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Biology of Reduviidae of Cocoa Farms in Ghana

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ABSTRACT: In the cocoa farms the members of family Reduviidae are distributed in a variety of habitats associated with particular food, defense and breeding requirements for various species. In general the ectrichodiines are exclusively litter dwellers and reduviines occur only under the loose bark of primary forest trees. The members of subfamily Harpactorinae are associated with herbs, shrubs and the foliage of cocoa trees. A group of harpactorines comprising *Authenta, Margasus, Nagusta* and *Odontogonus* has been found to be completely arboreal.

The food and feeding behavior of the cocoa farm Reduviidae were explored and data on the insects preyed upon by the Reduviinae obtained for the first time. In one locality at Tafo, one species of this subfamily utilized 24 different species of ants belonging to four subfamilies. As a preliminary to feeding, the reduviids were generally observed to exhibit grooming behavior which at times was repeated once the bug had finished feeding.

Coloration, mimicry and scent glands were considered to contribute greatly to the primary defense of the Reduviidae found in the cocoa farms. The majority of Reduviidae living in cocoa canopy or concealed situations such as leaf litter tended to be dark-colored, usually matching their surroundings. The reduviids at shrub level are conspicuously colored and their adults exhibit a behavior pattern highly suggestive of certain wasps. Excepting the Emesinae and Tribelocephalinae, where the scent glands are completely absent, repugnatorial glands producing generally a pungent secretion were found in all the reduviidae occurring in cocoa farms. A unique system of glands situated at the base of dorso-abdominal hairs was discovered for the first time. This system produces secretions which assist in sticking camouflage material to the back of reduviine larvae. Early instars of some species of Harpactorinae were observed to mimic smaller species of ants such as *Pheidole* and *Anochetus*.

Courtship, mating and oviposition in Reduviidae were studied and the significance of the precopulatory riding position, parental care and laying of eggs singly or in groups is discussed.

Cocoa capsids are attacked by a number of parasites and predators including ants, reduviids (assassin bugs), mantids, long-horned grasshoppers and crickets. Williams (1954) showed that predators are a significant factor in the natural control of capsid numbers. He furnished quantitative data which suggested that the assassin bugs and mantids together account for more than one and a half times the capsid mortality caused by ant predation. Leston (1969), however, considered that ants afford considerable protection to cocoa trees against capsid damage. Marchart (1969), on the other hand, presented experimental evidence in support of his contention that ants are ineffectual against capsids. One point which is very clear from the work of these authors is that each predatory species individually causes an appreciable mortality of the capsids. Smith (1968) has stressed that it is these "partial controls" that are so important in integrated control programs.

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Although discussion about the relative importance of these predators continues, not much is known about their natural history. For example, little is known about the life cycles of mantids and practically no published accounts exist of their larvae. There is even uncertainty over the number of instars in the larval life of a mantid (R. Kumar, pers. comm.), and in several species females have seldom been recorded. Similarly, a large number of common ants live in cocoa forest, but the details of the biology of only a few species have been investigated. The family Reduviidae, with which the present work is concerned, is a large group of mostly predacious bugs distributed primarily in tropical regions. They have been described as "formidable enemies" of capsids (Squire, 1947). On the basis of field observations, Mayné and Ghesquière (1934), Golding (1941), Squire (1947), Alibert (1951) and Forsyth (1966) have listed reduviid enemies of cocoa capsids in West Africa. Very recently radioisotope tagging has shown that at least three genera of Reduviidae prey upon *Distantiella theobroma* (Distant) in the field (Marchart, 1969; Collingwood, 1971). However, as in the case of mantids, very little is yet known about their habitats, habits and larval stages. Although these larval stages are frequently encountered in pyrethrum knock-down samples which are obtained to study the complex insect fauna inhabiting the cocoa forest canopy, no attempt has been made to formulate keys that might aid in the identification. The present work attempts to furnish some information on the biology of the assassin bugs occurring in cocoa farms.

The larval stages will be published elsewhere.

MATERIALS AND METHODS

Methods for the study of habitats.—The distribution of Reduviidae in cocoa farms was studied at Aburi, Mampong, Ammonokrom and Tafo (all within 70 miles N of Legon, Ghana) (Fig. 1) in the following habitats: ground — in litter (leaf, wood chips, dead wood, open and shade); herbs — open, shade; shrubs — open, shade; cocoa — open, shade [(1) trunk, (2) foliage]; other trees — (1) foliage, (2) trunk, (3) subcortical.

