quiet, but sometimes walked away or gave small shudders, kicked, or waved an antenna toward the wasp.

A further indication that females of both species of wasps hunted defending bugs rather than their eggs was that they were often seen attacking masses of nearly mature or already hatched eggs which were unsuitable for parasitization.

Females of *P. semiflaviventris* and perhaps also *T. bodkini* hunt mainly by day (Table 7); the numbers of *P. semiflaviventris* found in the morning and at night are both significantly lower than the number found in the afternoon (p<0.01), but the difference between morning and evening counts is not significant. The *T. bodkini* numbers show the same trends, but the differences are not sig-

nificant (0.1>p>0.05). One possible explanation for these data is that the wasps begin hunting in the morning and tend to stay near an egg mass and battle with the defending bug once one is found, thus "piling up" around the egg masses as the day progresses, and then many wasps leave egg masses in the evening. Most of the *P. semiflaviventris* females seen near eggs in the evening appeared not to be attacking. None were backing in toward the eggs with their abdomens extended and some were facing partially away from the bug, a position seldom seen during the day. Most had their antennae quiet and directed toward the substrate.

EXPERIMENTAL AND NATURAL ISOLATION OF EGG MASSES IN TREES.—Repeated observations of walking female wasps (especially *T. bodkini*) suggested that the wasps might walk while hunting their hosts. This hypothesis was tested in two ways and both types of evidence indicated that it was false, that the wasps fly rather than walk as they hunt. Young (<4 days old) egg masses (and the bugs

TABLE 8.—*Lack of effect of experimental isolation of egg masses from walking insects on parasitism rates* (rates from *Cassia* sp. are from three separate experiments in the same tree using nearly equal numbers of control and experimental egg masses in each case; those from *P. dulce* are from three adjacent trees observed simultaneously)

Wasp species	Cassia sp.		P. dulce	
	Isolated	Control	Isolated	Control
T. bodkini	18%	19%	12%	13%
P. semiflaviventris	44%	45%	2%	1%
Number of egg masses	51	89	30	29

defending them) were experimentally isolated from walking wasps in both *Cassia* sp. and *P. dulce* trees by coating a small area at the base of the branchlet bearing the leaf with the egg mass (see arrows in Figure 2) with Tack-Trap. The eggs were collected about a week later and the parasitism rates were determined. Parasitism in isolated groups did not differ from control rates in other groups of the same age from the same trees (Table 8).

Cassia sp. branchlets had pinnately arranged leaves (Figure 2*f*), and egg masses on leaves near the tips were thus naturally more isolated from the bases of the branchlets (where a wasp hunting on foot would presumably first arrive). Again the degree of isolation of the egg mass did not affect the parasitism rate. Of 56 masses which had less than the median number of *T. bodkini* for the tree where they were found, 25 were in the basal half of the branchlet and 31 in the distal half; corresponding numbers for *P. semiflaviventris* were 29 and 36 and neither differed significantly from the totals of 57 masses in the basal half and 75 in the distal half. Nor was there any correlation with the absolute distance from the base of the branchlet: of 58 masses with more than the median number of *T. bodkini*, 29 were more than four leaves from the base and 29 were on the basal four leaves; corresponding figures for *P. semiflaviventris* were 38 and 26 (total of 57 of 129 masses more than four leaves from the base).

Movements between Trees.—The possibility that wasps tended to stay in the trees where they emerged was tested by experimentally removing all or nearly all wasps before they emerged in alternate *T. catappa* trees growing in a row along the side of a small park (distances between the edges of adjacent trees ranged from 0.9 to 3.1 m). In four experimental trees I made biweekly collections of all or nearly all egg masses after they were more than approximately 5 days old (i.e., were no longer susceptible to further parasitism, but before the wasps emerged from parasitized eggs). Parasitism rates in these trees were monitored by examining collected eggs (parasitized eggs were distinguished by the membranes deposited next to the chorion by the wasp larvae; see Figure 11), while the rates in five control trees were determined from weekly collections of eggs from which both bugs and wasps had already emerged. The numbers of wasps emerging on the experimental trees were

thus reduced drastically, while the control populations were undisturbed.

The results of this treatment were measured in two ways. The parasitism rates of the eggs laid each week in both experimental and control trees were determined, taking into account that eggs laid in a given week were collected about two weeks sooner on experimental trees than on control trees. Figure 8 shows how the rates changed: by the last two weeks of the experiment the difference between the control and experimental rates for *P. semiflaviventris* was significant (p<0.002, Willcoxon Sum of Ranks Test), but *T. bodkini* rates were unchanged.

The fact that *P. semiflaviventris* rates declined gradually over several weeks rather than dropping more suddenly suggests that the wasps live an appreciable length of time and only slowly died out of or migrated away from the experimental trees.

The same lack of movement by *P. semiflaviventris* was found by using a second technique—counting the numbers of wasps seen attacking bugs
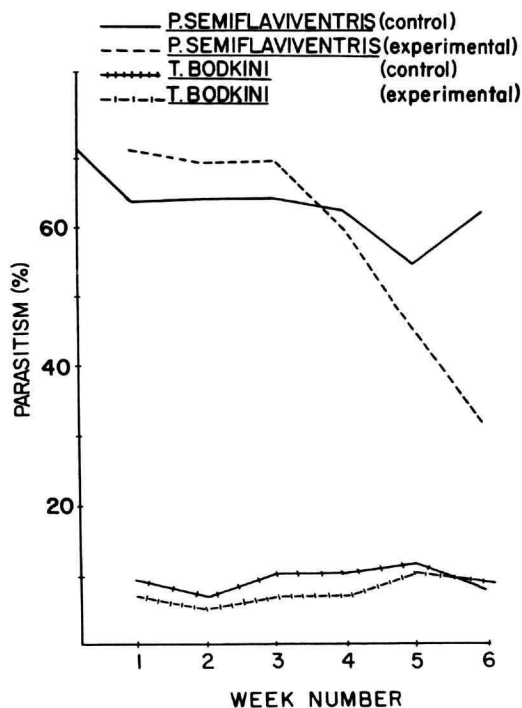

FIGURE 8.—Effect that removal of wasps from *T. catappa* trees before they emerged had on the parasitism rates in those trees.
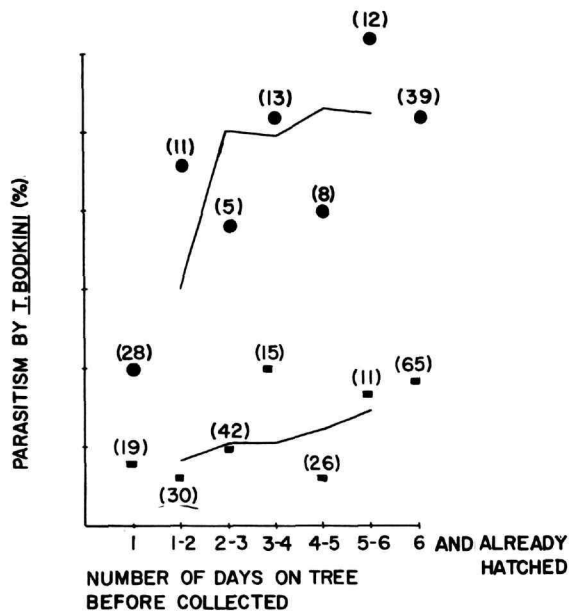
FIGURE 9.—Rates of *T. bodkini* parasitism in a *P. dulce* tree as a function of the length of exposure to wasps.

defending young (< about 4 days old) eggs. During two weeks of biweekly visits, 84 of 113 masses on the control trees had *P. semiflaviventris* females nearby, while only 14 of 78 masses on the experimental trees had wasps near them (p<0.01; the eggs observed were those represented in weeks 4 and 5 in Figure 8). The sample of *T. bodkini* was not large enough to analyze.

Both types of data show that *P. semiflaviventris* females tend to stay and hunt in the tree where they emerge, thus forming a "viscous" population; the less conclusive data on *T. bodkini* suggest that females of this species do not. One further observation supported both of these ideas. In one *P. dulce* tree which I searched weekly, the number of new egg masses fell from 72 to 5 in a span of three weeks. The rate of parasitism of these masses by *P. semiflaviventris* rose from 13% to 30% (the rates for the last two weeks differed from those for the week before the population of eggs began to decline; p<0.01, Willcoxon Sum of Rank Test). There was no change, however, in *T. bodkini* rates during this period; 15% of the eggs were parasitized at the beginning and 15% at the end. These data are in accord with the results of experimental removal of wasps since an increase in parasitism rates would be expected if the wasps tended to stay in the tree where they emerged; the relatively large numbers of wasps produced from the numerous previous egg masses would concentrate their hunting on a smaller number of egg masses and thus raise the average rate of parasitism.

CHANGES IN PARASITISM RATES WITH LENGTH OF EXPOSURE TO WASPS.—It was possible to deduce how much time had passed since a given egg mass was laid by noting how long it took the eggs to hatch in captivity, and parasitism rates could thus be determined for eggs which had been exposed to wasps for varying lengths of time. Figure 9 presents the results of two such studies of *T. bodkini* parasitism in the same *P. dulce* tree at different times.

TABLE 9.—*Parasitism rates on different species of tree* (egg masses on leaves only, from trees with >10 groups of eggs, and from Cali unless specified)

Wasp species	P. dulce	Cassia sp.		Canagium odoratum	T. catappa
		Cali	Bucaramanga		
T. bodkini					
Range	4%–26%	1%–29%	0%	11%–27%	0%–12%
Average	15.8%	12.6%	0%	17%	5.6%
Median	15%	13%	0%	21%	6%
P. semiflaviventris					
Range	0%–40%	2%–61%		39%–67%	57%–85%
Average	7.9%	41.3%	71.6%	54%	70.9%
Median	4%	43%		46%	70%
Number of trees	18	10	24	8	21
Number of samples	48	25	24	8	22
Number of eggs	35,099	18,411	5503	3215	26,302

TABLE 10.—*Parasitism rates on branches and leaves of the same trees* (trees with >10 groups on both leaves and branches in the case of *P. dulce*, and >5 in the case of *T. catappa*)

Wasp species	P. dulce		T. catappa	
	Branches	Leaves	Branches	Leaves
T. bodkini				
Range	31%–43%	15%–28%	0%–17%	0%–25%
Average	34.9%	20.6%	9.1%	4.6%
Median	34%	24%	7%	7%
P. semiflaviventris				
Range	0%–16%	0%–37%	2%–62%	40%–85%
Average	6.5%	9.9%	37.5%	71.6%
Median	3%	4%	37%	72%
Number of trees	8		15	
Number of samples	11		27	
Number of eggs	7463	13,313	3845	15,735

Although the final rates of parasitism were quite different, in both cases parasitism was essentially complete two days after the eggs were laid.

VARIATION IN DIFFERENT TREE SPECIES.—Table 9 shows that the rates of parasitism by *P. semiflaviventris* varied within different ranges in different species of tree. It may be significant that higher *P. semiflaviventris* rates occurred in trees with larger leaves (see Figure 2). Cocoa, which has large leaves, also apparently has high *P. semiflaviventris* rates (Callan, 1944a; Sepulveda, 1955). Parasitism rates by *T. bodkini* showed less correlation with tree species, although rates on *T. catappa* were significantly lower than those on *P. dulce* (p<0.01, Willcoxon Sum of Ranks Test). Competition between the two wasp species probably influenced the rates on different tree species to some extent.

VARIATION AT DIFFERENT SITES IN GIVEN TREES.— *Branches vs. Leaves*: The parasitism rates by both species of wasp differed for both *P. dulce* and *T. catappa* according to whether the bug eggs were on leaves or branches, as shown in Table 10. The *T. bodkini* rate was higher for egg masses on branches than for those on leaves in both species of trees, while the *P. semiflaviventris* rate was consistently lower.

Suckers vs. Trees: The rates of parasitism by *T. bodkini* were consistently lower in groups of eggs on the leaves of suckers at the bases of *P. dulce* trees (Figure 2a) than on the leaves of the same trees. When the numbers of eggs parasitized in groups of 26–28 eggs found on suckers around four

trees were compared with the median numbers of eggs parasitized by *T. bodkini* on the leaves of each tree and its suckers, 18 of the sucker masses were lower than the medians for their respective trees and 3 were higher (p<0.01). In another sample from one of these trees, the parasitism of masses from the suckers (N=14) was also lower than that of masses from the tree (N=21) (p<0.01, Willcoxon Sum of Ranks Test).

OVIPOSITION

BEHAVIOR.—Oviposition behavior actually forms a part of the attack behavior described below, but is considered separately here in order to simplify the descriptions. It should be kept in mind that some of the "ovipositions" I saw may have been only probing behavior with the abdomen and/or the ovipositor which did not result in eggs being laid. At least some "ovipositions," however, did result in the production of wasps from otherwise virgin eggs.

T. bodkini: When recently laid *A. tripterus* eggs were placed in a jar with 2-day-old fertilized female *T. bodkini* wasps that had emerged in captivity, the wasps showed no signs of being attracted to the eggs, several times passing very close to them without touching them. But as soon as a wasp did encounter eggs, she began to oviposit into them. Both these wasps and others found attacking egg masses in nature and induced to oviposit in undefended groups showed rather consistent behavior. The

TABLE 11.—*Frequency of superparasitism by wasps attacking undefended eggs*

Wasp species	Number of ovipositions in each egg				Number of egg masses	Number of female wasps
	0	1	2	3 or more		
T. bodkini						
Observed	273	185	16	2	17	9
Random	299	138	33	6		
P. semiflaviventris						
Observed	131	62	22	5	8	5
Random	132	65	19	5		

wasp began by walking over the group, antennating successive eggs. After pausing and antennating one egg for a second or more, she made a brisk 180° turn and placed the tip of her abdomen on the egg, then moved forward until the tip was against the near edge of this egg (or occasionally against an adjacent one). She stayed motionless, crouching low with her antennae folded down (Figure 1) for 10–30 seconds. Wasps in this position usually did not respond to being pushed or nudged. Then, before leaving, the wasp nearly always wiped the tip of her abdomen from side to side, one or more times, across the surface of the egg.

This "marking" behavior was similar to that observed by F. Wilson (1961) in *Asolcus basalis* and appeared to have the same function—to prevent multiple ovipositions in single eggs. The number of times females which were allowed to parasitize unguarded masses oviposited into each egg in the mass was determined for 17 masses. The numbers of eggs which would have been attacked 0, 1, 2, or 3 and more times if the wasps had been choosing host eggs randomly was calculated using the formula in Wilson's paper (the number of ovipositions per group varied, so these numbers were calculated for each egg mass and then summed) and compared with the observed numbers of ovipositions (Table 11). The wasps reoviposited in
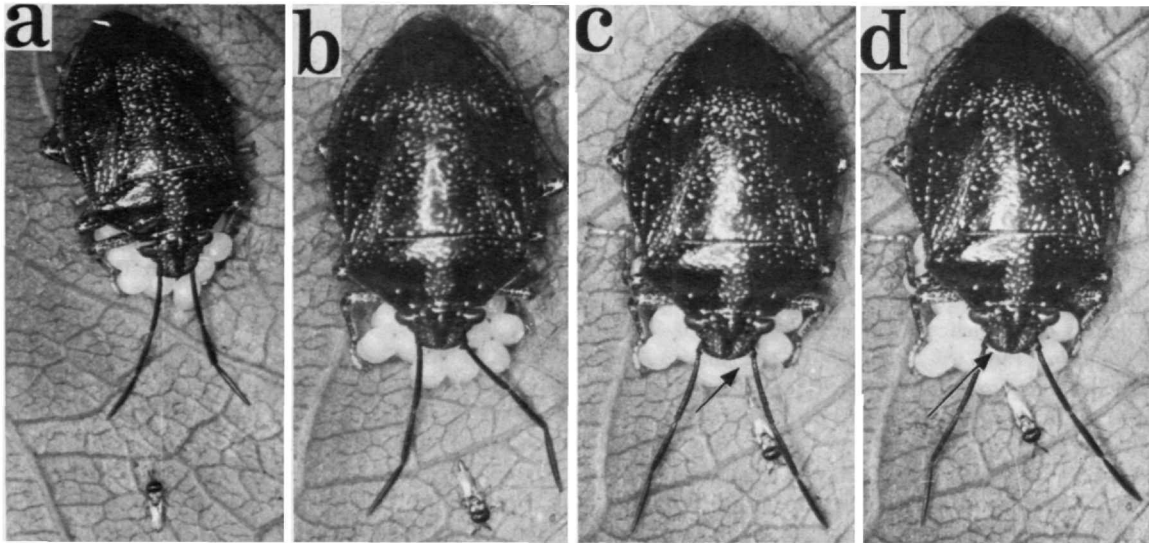

FIGURE 10.—Female *P. semiflaviventris* wasps attacking bugs defending their eggs: *a*, wasp looking in toward bug; *b*, wasp backing in with her abdomen extended; *c*, wasp ovipositing into egg in exterior row of mass (arrow); *d*, wasp ovipositing into egg in interior of mass (arrow).

eggs less often than if they had chosen eggs at random, thus indicating that the marking did prevent multiple ovipositions.

Usually females laid several eggs at first, with only very short pauses between ovipositions, but gradually they spent more and more time walking over the mass antennating eggs between ovipositions and finally, after less than an hour, left. In most cases the number of eggs laid in the first burst seemed to depend on the age of the bug eggs, newer groups being more thoroughly attacked. The wasp usually left before parasitizing all the eggs in a mass and usually it flew rather than walked away.

On several occasions I saw more than one female *T. bodkini* waiting near a gravid bug or attacking a single egg mass, but in no case was there any sign of aggression between them. In one case in which both a *T. bodkini* and a *P. semiflaviventris* were attacking an undefended mass, however, the *T. bodkini* moved toward the other female several times and appeared to be responsible for her leaving the eggs.

P. semiflaviventris: It was more difficult to induce *P. semiflaviventris* to oviposit. Females which emerged in captivity did not attack groups either with or without bugs defending them. Those found attacking masses in nature would only seldom lay into undefended eggs. In order to conduct studies of development rate and interspecific competition within the egg, it was necessary to glue eggs with known histories (known virgin eggs, for example) next to a bug whose eggs were being attacked by a *P. semiflaviventris* female. By pushing the bug over onto the other group (which she

then defended), the wasp's attention could be drawn to them and she would oviposit in them.

Oviposition by *P. semiflaviventris* differed from that of *T. bodkini* in a number of respects. Oviposition lasted for only approximately four seconds and was always performed with the abdomen extended (Figure 10c). The female did not climb onto the egg mass, staying on the leaf instead. She also failed to antennate eggs before laying in them, moving directly from one to the next with her extended abdomen. Marking behavior was never performed. Often a wasp laid a series of five to ten eggs, backing along the base of the egg mass and parasitizing both edge and internal eggs; to reach the latter, she inserted her abdomen between the bases of edge eggs (Figure 10d). The wasp's extended abdomen was very flexible; when she came to a corner of the egg mass, she curved the tip around the corner and parasitized the first edge egg on the next side before bringing her body around the corner.

Counts of the numbers of eggs reparasitized in eight different masses confirmed that *P. semiflaviventris* females do not differentiate eggs which they have already parasitized from others (Table 11).

Although I observed more than one *P. semiflaviventris* female attacking a single egg mass simultaneously many times, there was never any sign of aggression between them.

SUCCESS.—The results of ovipositions by both wasp species are summarized in Table 12, which shows that each species can displace the other and that the winner in any given case is not predictable. Some of the eggs found in nature may have been previously parasitized, but 15 of the eggs into

TABLE 12.—*Results of ovipositions by wasps in bug eggs found in nature*

Age of eggs	Species that emerged from the egg			Fail to develop	Number of eggs
	A. tripterus	T. bodkini	P. semiflaviventris		
Eggs <4 days old oviposited in by—					
T. bodkini	19%	65%	4%	11%	200
P. semiflaviventris	33%	0%	53%	15%	40
Both species	12%	24%	52%	12%	42
Eggs >4 days old oviposited in by—					
T. bodkini	90%	0%	0%	10%	34
P. semiflaviventris	97%	0%	0%	3%	27

which both species oviposited were known to have been virgin except for the observed ovipositions; these eggs produced six *T. bodkini* and nine *P. semiflaviventris*. Even within a given mass of virgin eggs where all ovipositions by each species occurred at the same time, some eggs produced one species of wasp and others the other. The rates of parasitism for doubly parasitized eggs differ from those for singly parasitized eggs (p<0.01 for both species), suggesting some form of competition between the larvae inside the bug egg, with the winner eating the loser as in other scelionids (e.g., Kamal, 1937; Pickford, 1964). Older bug eggs were much less susceptible to parasitism (p<0.05 for both species). Other scelionids such as *Telenomus gifuensis* also parasitize younger pentatomid eggs more successfully than older ones (Hikada, 1958).

It was clear, in addition, although no measurements were made, that the time between *T. bodkini* ovipositions (i.e., the time the wasp spent investigating eggs) was much greater on masses of older eggs than on new ones. Both species were found attacking mostly newer masses in nature.

The first egg laid by *T. bodkini* females tended to be a male. Of 24 masses in which only one egg was parasitized by this species, 20 produced males and 4 females. Assuming the frequency of males in Table 14 and a random assignment of sex to the first egg, these numbers should be 6 and 18; the difference is significant (p<0.01).