Methods for the study of the habitats were as follows: (1) searching; (2) sweeping; (3) pyrethrum knock-down (done jointly with Dr. A. King, member of the International Capsid Research Team, Tafo).

HABITATS

In cocoa farms the members of the family Reduviidae are distributed in a variety of habitats which are associated with particular food, defense and breeding requirements of the various species. Thus, ant-feeding larval reduviids occur under the loose bark of trees and pile corpses of ants and other material on their backs. Species feeding almost exclusively on cotton stainers mimic and live with them at ground level; species feeding on millipedes and other litter dwellers exclusively inhabit the leaf litter, while those with diverse habits are more widely distributed. As a result of the present work, the habitats of Reduviidae in cocoa farms can be classified as below. The writer is aware of the habitat classification put forth by Elton (1966) and other authors, but for the present work, it seemed best to follow the scheme adopted here.

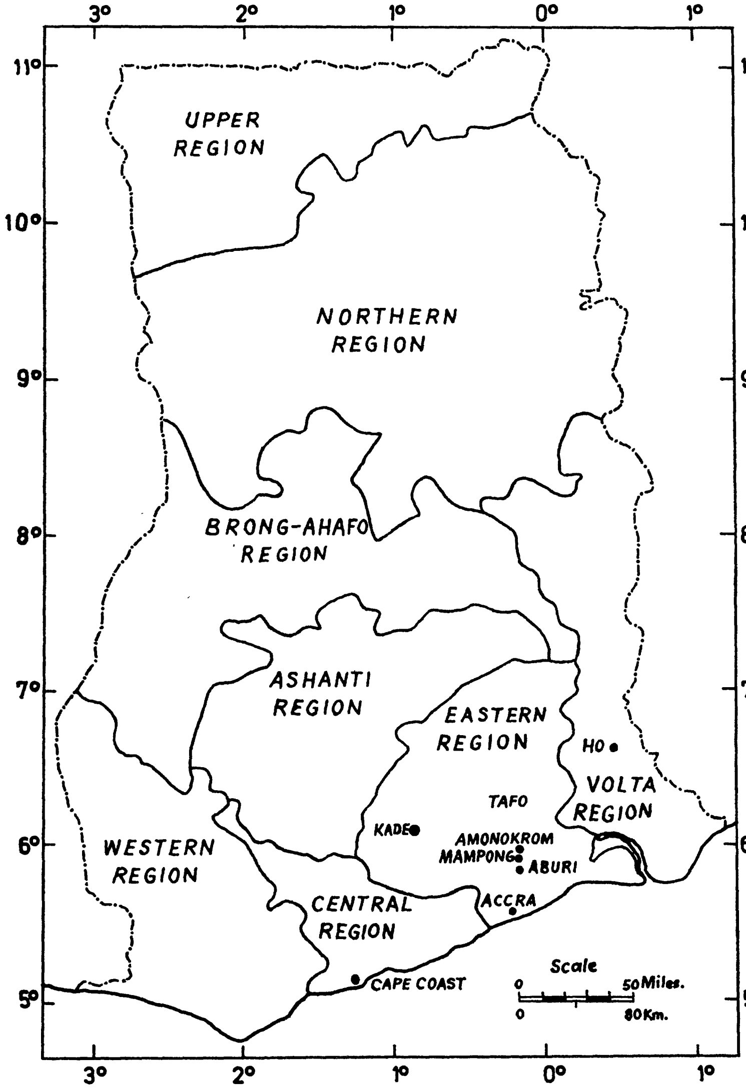

Fig. 1.—Map of Ghana showing localities where Reduviidae were collected

Ground.—This habitat in cocoa farms comprises mainly dead leaves from the cocoa trees, shade trees, herbs and shrubs along with broken branches and dried pods. Only species of Reduviinae, Piratinae, Ectrichodiinae and Harpactorinae (only one genus, *Phonoctonus*) were found in this habitat. At Tafo, the habitat of the below-mentioned species inhabiting leaf litter in the shade is as follows: *Ectrichodia barbicornis* (Fabricius) (Ectrichodiinae), *Microstemma atrocyanea* Signoret (Ectrichodiinae) (in soil under litter); *Acanthaspis sulcipes* Signoret, *Platymeris horrida* Stål (both Reduviinae); *Ectomocoris pretiosus* Schouteden (Piratinae) (also found crossing untarred road from one farm to another); *Phonoctonus* spp. (Harpactorinae) (in litter with *Dysdercus* spp.). All, with the exception of *Phonoctonus,* are negatively phototactic. Leaf litter forms a suitable temporary habitat for the larvae of reduviid species that inhabit various types of vegetation in cocoa farms. Actually this should more appropriately be called a shelter habitat. When disturbed or attacked, larvae from the vegetation fall and burrow into the leaf litter where they may feed on suitable prey. The larvae of the following Harpactorinae, whose normal habitat is herbs and shrubs, have been collected in litter: *Vestula lineaticeps* (Signoret), *Pisilus tipuliformis* (Fabricius), *Rhinocoris bicolor* (Fabricius), *R. loratus* (Stål), *Sphedanolestes leucocephalus* (Fabricius).

Herbs.—This habitat includes clustered and scattered food plants, different varieties of short grasses and other plants. The plants forming this type of growth belong to the families Araceae, Commelinaceae, Cucurbitaceae, Devalliaceae, Graminae, Papilionaceae, Piperaceae and Urticaceae. *Harpagocoris joveri* and *Rhinocoris carmelita* are the only species associated exclusively with this habitat. The former is always found in sunny areas while the latter occurs in shade, often on cocoa foliage and on the trunk. Pyrethrum knock-down samples almost always contain specimens of this species.

Shrubs.—These form the undergrowth of the cocoa farms and consist of scattered woody plants. In Ghana, where cultural practices are virtually nonexistent, this type of growth belongs to the families Acanthaceae, Apocynaceae, Combretaceae, Euphorbiaceae, Moraceae, Papilionaceae, Rubiaceae, Solonaceae and Urticaceae. The species of Reduviidae found in this type of habitat are listed in Table 1. Of these, *Vestula lineaticeps* flies to cocoa foliage to feed on capsids and ants. It is frequently encountered in pyrethrum knock-down samples. In cocoa farms devoid of herbs and shrubs (there are very few such farms), none of the reduviid species listed for these habitats occur.

Cocoa trees.—The trunks of cocoa trees do not form a natural habitat for many species of Reduviidae, though specimens occurring in other habitats may be encountered resting there or preying on available food. However, *Lisarda vandenplasi* Schouteden (Salyavatinae) is frequently encountered on cocoa tree trunks where it is highly cryptic.

The foliage of the cocoa trees, however, provides an important habitat for a number of reduviid species which are strictly arboreal. These are listed in Table 2.

Other trees.—Most cocoa farms examined in this study are in well-shaded areas and include dead or living primary forest trees. Under the loose bark of these trees a number of species of the subfamily Reduviinae live. The bugs prefer dry bark and are seldom encountered under moist bark or on rotten felled trees. An exception to this

TABLE 1.—Reduviidae inhabiting the shrubs

Locality	Family	Name	Habitat	
			Open	Shade
Aburi, Mampong, Amonokrom, Tafo	Harpactorinae	*Pisilus tipuliformis* Fabricius		Shrubs, cocoa-yam leaves
Tafo	Harpactorinae	*Phonoctonus fasciatus* Beauvois		Shrubs, at times on cocoa leaves
Tafo	Harpactorinae	*Phonoctonus lutescens* Guérin et Percheron		Shrubs, at times on cocoa leaves
Tafo	Harpactorinae	*Phonoctonus subimpictus* Stål		Shrubs, at times on cocoa leaves
Tafo	Harpactorinae	*Rhinocoris albopilosus* (Signoret)	Shrubs	
Aburi, Mampong, Amonokrom, Tafo	Harpactorinae	*Rhinocoris bicolor* (Fabricius)	Shrubs	
Aburi, Mampong, Amonokrom, Tafo	Harpactorinae	*Rhinocoris carmelita* (Stål)	Weeds, short grasses	Shrubs, cocoa-yam leaves
Aburi, Mampong, Amonokrom, Tafo	Harpactorinae	*Rhinocoris loratus* (Stål)	Shrubs, cocoa-yam leaves	
Tafo	Harpactorinae	*Rhinocoris rapax* (Stål)	Shrubs	Shrubs with top shade
Aburi, Mampong, Amonokrom, Tafo	Harpactorinae	*Sphedanolestes leucocephalus* (Fabricius)		Shrubs
Aburi, Mampong, Amonokrom, Tafo	Harpactorinae	*Vestula lineaticeps* (Signoret)	Shrubs, grass, weeds, cocoa-yam and cocoa leaves	Shrubs, grass, weeds, cocoa-yam and cocoa leaves

statement is, however, the case of *Sphedanovarus camerunensis* Breddin, which was collected from the moist bark of dead forest trees with partial shade from the cocoa canopy. The habits of bark-dwelling species were studied in considerable detail and are discussed elsewhere. The species studied are listed in Table 3. Generally, they are found