STAGES IN THE EGGS OF *A. tripterus*

Table 13 shows the developmental times of both wasp species. The membranes referred to were deposited against the chorion of the bug egg. The membranes of the two species were distinct; that of *P. semiflaviventris* was solid black on the bottom and sides (Figure 11a), while that of *T. bodkini* was clear on the bottom and had alternating black and transparent circular bands like barrel hoops along the sides (Figure 11b). The membranes stayed intact after the wasps left the eggs, and rates of parasitism by both wasp species could thus be determined by examining empty eggs. Although the most common coloration of the membranes was black, both species rarely (especially in *T. catappa* trees) produced lighter, more brownish membranes, which were occasionally only slightly clouded. Even in these cases, however, species

TABLE 13.—*Developmental times of* T. bodkini *and* P. semiflaviventris *in days* (measured from moment of oviposition by wasp; eggs checked at least once every 12 hours)

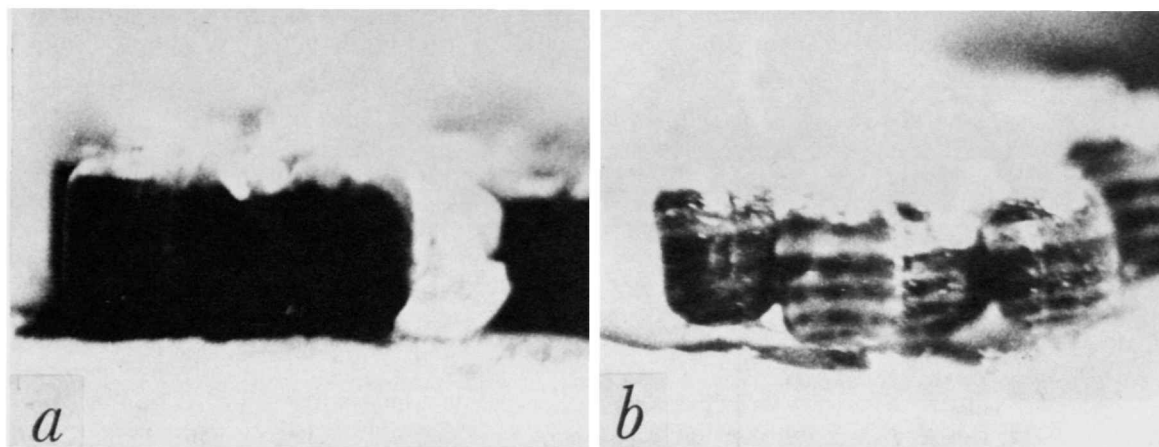| Stage	T. bodkini	P. semiflaviventris
Larva with membrane	3.5– 6.6	3.8– 7.9
White pupa	5– 6.8	5.8– 8.9
Red-eyed pupa	6.1– 8.2	6.8–10.2
Black pupa	7.2–11.8	7.9–12.7
Emergence	10–12.3	9.7–13.4

FIGURE 11.—Membranes left in bug eggs by: *a*, *P. semiflaviventris*; *b*, *T. bodkini*.

TABLE 14.—*Sexes of wasps raised from* A. tripterus *eggs collected in the field*
(28 of the 49 groups were parasitized by both species of wasp; averages calculated
on the basis of the number of masses parasitized by a given species)

	T. bodkini	P. semiflaviventris
Average number of males/mass	1.5	3.1
Average number of females/mass	4.8	13.3
Ratio of male:female	1:3.2	1:4.3
Maximum number of females/mass	22	23
Number of masses with more than 1 male	13	19
Number of masses with females but no males	3	6
Range of number of wasps/mass	1–25	1–25
Total number of masses	39	38
Total number of wasps	245	527

identity could nearly always be distinguished by the circular stripes and the paler bottoms of *T. bodkini* membranes. The function of the membranes and the reason for the variations in their color are not known. Species of the scelionid genus *Asolcus* also produce characteristic membranes (Cumber, 1964).

The wasp larvae did not defecate until they had finished feeding, and then deposited a slab of feces along one side of the egg. In all cases the feces were placed ventrally with respect to the wasp pupa and adult, with the wasp nearly always facing the cap of the egg. In only one of several thousand eggs examined was there more than one wasp in a single bug egg.

EMERGENCE FROM THE EGG

Males developed in less time than females and the first wasp to emerge from the egg mass was a male in each of 40 cases for *T. bodkini* and in 44 of 45 for *P. semiflaviventris*. The wasps emerged by cutting away the egg cap with their mandibles. They sometimes opened the egg in less than an hour, but other times paused for up to several hours before completing the task. The two species differed slightly in the form of the cut made in the cap: *T. bodkini* cut mostly along the edge of the cap, while *P. semiflaviventris* tended to start in the center and cut in ever-widening arcs until a sufficiently large hole was produced. *P. semiflaviventris* tended to emerge more in the night and early morning than the day; of 214 wasps which emerged in captivity over a period of a week, 149 emerged between 7 PM and 9 AM ($p < 0.01$).

SEX RATIOS

Males of both species were less common than females, but nearly every egg mass parasitized produced at least one male wasp (Table 14), perhaps due to tendencies to lay male eggs first. Only rarely were males as common as females in a given mass of eggs (once in each species for the groups in Table 14), indicating, since unfertilized hymenopteran eggs generally produced males (e.g., E. O. Wilson, 1971), that either unfertilized females were rare or that they do not oviposit.

MALE BEHAVIOR

FIGHTS.—Males of both wasp species fought for possession of egg masses. Unfortunately, they were usually disturbed when the leaf which the egg mass was on was placed under a microscope, so the descriptions below are only fragmentary.

Males stayed on the tops or at the sides of the egg masses from which they had emerged, walking over the eggs and grooming periodically, but generally remaining quiet. They could distinguish eggs from other objects, as they almost always climbed onto eggs and stayed on them when introduced into vials containing several egg masses on leaves. In this situation they mounted and stayed on completely hatched masses as well as on ones about to produce female wasps.

I witnessed both inter- and intraspecific aggressive encounters, and the frequency with which more than one male emerged from a given egg mass (Table 14) indicates that both types of fights are common in Cali.

The males' weapons were their mandibles and,

although fights did not usually result in injuries, they were capable of biting off the antennae and legs of opponents. Aggressive males often opened their mandibles as they looked toward other males and, in at least some cases, it was possible to predict the outcome of an encounter by observing which male opened his mandibles more. Less aggressive males were not as active as others, often keeping their antennae lowered and still, and crouching low on the egg mass or next to it.

When one male was much more aggressive than the other, interactions did not usually involve physical contact, the loser running off the egg mass as the other moved toward him. In these cases the more aggressive wasp did not pursue the other more than 1–2 cm from the egg mass. In more evenly matched pairs, the second wasp turned and lowered his head toward his opponent's rush or even moved toward him; the two wasps locked mandibles and apparently struggled, moving from side to side and backward and forward, with one male finally appearing to dominate, pushing the other backward off the egg mass.

MATING.—Mating probably normally occurs the moment the female leaves the egg, and I saw more than ten matings of this type in each species. As the female began to climb out of the egg after cutting open the top, the male eased himself onto the top of her thorax. He immediately began to antennate the front of her head and her antennae, and she responded by folding her antennae ventrally and staying motionless. Then the male moved backward and bent his abdomen slightly downward to make contact with the tip of her abdomen. Often the male moved forward one or more times to reantennate the female's head before achieving genital coupling. Both animals usually remained nearly motionless during the ten seconds while they were coupled and then the male dismounted.

There were two small differences in the mating behavior of the two species. Occasionally *P. semiflaviventris* males rubbed their hind legs briskly along the dorsal and lateral surfaces of the female's abdomen while antennating her head. Female *T. bodkini* nearly always walked several centimeters away from the egg mass immediately after mating, while *P. semiflaviventris* females did not move away.

Males of *T. bodkini* copulated with virgin females in plastic vials, and one male mated with

four females during his first minute in such a situation. These matings were slightly different and suggest that mating away from the egg mass is possible in nature. The female remained nearly motionless as the male approached, antennated her briefly, and mounted her. In one case, the female moved away, and the male approached again, more slowly and with more antennation before mounting. Several times a female began to walk as the male mounted on her attempted genital contact, and he responded by moving forward to antennate her antennae until she folded them and became quiet again, then moved back to attempt genital contact.

Males could copulate several times and I saw one *T. bodkini* male mate with 12 females, and one *P. semiflaviventris* male mate with 7 females. The females mated only once and *T. bodkini* females, kept in a vial where they could not escape from a male, avoided additional contacts by moving away when another wasp came near. Males in this situation approached both virgins and nonvirgins, but usually did not attempt to follow wasps which moved away. I saw one male *P. semiflaviventris* mount immobile nonvirgins at the edge of an egg mass three times; in each case the female stayed motionless and the male dismounted without attempting to copulate.

I also saw two *P. semiflaviventris* females emerge from an egg mass patrolled by a *T. bodkini* male. In both cases the male antennated the female as she emerged, but did not mount her. In one case the male did not allow the female to stay near the edge of the egg mass, chasing her away. In groups collected in nature while the wasps were emerging, there was only a slight, insignificant tendency $(0.25 < p < 0.1)$ for fewer female *P. semiflaviventris* (per empty egg parasitized by *P. semiflaviventris*) to cluster near masses patrolled by *T. bodkini* males $(N = 13)$ than near other groups $(N = 29)$, indicating that such behavior by *T. bodkini* males is far from universal. Cumber (1964) found that males of two species of *Asolcus* would mount females of the other species, but in neither case was fertilization accomplished.

CLUSTERS OF FEMALES

Females of both species stayed near the egg mass for several hours after emerging and mating, al-

though they readily walked and flew away when disturbed. Female *T. bodkini* were always dispersed, each several centimeters from the egg mass; on *P. dulce* trees they were usually each on a different leaf near the leaf with the egg mass. The avoidance of other wasps by recently mated females is probably responsible for this pattern. Females of *P. semiflaviventris,* in contrast, usually stayed in contact with the base of the egg mass, each one remaining immobile amidst the bug nymphs as the female bug stood guard over them all.

As noted above, female bugs guarding nymphs scraped less often in response to artificial stimuli than those over eggs (Table 6). I never saw a female bug drive off either female or male wasps which had emerged from her egg mass. Bugs guarding masses from which wasps were emerging gave no response to immobile wasps and only waved their antennae toward moving wasps. The bugs often raised themselves off the surface of the egg mass when touched ventrally by a wasp walking over the eggs. This response probably serves to give moulting first instar nymphs room to emerge from their old cuticles after they climb onto the eggs and hook their claws there (females with moulting nymphs under them were seen in this position several times), but it also facilitated the movements of male wasps over the egg mass.

Interactions between Wasps and Bugs

WASPS VS. BUGS GUARDING EGGS

DIRECT OBSERVATIONS.—I observed parts of more than 20 interactions between female wasps of each species and bugs guarding eggs. Behavior of individual wasps varied somewhat, but the two species were quite distinct.

T. bodkini: Female *T. bodkini* waited near bugs, staying out of range of the bug's antennae and facing in toward the eggs. One common tactic was to rush to the egg mass and turn quickly to lay into an egg in the edge of the mass. I had the strong impression that wasps tended to make such rushes just after I disturbed the bug by seizing the leaf with my hand; on several such occasions the bug, apparently distracted momentarily, failed to respond to the wasp. Another tactic was to wait several minutes on the other side of the leaf, then come over the edge and quickly rush to the egg

mass. Usually the bug responded to rushes by scraping, kicking, waving her antennae, and occasionally shuddering as described above. Often this behavior served to drive the wasp out of range of the bug's antennae and bugs occasionally succeeded in knocking wasps completely away from the egg mass with a kick.

On several occasions a wasp appeared to hurry her oviposition in a way never seen in attacks on undefended eggs, omitting antennal inspection of the bug egg, and simply moving her abdomen directly from one egg to the next.

The bugs were unable to effectively defend the rear edge of the egg mass, i.e., the edge under the bug's abdomen (Figure 1, arrow in Figure 5a). They apparently could not bend their hind legs so as to scrape along that edge, and thus a wasp which was able to insinuate herself into this area was usually able to parasitize several eggs along the back row with little interference from the guarding bug. After ovipositing in the back row, *T. bodkini* females often attempted to move stealthily along the lateral edge of the group. Usually, however, these attempts were unsuccessful, as the bug responded by kicking at the wasp with a hind leg or scraping.

It is interesting that even when a bug gave clear indications (kicks, shudders, etc.) that she sensed that there was a wasp at the rear edge of her egg mass, she never turned to assume a new orientation over the eggs. That is, the bugs never turned so as to bring their front legs to bear on the unprotected back side of the mass. To do so of course would result in leaving another side of the mass open to attack, and the lack of turning implies a sacrifice of the back eggs in order to insure the relative safety of the others. This failure to turn was probably an important factor in keeping *T. bodkini* rates at relatively low levels in some situations.

P. semiflaviventris: Attacks by *P. semiflaviventris* females were quite different. The general tactic of this species was to move to about a body length from the edge of the egg mass (generally within range of the bug's antennae), quickly turn 180°, and then extend the abdomen to about twice its normal length and back in slowly toward the mass, attempting to contact an egg with the tip of her abdomen (Figures 1, 10b, 10c). Upon reaching the mass, the wasp laid in the first bug egg she touched, then moved to lay in an adjacent egg in

the edge of the mass or to thread her abdomen between two edge eggs and parasitize an interior egg (Figure 10d). Wasps attacked from all sides of the bug, not just the rear. This species also seemed to attack especially often just after I disturbed the bug.

DEDUCTIONS FROM PATTERNS OF PARASITISM WITH-IN EGG MASSES AND WITHIN TREES.—The patterns of parasitism in empty (hatched) egg masses with the common "compact" shape (Figure 12) confirmed the direct behavioral observations of wasp-bug interactions. Since defending female bugs nearly always positioned themselves over such groups in a standard way, detailed analyses of the directions from which the wasps attacked could be made.

For instance, the eggs in position C in Figure 12b formed the rear, more poorly protected edge

of the mass, and eggs in these positions were parasitized by T. bodkini approximately four times more heavily than those in any other part of the mass. Parasitism by P. semiflaviventris on the other hand was not confined to the rear edge, but was distributed on all sides of the group. The central eggs were seldom parasitized by either species.

The patterns of parasitism of these groups also brought out several more subtle details of the interactions between P. semiflaviventris and the defending bugs. Excepting the back edge, edge eggs (A, B, and D in Figure 12b) were generally more heavily attacked than eggs on the first interior row (E, F, and G, but not H—see below) ($p < 0.05$ excluding H). Since attacking wasps arrived first at edge eggs and only later at interior eggs, the difference between the two positions
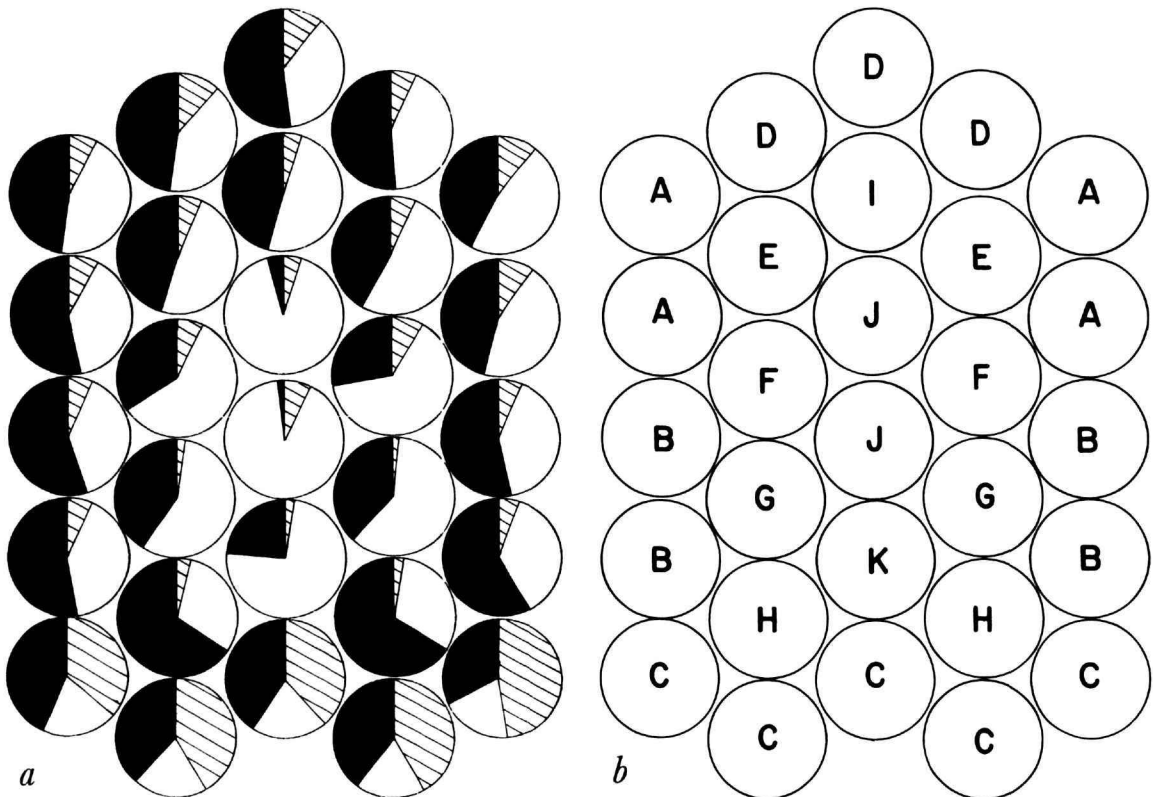

FIGURE 12.—Pattern of parasitism of "compact" egg masses: a, parasitism rate for each position (hatched = T. bodkini, black = P. semiflaviventris, white = no parasitism); b, positions grouped according to similarities in parasitism rates.

probably results from the bugs interrupting some attacks by the wasps.

The two eggs farthest from any edge (J in Figure 12b) were least parasitized by *P. semiflaviventris* (p<0.01). Probably the wasps were unable to extend their abdomens far enough to reach these eggs. Eggs in position K were more heavily parasitized than the central eggs (p<0.01), but less heavily parasitized than other first row interior eggs (E, F, G, and H) (p<0.01). The wasps were probably capable of reaching these eggs with their extended abdomens, but perhaps often failed to curve them so as to reach this position.

Anterior lateral edge eggs (A) were less parasitized than posterior lateral edge eggs (B) (p<0.05). This difference may result from the bug's more consistent and efficient scraping along the front edge of the egg mass with her front legs.

In addition, first row interior eggs at corners (I, E, and H) were more heavily parasitized than other first row interior eggs (F, G) (p<0.01). Such corner eggs were probably more accessible to wasps; for instance, a wasp could reach position E by going between the bases of either A and D or A and A, but would have access to F only between A and B. The position with the highest rate of parasitism, H, had three access routes, in addition to being accessible from the poorly guarded rear edge of the mass.

The bugs were clearly less successful in defending the eggs at the front and sides of their groups against *P. semiflaviventris* than against *T. bodkini*, probably as a result of several factors. Female *P. semiflaviventris* kept their bodies out of range of the bug's scraping legs while ovipositing, exposing only the small tips of their extended abdomens. The bug thus had a smaller target to hit, and one which offered much less purchase for its legs. The tip of the wasp's abdomen may have been difficult for the bug to see (it was darker than the rest, and I had trouble seeing it), and this, combined with the ability of the female *P. semiflaviventris* to lay eggs very quickly, also meant that just a moment's lack of vigilance could cost the bug one or more eggs. Often bugs responded to the presence of an attacking *P. semiflaviventris* by continually scraping along the edge of the egg mass, even when the wasp was not near enough to oviposit. Once a wasp succeeded in getting her extended abdomen between two edge eggs and was
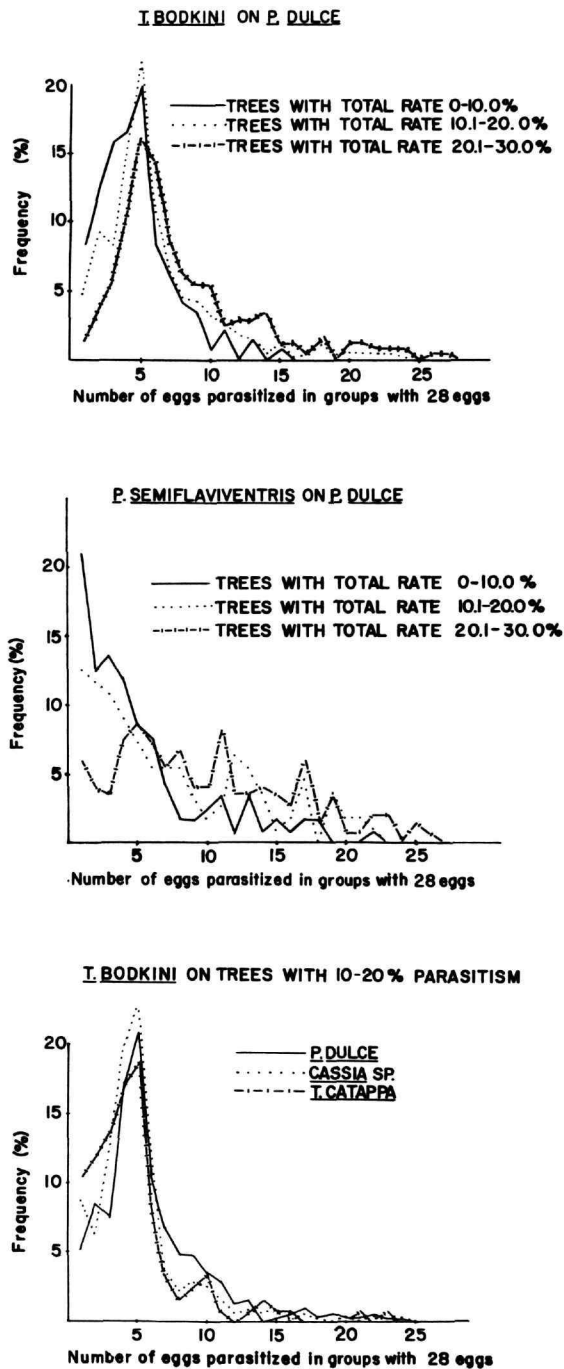

FIGURE 13.—Number of eggs parasitized/mass as a function of the total parasitism rate of the tree.

ovipositing in an interior egg, she was well braced by the eggs and not easily moved; on several occasions I saw a bug scrape right over a wasp in this position without dislodging it.