TABLE 2.—Reduviidae inhabiting cocoa trees

Locality	Family	Name	Habitat
			Open or Shade
Tafo	Harpactorinae	*Authenta fulvipennis* Horvath	canopy
Tafo, Aburi, Mampong	Harpactorinae	*Margasus afzelli* (Stål)	canopy, generally at low level
Tafo, Mampong	Harpactorinae	*Margasus impiger* Bergroth	canopy, generally at low level
Tafo	Harpactorinae	*Nagusta punctaticollis* (Stål)	canopy
Tafo	Harpactorinae	*Odontogonus dimensis* Schouteden	canopy but descends at times to cocoa tree trunks
Tafo	Emesinae	2 undetermined species	canopy

TABLE 3.—Reduviidae inhabiting other trees (primary forest trees)

Locality	Family	Name	Habitat	
			Open	Shade
Mampong, Tafo	Reduviinae	*Acanthaspis vitticollis* Reuter		Under loose dry barks of live or felled primary forest trees
Tafo	Reduviinae	*Cethera maculipennis* Breddin		Under loose dry barks of dead primary forest trees
Tafo	Reduviinae	*Cethera musiva* Germar		Under loose dry barks of dead primary forest trees
Tafo	Reduviinae	*Sphedanovarus camerunensis* (Breddin)		Under loose moist barks of dead primary forest trees
Aburi, Tafo, Ho (Volta region), Kade	Reduviinae	*Tetroxia nigrispinosa* Villiers		Under loose barks or on dead and live primary forest trees

at heights of 0.6-1.85 m. In any case, loose bark seldom occurs at a level higher than 3 m. Specimens of *Acanthaspis vitticollis* on many occasions were observed to be coming down the trunks of cocoa trees, probably returning from feeding trips in search of ants.

HABITS

FOOD AND FEEDING BEHAVIOR

Food.—It is generally accepted that Reduviidae have no decided food preferences. A large number are predacious and they will attack most insects and other arthropods which fall within certain size limits. There are, however, certain well-established exceptions; for instance, the members of the subfamily Ectrichodiinae feed exclusively on millipedes (Miller, 1953) while species of *Triatoma* and *Rhodnius* feed on warm-blooded mammals. The food of the common cocoa-farm Reduviidae may best be considered under the different subfamilies:

Ectrichodiinae: Specimens of *Ectrichodia barbicornis* and *Nularda nobilata* were fed and kept alive in the laboratory for several weeks on a diet of millipedes. They rejected insects and other arthropods even when starved.

Emesinae: Only two undetermined species were collected in cocoa farms. Being arboreal, no observations could be made on their food in the field. Another species, *Eugubinus annulatus* (Villiers), was extensively collected at Legon from the webs built by spiders near the roofs of verandahs. After a good deal of experimentation, *E. annulatus* was found to accept only mosquitoes (*Aedes* spp.) and *Drosophila* spp. Gillet (1957) was also able to rear *Bagauda gilletti* Miller on species of *Aedes.* Wygodzinsky (1966) in his monograph has given a detailed account of the food of emesine bugs.

Reduviinae: *Acanthaspis vitticollis* is the commonest reduviine in cocoa farms. Its larvae are commonly associated with *Tetroxia nigrispinosa,* a species which resembles it closely and belongs to the same subfamily. The two species may, however, after some practice, be readily distinguished. *Acanthaspis vitticollis*, to camouflage itself, piles and carries on its back corpses of ants and some other insects, while *Tetroxia nigrispinosa* utilizes mostly soil particles and bits of plant parts. In the laboratory, *Acanthaspis vitticollis* was reared on a diet of *Oecophylla longinoda* (L.) (Formicidae : Hymenoptera) workers. All efforts to rear *Tetroxia nigrispinosa* on a diet of common insects and other arthropods failed and its food remains unknown. It was found that after sucking the ants, *Acanthaspis vitticollis* always attached them to its back. Similar observations have been made on other species of Reduviinae by Immel (1954 and 1955), Miller (1953), Odhiambo (1958), Villiers (1948) and others. It was observed that after each molt, the camouflage carried during the previous molt was transferred to the back of the newly molted bug. Thus an analysis of the corpses may reasonably be expected to give some idea of the food of the bugs under field conditions.