Several additional details of bug-wasp interactions can be deduced from Figure 13, which shows how the numbers of eggs parasitized in masses of 28 eggs varied according to the total parasitism rate in *P. dulce* trees. The total rate for a tree is probably a fair indication of the density of wasps which were searching for eggs there and thus what is said below concerning total parasitism rates probably also applies to the density of searching wasps in a tree.

In both wasp species the number of egg masses missed declined as the total parasitism rate for the tree rose (it should be kept in mind that my assumption that unparasitized egg masses were never found by wasps was undoubtedly incorrect in some cases in which the bug succeeded in repelling a wasp before it laid a single egg; such interactions may have been more common in the case of *P. semiflaviventris*); at the same time, the number of eggs parasitized per group rose for both species. The curves for *T. bodkini* show strong peaks in the region of five eggs, almost certainly due to the

fact that the back edges of egg masses, the usual site of *T. bodkini* parasitism, usually consisted of about five eggs; the curves for *P. semiflaviventris* show no such tendency.

The low numbers of eggs per group parasitized by *P. semiflaviventris* in trees with low total rates are surprising, indicating that the defense of the bugs against single attacks by *P. semiflaviventris* was quite effective, perhaps more so than that against single attacks by *T. bodkini* females. The higher rates of parasitism which *P. semiflaviventris* achieves on some trees would thus seem to be due to multiple attacks, a conclusion supported by the shift to the right of the *P. semiflaviventris* curves in trees with higher total rates. The curves for *T. bodkini* also move to the right, but more slowly, probably because each subsequent female wasp tends to attack the same five eggs in the rear edge of the egg mass; *P. semiflaviventris* females, not being so restricted, probably attacked more efficiently, reparasitizing eggs much less often.

It was not uncommon to see more than one female wasp attacking a single bug (up to 10 female *P. semiflaviventris* were seen around a single bug in *T. catappa* trees), and it seems possible that a sort of "social facilitation" may occur in such situ-

TABLE 15.—*Patterns of parasitism of "compact" egg masses by* P. semiflaviventris *in different species of tree* (the numbers are the number of wasps from the given position divided by the total number of wasps from eggs in that tree species not counting those from position C; the positions are those indicated in Figure 12b)

Position of egg	P. dulce	Cassia sp.		Canagium odoratum	T. catappa
		Cali	Bucaramanga		
A	.20	.19	.22	.19	.21
B*	.28	.22	.21	.22	.21
C	.23	.30	.23	.12	.21
D	.12	.16	.17	.15	.16
E	.08	.08	.08	.10	.07
F	.07	.05	.07	.07	.09
G	.08	.07	.08	.09	.08
H*	.17	.16	.11	.11	.11
I	.06	.04	.05	.05	.04
J	.00	.01	.01	.00	.01
K	.03	.03	.03	.02	.02
Total wasps (not counting those from position C)	208	545	1297	682	773
Total number of egg masses	87	73	86	50	50
Total parasitism by *T. bodkini*	14%	8%	0%	20%	9%

* Difference between *P. dulce* and *T. catappa* significant (p <.05).

ations, with a given wasp's presence aiding other attacking females by distracting the bug's attention.

EFFECT OF TREE SPECIES.—Battles between bugs and *P. semiflaviventris* wasps for "compact" egg masses were only slightly influenced by the species of tree where they occurred. Since the rates of parasitism by *T. bodkini* differed in different tree species, the eggs at the back edges of the masses (position C in Figure 12), where the great majority of *T. bodkini* parasitism occurred, were excluded from the analysis to avoid the effects of interspecific competition. The percentage contribution from each position in the mass was calculated by placing the total parasitism in a given position over the total number of *P. semiflaviventris* produced in compact masses in that particular tree species minus those from position C. When the resulting patterns of parasitism in different tree species are compared as in Table 15, it is clear that the general pattern was very similar. Two differences are significant, however; the numbers of wasps from the two posterior lateral positions B and H are higher in *P. dulce* than in the other trees. These differences may stem from a wasp's being able to "surprise" the bug more easily on small leaves by hiding for several minutes on the other side of the leaf, then peeking over the edge and quickly beginning to lay before the bug sees her. This tactic might be more effective on smaller leaves and in the rear part of the egg mass where the bug's antennae and eyes would be less likely to sense the wasp.

A detailed analysis of this type was not possible in the case of the *T. bodkini*, but Figure 13c indicates that the tree species also failed to substantially modify the bug's interactions with this species of wasp.

EFFECT OF SHAPE OF EGG MASS.—The effect of the shape of an egg mass on its susceptibility to wasp attack was determined by counting the numbers of eggs parasitized in already vacated egg masses of different shapes. Of 209 "compact" masses from 17 *P. dulce* trees, 124 had fewer than the median number of *T. bodkini* wasps for masses of 28 eggs in their respective trees (p<0.01, all trees had a median parasitism greater than 0). Presumably this reduction in parasitism resulted from the bugs being better able to defend a smooth-sided, compact group than more irregular, strung-out masses which had more "edge" eggs and more nooks to protect attacking wasps from the bug's feet. The form of the mass did not have a significant effect on parasitism by *P. semiflaviventris*, however.

WASPS VS. OVIPOSITING BUGS

DIRECT OBSERVATIONS.—On three occasions I found wasps (three *T. bodkini* and one *P. semiflaviventris*) parasitizing eggs while the bug was still ovipositing. Except for kicking at the wasp when it touched her, and perhaps moving farther back over the eggs between ovipositions, none of the bugs appeared to modify her oviposition behavior. The bugs were apparently unable to see the wasps (which were always behind them) and in two cases did not appear to sense the wasp's presence during the early part of the interaction. The kicks of the bugs at the wasps were essentially blind, evidently directed mainly by contact. For instance, on one occasion the bug moved forward to lay an egg, then back, and kicked at the side where she had touched a wasp just before moving forward, but meanwhile the wasp had changed sides; later the bug also kicked several times more after she succeeded in kicking the wasp clear of the eggs. Although the bugs finally kicked away all four wasps before finishing ovipositing, their defensive behavior was poorly organized; several times a bug brushed or kicked an ovipositing wasp repeatedly and, failing to dislodge it, ceased responding to it.

The behavior of the two species of wasp was quite distinct in this situation. The *P. semiflaviventris* female behaved very much as if attacking a group with a female bug in normal defensive position; she stayed on the leaf, backed in and probed with her extended abdomen, and laid several eggs in succession without inspecting them with her antennae. She showed no response to the bug's periodic moves forward and back over the egg mass.

The behavior of the *T. bodkini* females differed from both that of *P. semiflaviventris* and from that of *T. bodkini* females attacking eggs with a bug in normal guarding position. They stayed on the tops rather than the sides of the eggs, and moved over them antennating the cap of each. All three wasps appeared to try to avoid touching the bug. Although each wasp spent the majority of her time on the rearmost eggs (which were not covered by

the bug's abdomen), she did not oviposit there—presumably because she had already parasitized those eggs. When the bug moved forward to lay another egg, the wasp also moved to the front part of the group, inspected, and then turned and oviposited in an egg there. Since the bug laid an egg in less time than it took *T. bodkini* to oviposit, the bug sometimes moved back over the mass while a wasp was still ovipositing. The bugs often sensed the wasps at this time, and two of the wasps were kicked clear of the eggs after being discovered at this stage. In other cases, the wasp crouched low and stayed very still under the bug's thorax, only moving again when the bug moved forward to lay its next egg. On one occasion I was sure that the wasp marked the egg it had just parasitized, but on several other occasions the marking was either very limited or did not occur. One of the *T. bodkini* females, kicked clear of the eggs by the bug, landed on my hand holding the branch, and after cleaning herself briefly, she flew away.

DEDUCTIONS FROM PATTERNS OF PARASITISM WITHIN EGG MASSES.—Attacks made during the bug's oviposition may explain one additional pattern of parasitism of the "compact" group form. The interior eggs in the anterior part of the mass (positions E, F, and I) were more heavily parasitized by *T. bodkini* than those in the posterior part (G, J, and K) ($p < 0.05$, H is omitted since the high rate of parasitism by *P. semiflaviventris* may influence the *T. bodkini* rate). Interior eggs are probably nearly inaccessible for *T. bodkini* once the bug finishes ovipositing, and the eggs in the front part of the group are laid first (e.g., Figure 4) and are thus both exposed longer to attacks during ovi-

position and more poorly defended by the ovipositing bug.

Competition between Species of Wasps

WITHIN BUG EGGS

Comparisons of the patterns of *P. semiflaviventris* parasitism of "compact" groups from sites with different rates of *T. bodkini* parasitism showed (assuming that wasp-bug battles were essentially the same in all sites—see Table 15) that the two wasp species compete for eggs. The sites chosen for their different *T. bodkini* parasitism rates were these: *Cassia* sp. trees in Bucaramanga (*T. bodkini* absent), *P. dulce* tree leaves in Cali (*T. bodkini* in moderate numbers), and *P. dulce* branches in Cali (*T. bodkini* in high numbers). In all cases, the parasitism by *T. bodkini* was concentrated in the rear edge of the egg mass (position C in Figure 12*b*). As shown in Table 16, parasitism by *P. semiflaviventris* in these rear eggs was significantly reduced where *T. bodkini* was more common.

The complementary comparison of patterns of *T. bodkini* parasitism of "compact" masses in tree species with high and low *P. semiflaviventris* rates (*T. catappa* vs. *P. dulce*) showed no difference. This probably results from the tendency noted above for *P. semiflaviventris* to attack all sides of the mass more or less equally, and in turn indicates that the lower rates of *P. semiflaviventris* in rear eggs on *T. catappa* and *Cassia* sp. (Figure 12*a*) probably also resulted from competition with *T. bodkini*.

In general, these data show conclusively that *T.*

TABLE 16.—*Influence of interspecific competition on patterns of parasitism in "compact" egg masses* (all samples from Cali, Colombia, unless otherwise indicated)

Wasp species	Cassia sp. in Bucaramanga	T. catappa	P. dulce trees	
			Leaves	Branches
P. semiflaviventris				
Total parasitism rate	70%	68%	11%	6%
Percent of total that came from position C	23%[a]	17%[a]	18%[b]	9%[b]
T. bodkini				
Total parasitism rate	0%	9%	15%	41%
Rate of parasitism of eggs in position C	0%	32%	54%	90%
Number of masses	86	50	87	69

[a,b] Pairs differ significantly ($p < .01$).

bodkini sometimes displaces *P. semiflaviventris,* but not vice versa. The fact that neither species dominated consistently over the other when both laid into the same, otherwise virgin, eggs indicates, however, that each species sometimes displaces the other in nature.

FIGHTS BETWEEN MALES

Since the first wasps to emerge were nearly always males, it was possible to deduce the results of interspecific fights which had occurred in nature. In masses from which at least one wasp of both species had emerged, but from which some wasps of both species had yet to emerge when the mass was collected (all wasps and eggs were immediately killed with alcohol to prevent additional emergals before I counted them), the numbers of males of both species were significantly reduced ($p < 0.01$, Table 17). Thus, males of each species significantly displaced those of the other.

It appears that *T. bodkini* males may be superior fighters. The total rates for those egg masses parasitized by both species of wasp were 18% *T. bodkini* and 45% *P. semiflaviventris*. Assuming the sex ratio in Table 5, this would imply an average of 1.3 *T. bodkini* males/egg mass, and 2.4 *P. semiflaviventris* males/egg mass. If the two species were equally good fighters, the results of the 20 cases in which only one male was left on the egg mass (Table 17) would have been 7 *T. bodkini* and 13 *P. semiflaviventris*, rather than the observed 11 and 9 ($0.05 < p < 0.1$).

In addition, *P. semiflaviventris* males were more tolerant of the presence of conspecific males than were *T. bodkini* males. Of 48 masses which had *T. bodkini* males, only 4 had more than one, while 9 of 33 masses had more than one *P. semiflaviventris* male ($p < 0.05$). On several occasions I saw

a *P. semiflaviventris* male avoid an attack by an advancing conspecific by behaving like a female, lowering his antennae to the substrate, and remaining motionless. Such "feigning" behavior might be more effective in *P. semiflaviventris* than in *T. bodkini* since *P. semiflaviventris* females usually stay clustered around egg masses after emerging while *T. bodkini* females disperse.

There was no indication that males search out egg masses other than those where they emerge, as males were never found on masses from which at least one wasp of that species had not emerged (Table 17). Thus the exclusion of males of a given species by the other eliminated the chances of females of that species to mate near that egg mass, although the possibility remains that they mate away from the eggs.

Experimental Removal of Bugs Guarding Eggs

Both the patterns of parasitism of egg masses by the wasps and my repeated observations of bugs repelling attacking wasps show that the defensive behavior of the bugs lowers the number of eggs parasitized by wasp females which have found the egg mass. The observations reported in the sections on the oviposition and hunting behavior of the wasps suggest, however, that both species, and especially *P. semiflaviventris*, use the presence of guarding bugs to locate egg masses. The possibility thus arises that the net influence of the guarding bug on her eggs is negative—that her betrayal of their position by standing over them outweighs the benefits she confers on them with her defensive behavior.

This possibility was tested by removing bugs from some young egg masses (eggs without visible embryonic eyes and thus less than about four days old and still susceptible to parasitism), and leaving

TABLE 17.—*Male wasps present on egg masses from which some but not all of the wasps had emerged*

Species emerged	T. bodkini	P. semiflaviventris	Both	None	Total
Masses from which males of both species had emerged	11	9	8	2	30
Masses from which only T. bodkini had emerged	30	0	0	1	31
Masses from which only P. semiflaviventris had emerged	0	38	0	3	41

TABLE 18.—*Results of removal of female*
A. tripterus *guarding eggs on antless trees*

Wasp species	T. catappa	Cassia sp.
Parasitism by *T. bodkini*		
Control	4.5%	11.8%
Without female	7.2%	18.1%
Parasitism by *P. semiflaviventris*		
Control	64.4%	61.4%
Without female	29.1%*	46.4%*
Number of control egg masses	27	23
Number of experimental egg masses	22	39

* Experimental differs from control (p <.05, using Willcoxon's "Sum of Ranks Test").

the females guarding other similar masses in the same trees to serve as controls. Both test and control groups were identified by marks placed on adjacent leaves, and parasitism rates were determined 1–2 weeks later. The first test of this kind was conducted in two *P. dulce* trees, and a total of 48 test and 41 control groups were recovered. Nearly all of the experimental egg masses had vanished, however, when I recovered the leaves; in most cases there was nothing but a greasy stain remaining on the leaf. Of those few eggs recovered, not one produced a bug (most failed to develop). I observed several species of insect feeding on undefended eggs in this species of tree (Table 22), and they (perhaps especially the ants) were probably responsible for the losses.

These results show that the defense of the bugs against generalized egg predators is highly effective and that the overall effect of their defense is undoubtedly positive. The possibility remained, however, that the effect of the bugs with respect to the parasitic wasps is negative. This was tested by more

or less excluding ants from one *T. catappa* tree and one *Cassia* sp. tree (twigs harboring *Pseudomyrmex* colonies were removed and a ring of "Tack Trap" was laid around the trunk to prevent other species from climbing into the tree) and then repeating the experiment just described.

The results, presented in Table 18, show that the net effect of the presence of the bugs is indeed negative; it aids rather than hinders *P. semiflaviventris* and has no significant effect on *T. bodkini*. Thus the bugs were "wasting their time" with respect to both species of wasp, since they could have been investing it in feeding to produce more eggs.

Other Factors Affecting *A. tripterus* Survival

UNHATCHED EGGS

Often some eggs in a mass failed to produce either bugs or wasps. In some cases it was possible to determine whether a young bug or a wasp had died before emerging; in others, where it was not possible, the egg was termed "undeveloped." Some such eggs may have been infertile, while others probably contained dead bug embryos or parasites which died before discoloring the egg's vitelline membrane. The frequencies of both failures of identifiable bugs and wasps to emerge and of undeveloped eggs were correlated with the site of the egg mass.

DIFFERENCES BETWEEN SPECIES OF TREE.—Eggs laid during the same four-week period failed to develop more often on the leaves of a *P. dulce* tree than on those of two nearby *Cassia* sp. trees (Table 19). The frequency of undeveloped eggs was also correlated with tree species when data taken from

TABLE 19.—*Frequencies of deaths within the bug eggs on leaves of different tree species during the same four-week period* (A) *and during various periods* (B)

	P. dulce	Cassia sp.	Canagium odoratum	T. catappa
Died within the egg (A)				
Bugs	5.2% (N=3262)	.9% (N=1063)		
T. bodkini	19.7% (N=761)	.9% (N=327)		
P. semiflaviventris	42.2% (N=491)	2.7% (N=1251)		
"Undeveloped"	6% (N=4777)	1% (N=2778)		
Frequencies of "undeveloped" (B)	4.9% (35,099 eggs, 18 trees)	1.2% (18,411 eggs, 10 trees)	2.1% (3,215 eggs, 8 trees)	2.7% (26,302 eggs, 21 trees)

various trees at different periods were compared (Table 9). Hatching was consistently poorer on *P. dulce* than any other species of tree, but the level of significance cannot be determined since the effects of parasitism on the production of "undeveloped" eggs are unknown.

DIFFERENCES BETWEEN LEAVES AND BRANCHES.—In *P. dulce* trees, eggs laid on branches failed to develop more frequently than those on leaves. Thus, in 12 samples from 14 trees, the frequency of undeveloped eggs in branch egg masses was higher than that in leaf masses in 13 cases, lower in 7, and equal in 3 (p<0.1), and the total frequencies of undeveloped eggs were 7.7% on branches (N= 7463) and 4.3% on the leaves (N=13,313) of these trees. Data from eggs on *T. catappa* trees did not follow this pattern: 2.4% of the eggs on branches (N=3845) and 3.2% of those on leaves (N=15,735) of six trees were undeveloped. In this case at least, the differences in developmental failures are not due to differences in parasitism, since the differences in parasitism rates on leaves and branches of both tree species are similar (Table 10).

LEAVES AND EGG MASSES THAT FELL FROM TREES

Substantial losses of entire egg masses were observed during weekly checks in several trees. Each leaf which had an egg mass on it was marked (in the case of *P. dulce,* an adjacent leaf was usually marked), and the mass was collected after all bugs and wasps had left it. In a span of five weeks, 290 leaves marked on three *P. dulce* trees were recovered; 31% had lost their eggs. On two *Cassia* sp. trees, 16% of 145 marked leaves recovered during the same period were without eggs, indicating that this type of egg loss was less common (p<0.01) in *Cassia* sp.

These figures show a clear difference between the tree species, but they are only approximations of the true rates of loss because of several complications in taking the data: (1) marked leaves lacking eggs were probably less easily noticed, and therefore underrepresented; (2) some egg masses probably fell after the last bugs and wasps left, but before I returned to search the tree—these losses would be biologically insignificant; and (3) in the case of *P. dulce,* the entire leaf rather than just the egg mass may have fallen in some instances, leaving only the adjacent marked leaf. (Repeated observations of new eggs on yellow, ready-to-fall leaves on *P. dulce* and *Cassia* sp. trees [these trees continually shed a few scattered leaves] suggest that the bugs did not distinguish such unsatisfactory sites from others.) In balance, the data on losses by falling are probably somewhat below the true rates.

One other factor appeared to influence the loss of egg masses by falling. In all four study species of tree (and especially in *P. dulce*), a greater proportion of the older masses were on branches than on leaves (Table 20; guarded masses differ from unguarded masses, p<0.01) indicating that eggs stayed stuck to branches longer before falling. Egg masses also .appeared to stay glued to *T. catappa* and *Canagium odoratum* leaves longer than to *P. dulce* and *Cassia* sp. leaves, perhaps due to the greater mechanical protection afforded by the larger size of the leaves (Figure 2).

LOSSES OF FIRST INSTAR NYMPHS

VARIATION WITH SITE.—The numbers of first instar nymphs lost from groups at different sites were determined in two ways. Direct measurements of losses during the entire first instar period were determined in cases where the nymphs were found just moulting to the second instar by comparing

TABLE 20.—*Distribution of young and old egg masses on branches and leaves of* P. dulce *trees (total of 18 samples from 16 trees; the ages of unguarded masses were judged by the accumulations of dirt and fungus on them)*

Ages of eggs	Percent of masses found on—		Total number of
	Branches	Leaves	egg masses
Guarded egg masses	18	82	832
Unguarded and empty,but relatively new eggs	51	49	334
Old, weathered, empty eggs	58	42	283

for each mass the numbers of eggs that had pro-
duced bugs with the numbers of nymphs present;
indirect measures were obtained by comparing the
numbers of hatched eggs and the numbers of first
instar nymphs and then (assuming that on the
average these nymphs were halfway through the
first instar and that the rate of loss throughout the
instar was uniform) multiplying the losses by 2.
The results of both types of counts are presented
in Table 21. It should be kept in mind that "losses"
did not necessarily mean deaths of nymphs, but
only that the nymphs were no longer near the egg
mass. The general low activity of the first instar
nymphs suggests that vanished nymphs had not
walked away, but had either fallen or been eaten.
Falling nymphs clung readily to surfaces which
they struck but, even so, the chances of survival of
the nymphs probably decreased greatly if they fell.