A total of 36 specimens of *Acanthaspis vitticollis* from different localities were collected and their camouflage material analyzed. The data obtained from this study may be summarized as follows:

Each specimen of *A. vitticollis* carried a variety of insects of which ants were the most frequent. The number of ants per specimen varied from 1-75 (mean, 12) and the number of species of ants per specimen varied from 1-10 (mean, 4). The following is the list of insect species found in the camouflage material.

Order Hymenoptera
Family Formicidae
Subfamily Formicinae: *Acantholepis* sp., *Camponotus acvapimensis* Mayr; *C. flavimarginatus* (Mayr); *C. vividus* (F. Smith); *Oecophylla longinoda* (Latr.) and *Polyrhachis laboriosa* Smith.
Subfamily Ponerinae: *Anochetus africanus* Mayr; *Anochetus* sp. and *Odontomachus* sp.
Subfamily Dorylinae: *Anomma nigricans* Illiger.
Subfamily Myrmicinae: *Cataulacus guineensis* F. Smith; *Cataulacus parallelus* F. Smith; *Crematogaster africana* Mayr; *C. clariventris* Mayr; *C. spuria* (Forel); *C. striatula* Emery; *Crematogaster* sp.; *Monomorium* sp.; *Macromischoides aculeatus* Mayr; *Pheidole speculifera* Emery; *Pheidole* sp. 1; *Pheidole* sp. 2; *Pristomyrmex* sp.; *Tetramorium guineense* (Fabricius); *Tetramorium* sp. 1 and *Tetramorium* sp. 2.
Subfamily Dolichoderinae: *Tapinoma* sp. and *Technomyrmex* sp.
Families Braconidae and Tiphilidae (undetermined species).
Order Diptera: Undetermined Drosophilidae and Tipulidae.
Order Coleoptera: Undetermined Platypodidae and Staphylinidae.

From analysis of this and other information, the following points may be made regarding the food of *A. vitticollis* in the field.

1. *A. vitticollis* feeds on a wide variety of ants. In the cocoa farms, around the Cocoa Research Institute, Tafo, the bugs utilized no less than 24 species of ants. It is clear that the bugs frequent areas where different species of ants occur. Exceptions to this statement were, however, five specimens which either carried *Crematogaster striatula* exclusively or in very high numbers. These departures from the normal pattern might be due to two reasons:

a. the bugs frequented an area where *C. striatula* is dominant. According to D. Leston (pers. comm.), if this ant is dominant in an area, it has the ability to keep out other ants from that area.

b. it is also likely that the bugs frequented the tree that had many *C. striatula* nests and it was easy for the bugs to prey on them. Both *C. striatula* and *A. vitticollis* live in dark, shaded areas, thus providing ideal situations for predation by the bug.

2. The bugs do not have preferences for any particular species of ants and they seem to move around in search of their food. The presence of many soil-nesting *Pheidole* species in the camouflage material is perhaps a pointer in this direction.

3. According to my field observation, *A. vitticollis* carries out its

feeding excursions during the daytime. However, *Macromischoides aculeatus,* an ant with a main activity period at night, was found in the camouflage material of 19% of the specimens. This suggests that the bugs are active at night as well.

4. *Oecophylla,* though a dominant ant in cocoa farms, is only rarely preyed upon (about 6% of the cases in the present study). This may be explained by the great mobility and ferocity of the ant. Under laboratory conditions, as mentioned earlier, *A. vitticollis* was reared exclusively on a diet of *Oecophylla.*

5. In addition to ants, as evidenced by camouflage material, *A. vitticollis* feeds on certain beetles, flies and wasps as well. However, no attempt was made to raise the bugs in the laboratory on such diets.