There were again significant differences in losses
from different species of tree and from different
sites within a given species (Table 21). The di-
rectly measured rate of loss from *P. dulce* leaves
was not quite significantly greater than that from
Cassia sp. leaves (0.06>p>0.05), but was greater
than that from *T. catappa* leaves (p<0.05). The
indirectly measured rate of loss from branches was
greater (p<0.01) than that from leaves in *P. dulce*.
Although none of the differences between direct
and indirect measurements were large enough to
be significant, the consistent tendency for indirect
measurements to be larger suggests that the as-
sumption that the rate of loss is constant through-
out the instar may be incorrect and that younger
nymphs may be more frequently lost.

It seemed that mechanical agitation, which
would be greater on smaller-leafed trees such as
P. dulce, might be a principal cause of loss, but
comparisons of losses (determined indirectly) on
one *P. dulce* just after a period of heavy daily rains
and after periods of milder weather were not sig-
nificantly different. First instar nymphs (as well as
older ones) were capable of clinging very strongly
to a substrate; when I tried to lift nymphs away
from their egg masses in captivity, some individuals
clung to and suspended groups of eggs and nymphs
corresponding to up to 50 times their own weight.

EXPERIMENTAL REMOVAL OF FEMALES GUARDING
FIRST INSTAR NYMPHS.—The effects of the bugs'
defense of first instar nymphs were measured by
removing defending females. The number of
nymphs was counted when the female was removed
and again two days later, and the total number
which would have been lost in seven days, the ap-
proximate duration of the first instar, was then
calculated by multiplying the observed losses by
3.5. The results of these observations (Table 21)
were that losses rose significantly (p<0.01, calcu-
lated on the basis of losses/day) on both *P. dulce*
and *Cassia* sp. when the female was removed. The
defense of the females, at least in *P. dulce* trees,
had the effect of especially reducing the likelihood
of losses of large numbers of nymphs from any
given group. Thus, of 39 unguarded groups on *P.
dulce* which lost nymphs during the 48-hour ex-
perimental period, 13 or 33% lost three or more
nymphs; of 108 control groups which had lost
nymphs (the average age of these nymphs was as-
sumed to be 3.5 days), only 24% had lost three or

TABLE 21.—*Losses of first instar* A. tripterus *nymphs from guarded and un-
guarded groups in 7 days at different sites* (methods used in arriving at these
numbers are explained in the text; numbers in parentheses are number of egg
masses and total number of nymphs hatched)

| | P. dulce | | Cassia sp. | T. catappa | |
	Leaves	Branches	Leaves	Leaves	Branches
Nymphs lost from defended groups					
Measured directly	6.3% (41, 808)		3.4% (23, 353)	2% (10, 99)	
Measured indirectly	11.7% (245, 4802)	32.2% (56, 726)	9.3% (146, 1969)	3.5% (79, 665)	8% (20, 170)
Nymphs lost from undefended groups	44.1% (51, 1078)		40.2% (22, 332)		

more nymphs (p<0.05 after adjusting for different time spans).

OTHER ENEMIES OF *A. tripterus*

The animals observed preying on various stages of *A. tripterus* in nature and captivity are listed in Table 22. In addition to the species listed, a fungus of the genus *Penicillium* attacked and killed both nymphs and adults in Palmira and Cali (Eberhard, in press). A parasitic wasp, *Hexacladia* sp. n. (?) (Encyrtidae) (det. C. M. Yoshimoto), was also

reared from both adults and large nymphs of *A. tripterus.*

Discussion

HUNTING BEHAVIOR OF THE WASPS

Precise descriptions of the searching behavior of parasitic insects are of great interest, but are rare (DeBach and Hagen, 1964). Several aspects of the hunting behavior of the two wasps are clear from the data of this study.

TABLE 22.—*Other enemies of* A. tripterus *(all attacks on eggs and first instar nymphs occurred in unguarded groups unless otherwise noted; e=egg, n_1=first instar nymph, n=other nymphs, a=adults, P.d.=Pithecelobium dulce, C.sp.= Cassia sp., T.c.=Terminalia catappa)*

Predators	Stage(s) of A. tripterus *attacked*		Trees in which enemy was found
	In captivity	*In nature*	
Hymenoptera			
Sphecidae			
Bicrytes variegata		n	*P.d., C.*sp.
Vespidae			
Polistes canadensis		n[1]	*P.d., C.*sp.
Formicidae			
Ectatomma ruidum		e	*P.d., C.*sp., *T.c.*
Crematogaster sp.		e	*P.d., T.c.*
Pseudomyrmex spp.		e	*T.c.*
Campanotus sp.		e	*P.d.*
Hemiptera			
Reduviidae			
Zelus sp.	n_1, n		*P.d., T.c.*
Pentatomidae			
Loxa sp.	e		*P.d.*
Podisus cloelia	e,n_1,n	n_1^2,n,a	*P.d.*
Supputius sp. near *typicus*[3]	e,n_1,n	e^2,n_1^2,a	*P.d., T.c.*
Coleoptera			
Coccinellidae			
Olla abdominalis Say (?)		e	*P.d.*
Curinus colombianus Chapin		e	*P.d., C.*sp.
Neuroptera			
Chrysopidae (1 species)		e,n_1	*P.d., C.*sp., *T.c.*
Araneae			
Theridiidae			
Achaearanea tesselata[4]		n,a	*P.d., C.*sp., *T.c.*
Anelosimus sp.		n,a	*P.d.*
Salticidae			
Species 1		n	*T.c.*
Species 2		a[1]	*T.c.*

[1] Recently moulted.

[2] Female *A. tripterus* present.

[3] Also preys on adult *Phanuropsis semiflaviventris* in nature.

[4] Also preys on *Bicyrtes variegata* in nature.

Females of *P. semiflaviventris,* but not *T. bodkini,* tend to stay and hunt in the tree where they emerge; experimental predation on unemerged wasps in given trees significantly reduced the parasitism by *P. semiflaviventris,* but not *T. bodkini.* Both wasps almost certainly use the presence of the defending female bugs to locate host eggs, and their responses to male and dead bugs suggest that the location and immobility of the bug are important. Both wasps hunt their host visually, and *P. semiflaviventris* hunts during the day.

Both species seem to be primarily aerial hunters. The lack of correlation between the relative isolation (both natural and experimental) of the leaf with the eggs and the parasitism rates on the pinnate leaves of *Cassia* sp. trees imply that most searching is not carried out on foot. A further, indirect indication that the wasps find bug eggs from the air is the tendency of the bugs to face the leaf tip rather than its base while guarding their eggs.

It is not easy to reconcile the tendency of the wasps to hunt in flight with the tendency of *P. semiflaviventris* to stay in the trees where they emerge. The wasps are very small, and relatively weak fliers, so that even moderate winds probably tend to wash them out of trees where they are flying. The wind in Cali is usually very weak in the mornings, but is often moderate to strong in the afternoons, sometimes reaching 15–20 kmph as early as 2:30–3:00 PM. Perhaps moderate or stronger winds cause *P. semiflaviventris* to stop hunting, perhaps the wasps do not normally hunt later than about 2:00 PM, or perhaps hunting flights consist of many short hops.

It is possible that hunting for eggs on branches involves behavior distinct from that of hunting on leaves, as on several occasions females of *T. bodkini* were seen walking along branches and responding to bugs as if they were searching for eggs.

It is clear that the species of tree somehow influences the hunting behavior of *P. semiflaviventris.* Parasitism by this wasp shows a general correlation with leaf size, being highest in eggs laid on larger leaves. Even though the defensive behavior of the bugs may be somewhat less effective against *P. semiflaviventris* on the small-leaved *P. dulce,* eggs on this tree are much less heavily parasitized than those in other trees. The relatively constant rates of *T. bodkini* in different tree species on the other hand suggest that its hunting be-

havior is not influenced by the tree species.

The rate of parasitism in a given tree species must be a function of both the facility with which a wasp finds egg masses (hunting efficiency) and the time it spends looking for them there (hunting effort). The relative weights of these two factors are unknown. It would seem that trees with larger and fewer leaves would, a priori, be easier to search; this would explain the variations in *P. semiflaviventris* rates, but would imply that *T. bodkini* hunts more in trees which are harder for it to search. Without more knowledge of the natural habitats of the wasps and bugs and of alternate hosts of the wasps, it is not possible to weigh these factors.

Although *T. bodkini* tends to disperse more randomly among different species of tree than does *P. semiflaviventris,* parasitism rates by *T. bodkini* were far from uniform, even in trees of the same species, and significant differences occurred in given trees at different times. These differences could be explained by (a) more wasps arriving to hunt in some trees than in others, (b) individual wasps searching more in some trees than in others, and/or (c) some trees being more easily searched than others of the same species. The most likely of these is (a), at least in those cases in which a given tree's parasitism rates varied over time.

COMPETITION BETWEEN THE WASPS

The two species of wasps compete with each other at two points in their life cycle; the males tend to exclude each other from egg masses and, probably as a result of larval competition within the egg, only one wasp grows from any egg parasitized by both species. It appears that neither species is completely dominant in either type of competition, although *T. bodkini* males may be somewhat superior fighters. Both types of competition are common in Cali.

The result of interspecific competition between males is that, at least on some trees, substantial numbers of females are left unfertilized. Analyses of the sexes of wasps from egg masses showed that unfertilized females seldom lay eggs (assuming that unfertilized eggs produce males, as is generally true for Hymenoptera). Whether unmated females mate away from the egg masses where they emerged (laboratory observations indicate that this is pos-

sible, at least in *T. bodkini*), or whether they never oviposit is not known. In any case, interspecific competition among males probably causes appreciable reductions in the rates of parasitism by both species in at least some situations.

It should be noted that this host-parasite system is somewhat unusual in that the bug's defense of its eggs probably buffers the competition between the wasps to some extent. By more or less excluding *T. bodkini* from most parts of the egg mass, the bug makes some eggs avilable to *P. semiflaviventris* even in areas of relatively high *T. bodkini* density. The bug's defense also lowers the premium on the searching ability of the wasps, since a wasp's ability to outmaneuver the bug once she has located an egg mass is also a factor in her competitive success. Thus the superiority of one species in hunting might be such that it would displace the other under different circumstances, but would fail to do so in this system because of its difficulty in overcoming the defenses of the bugs.

Net influence of the guarding behavior of the bugs on the total effectiveness of the wasp population's ability to parasitize eggs is not known. The bugs certainly delayed and repelled some wasps and caused many others to waste time trying to attack unsuitable eggs. But they also acted as beacons indicating the location of the eggs, and the balance of these factors is unknown.

EVOLUTIONARY RELATIONSHIPS OF THE WASPS

F. Wilson (1961) described various characteristics which are common to most wasps of the family Scelionidae. On comparing the two species of this study against his scheme (Table 23), it is clear that *T. bodkini* is less specialized (closer to the family norm) than *P. semiflaviventris* and that the main points of difference in both species are associated with oviposition.

The differences of both species from the family pattern are probably due to the unusual circumstances they encounter while ovipositing. They must overcome the defensive behavior of the guarding bugs, while at least some of the scelionids considered by Wilson attack unguarded eggs (Wilson, pers. comm.). It seems likely that characteristics #6, 7, and 8 would be disadvantageous during battles with defending bugs since they would slow the wasp's oviposition and thus give the bug more

TABLE 23.—*Characteristics of* T. bodkini *and* P. semiflaviventris *as compared with those of other scelionids* (F. Wilson 1961)

Family norm for Scelionidae	Same characters found in—	
	T. bodkini	P. semiflaviventris
1. Males emerge before females	yes	yes
2. Males stay on egg mass where emerged, fight with other males there	yes	yes
3. Copulation occurs as female emerges from host egg	yes	yes
4. More females than males	yes	yes
5. Each male can fertilize many females	probably	probably
6. Females fight each other while attacking an egg mass	almost never	no
7. Female marks host egg after ovipositing into it	sometimes	no
8. Female distinguishes already parasitized eggs from others	yes, at least sometimes	no

time to kick it away. This idea is supported by the fact that *T. bodkini* females perform more marking and inspection when on undefended eggs than when battling a bug.

F. Wilson (1961) also describes several other characteristics of *Asolcus basalis,* which he does not attribute to the rest of the family, and the species of this study share several of these, including the method of cutting the cap of the bug's egg on emergence, and the predominance of emergences in the morning (at least in *P. semiflaviventris*). They differ in that they oviposit much more quickly—approximately 4 seconds in *P. semiflaviventris* and 20–30 seconds in *T. bodkini* as against 3–4 minutes in *A. basalis.* Oviposition times of other scelionids which attack undefended eggs are also relatively long: 2.5 minutes in *Telenomus gifuensis* (Hidaka, 1958), 6–8 minutes in *T. fariei* (Lima, 1928), 5–20 minutes in *Hadronotus ajax* (Schell, 1943), and 0.5–2 minutes in *Platytelenomus* sp. (?) *hylas* (Moutia and Courtois, 1952). Egg marking behavior by *T. bodkini* is also much shorter (1–2 seconds) than that of *A. basalis* (about 20 seconds—F. Wilson, 1961). Again these differences appear to represent adaptations to overcome the bug's defense of her eggs. One other small dif-

ference is the rubbing movement made occasionally by *P. semiflaviventris* males mounted on females before mating.

P. semiflaviventris is more specialized to overcome the bug's defenses than is *T. bodkini*: in each case in which the two species differ from the scelionid norm, *P. semiflaviventris* is farther from the norm than *T. bodkini* and the ability of *P. semiflaviventris* to extend and curve its abdomen, an unusual feature for the family (*Scelio pembertoni*, a parasite of buried grasshopper eggs—Pemberton, 1933—also extends its abdomen when ovipositing), is also clearly an aid in penetrating the bug's defense. *P. semiflaviventris'* combination of "advanced" characters enables it to parasitize relatively well-defended areas of the egg mass, while the "less specialized" *T. bodkini* is more or less restricted to one poorly defended edge. *T. bodkini* attacks appeared to be more efficient in one situation, however—when the wasps parasitized eggs as they were being laid by the bug.

F. Wilson interpreted the various characteristics he described as being adaptations favoring the species, but it is possible and thus preferable (see Williams, 1966, for example) to explain them as adaptations to benefit the individual. Each female would be favored by the ability to distinguish and refrain from ovipositing into eggs already parasitized, and by her aggressiveness toward other females on a given egg mass. The same would hold for aggressiveness between males on egg masses. Aggressive males emerging early and staying to copulate with females from the same mass would

avoid having to hunt for females, and thus benefit from the likely high concentration there, and they would give their mates a maximum amount of time to hunt for hosts. Females which mated as soon as they emerged would have more time to search for hosts. And within this framework, a female would maximize the reproductive potential of her offspring by producing more female than male eggs, laying only the minimum number of male eggs necessary to insure the fertilization of the females in that egg mass.

SELECTION PRESSURES ON THE BEHAVIOR OF THE BUGS

THE CHOICE OF SITES FOR EGG MASSES.—The data relating the sites of egg masses to variations in parasitism, failure to hatch, losses from the tree by falling, and losses of first instar nymphs reflect the workings of natural selection on the bugs' choices of oviposition sites. The balance of these factors was not always the same in different trees, and the bugs did not always act in their own best interests.

Natural selection clearly favored laying eggs on branches rather than leaves in *T. catappa*, while losses were nearly even in *P. dulce* (Table 24). In both species of trees, however, the bugs laid on leaves much more often than on branches, and the difference between the tree species was the reverse of what survivorship data would predict, with *T. catappa* leaves being more heavily favored than those of *P. dulce* (Table 24). These data suggest

TABLE 24.—*Percent losses of* A. tripterus *offspring in different trees, on leaves and branches of the same trees and frequency of oviposition in these sites*

Cause of loss	T. catappa		P. dulce	
	Leaves	Branches	Leaves	Branches
Parasitism by—				
T. bodkini	8%	13%	21%	35%
P. semiflaviventris	64%	32%	10%	7%
Failure to develop	5%	3%	4%	8%
Eggs fall from tree	very small	very small	31%	very small
Loss of first instar nymphs	2-3%	8%	10%	20%
Total average survival	31%	52%	49%	45%
Frequency of oviposition	92.5%	7.5%	87%	13%
Number of egg masses	519		1221	
Number of trees	15		14	

the hardly surprising conclusion that the bugs evolved in circumstances very different from those in present-day urban Cali, and that they are probably presently evolving new behavior to adjust to this environment. Modified selective regimes in urban areas are probably common for many organisms (e.g., Ford, 1955; Waldbauer and Sternburg, 1967). Just what the original conditions were in which *A. tripterus* evolved a preference for ovipositing on leaves is a matter of conjecture.

Survivorship data also permit comparisons between species of tree. Thus the total survivorship through the first instar on *P. dulce* was about 48% (49% of the 87% on leaves plus 45% of the 13% on branches), that on *T. catappa* was about 33% (31% of 92.5% plus 52% of 7.5%), and that on *Cassia* sp. was about 45% (branch masses were almost nonexistent; average rates were 54% parasitism, 1% failure to hatch, 16% falling from the tree, and 5% loss of first instar nymphs). Natural selection on eggs and first instar nymphs favored bugs ovipositing in *Cassia* sp. and *P. dulce* trees over those laying eggs in *T. catappa*, but in fact trees of the latter species commonly had large populations of bugs and eggs.

DEFENSE OF EGGS BY FEMALES.—The striking fact that the defense of their eggs by the female bugs, which in various respects appears to be specifically designed to combat the parasitic wasps, nevertheless causes a net loss of eggs to at least one of the wasp species, suggests the following possible evolutionary history. The bugs are certainly descended from an ancestor that did not guard its eggs, although at least four other *Antiteuchus* species are presently subsocial. This ancestor's eggs were probably strong enough to withstand attacks by generalized predators such as ants, but were relatively defenseless against parasites such as scelionids, which were able to oviposit through hard shells. Bugs began guarding their eggs because of the selective advantage of repelling parasites. Their existing responses to disturbances (as seen in present-day nymphs and males)—antennating toward the source of disturbance, shaking the body, and perhaps kicking toward the disturbance—combined with suppression of the tendency to flee, served to drive away enough of the parasites to make guarding worthwhile, and incidentally drove off generalized predators also.

Over time the defensive responses of the bugs became more finely adjusted to the attack behavior of the parasites: they acquired the defensive movements of scraping and leaning toward the source of disturbance, perhaps later suppressing scraping after the nymphs had hatched out; they suppressed squirting defensive liquid, feeding, and the tendency to turn and face disturbing stimuli; and, perhaps, they modified several details of oviposition behavior, and began laying more compactly arranged egg masses, and facing toward the tips of such masses and toward the tip of the leaf. At the same time, the egg cuticle became thinner, as the eggs were now guarded from attacks of generalized predators as well as from parasites, and this material could be more advantageously used in other ways.

The wasps, especially *P. semiflaviventris,* evolved in response to the changes in the behavior of the bugs, modifying several aspects of their oviposition behavior to speed it up, and also beginning to use the presence of the bug as a cue to the location of egg masses. *P. semiflaviventris* also evolved a greatly extendible abdomen. The advances of the wasps have been such that at the present time the bug loses more eggs to parasites than it saves from them by guarding. The production of thinner egg shells, however, has trapped the bugs into remaining on their eggs, which are now susceptible to many other predators in addition to the parasites.

DEFENSE OF FIRST INSTAR NYMPHS BY FEMALES.— Since losses of unguarded nymphs were not prohibitively high (Table 21), the possibility arose that female bugs lost more than they gained by guarding nymphs. The cost of guarding behavior was calculated by comparing the lengths of time until the next oviposition in two cases: females taken from newly hatched (<12 hours old) first instar nymphs, and females from second instar nymphs (these had spent about a week guarding first instar nymphs and 0.5–1 day guarding second instar nymphs). The females from the new first instars reoviposited on the average 19 days later (giving a rate of egg production of 28/19 or 1.47 eggs/day), while the others averaged 17 days until reoviposition (1.65 eggs/day). Comparing the two tactics—desertion or nondesertion of first instar nymphs—in terms of time, deserters would spend $7+19=26$ days between ovipositions, and nondeserters $7+7+17=31$ days between ovipositions. The time difference multiplied by the rate of egg

production by deserters (5×1.47) gives the actual cost in eggs of guarding behavior—7.4 eggs each cycle.

The savings, in terms of nymphs, resulting from guarding behavior amount to about 30% of the nymphs hatched in both *P. dulce* and *Cassia* sp. trees (Table 21). For unparasitized masses of 28 eggs, this would amount to 8.4 nymphs per cycle. Thus, even without taking into account the advantages of protecting nymphs as they moult to the second instar (their bodies are soft and for a short while they are without defensive odor) and the

possible dangers to the female before she oviposited again, the benefits outweigh the costs of guarding first instar nymphs. This should be equally true for situations of high and low parasitism, unless parasitism rates are declining steadily.

Desertion rates were higher in *P. dulce* than in *Cassia* sp., even though the rates of loss of nymphs from unguarded groups were about the same in both species. Thus, at least in urban Cali, the stimuli which cause the bugs to desert their nymphs do not accurately reflect the likelihood of losses of unguarded nymphs.

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