Harpactorinae: The larvae and adults of *Hediocoris tibialis, Pisilus tipuliformis, Rhinocoris bicolor, R. carmelita, R. loratus, Sphedanolestes leucocephalus, Sphedanolestes* sp. and *Vestula lineaticeps,* as already stated, were reared on laboratory-cultured *Tenebrio* larvae, pieces of freshly killed and dismembered *Periplaneta americana* and *Zonocerus variegatus.* First and 2nd instar larvae were unable to feed on live *Tenebrio* and had to be provided with cut pieces of these beetles. Larvae of all stages, however, readily fed on *Drosophila,* and it is quite possible that, in the field 1st and 2nd instar larvae feed on similar insects.

In addition to the above-mentioned insects, the reduviids fed on a variety of insects that were offered to them. They are as follows: *Humbe tenuicornis* Schaum (Acridiidae: Orthoptera); unidentified member of family Sarcophagidae (Diptera); *Anomis leona* Schaus (Noctuidae: Lepidoptera); *Eumeta rougeoti* Boug (Noctuidae Lepidoptera); *Distantiella theobroma* (Distant) (Miridae: Heteroptera); *Sahlbergella singularis* Haglund (Miridae: Heteroptera); *Bryocoropsis laticollis* Schumacher (Miridae: Heteroptera); *Helopeltis corbisieri* Schmitz (Miridae: Heteroptera); *Sphaerocoris* sp. (Scutelleridae: Heteroptera); *Mylabris lemoulti* Pic. (Meloidae: Coleoptera); *Labidognatha coerulans* F. (Coccinellidae: Heteroptera); an undetermined species of family Elateridae (Coleoptera). In the field, in Ghana, the assassin bugs were noted to feed on a number of different insects. These observations together with those available in the literature are listed in Table 4.

Feeding behavior.—As a preliminary to feeding, the bugs at times clean their antennae and rostrum with the aid of the foretarsi. The same behavior may be repeated once the bug has finished feeding. When dilute acetic acid is applied either to the antennae or the rostrum, the bug at once responds by cleaning it off with the aid of its foretarsi. When the tarsi are cut off, the bug uses the tip of the tibia to clean the affected parts. When the forelegs are entirely cut off at the femoro-trochantal junction, the bugs move about until they find a suitable site on which to rub the rostrum or the antennae. When the acid is applied to the wings, the tarsi of the hind legs are used for wiping it off, and at the same time the wings are flapped. Similar

TABLE 4.—Field observations on the food of Harpactorinae

Name of species	Name of prey	Systematic grouping of the prey	Authority
Endochus africanus	*D. theobroma*	Miridae: Heteroptera	Marchart, 1969; Collingwood, 1971
Hediocoris tibialis	*Dysdercus* spp.	Pyrrhocoridae: Heteroptera	Forsyth, 1966
Margasus afzelii	*Oecophylla longinoda* (Latr.)	Formicidae: Hymenoptera	This study
Odontogonus dimensis	a. *Camponotus* sp.	Formicidae: Hymenoptera	This study
	b. Eggs of *Bathycoelia thalassina* (H.S.)	Pentatomidae: Heteroptera	This study
Pisilus tipuliformis	a. *Physopelta analis*	Largidae: Heteroptera	This study
	b. various undetermined flies	Diptera	This study
Phonoctonus fasciatus Beauvois, *P. lutescens* Guérin et Percheron, and *P. subimpictus* Stål	a. various Pyrrhocoridae	Heteroptera	This study and Stride, 1956
	b. other insects		
Rhinocoris bicolor	a. *S. singularis*	Miridae: Heteroptera	This study; Collingwood, 1971; Forsyth, 1966
	b. *D. theobroma*	Miridae: Heteroptera	
	c. *Scotinophora* sp.	Pentatomidae: Heteroptera	This study
R. loratus	a. *Dysdercus* sp. larvae	Pyrrhocoridae: Heteroptera	
	b. *B. laticollis* and *S. singularis*	Miridae: Heteroptera	Forsyth, 1966
	c. *D. theobroma*	Miridae: Heteroptera	Collingwood, 1971
Sphedanolestes sp.	*Helopeltis labaumei* Popp.	Miridae: Heteroptera	Forsyth, 1966
S. leucocephalus	An undermined wasp	Braconidae: Hymenoptera	This study
Sphedanovarus camerunensis Breddin	An undermined beetle	Staphylinidae: Coleoptera	This study
Vestula lineaticeps	a. *Crematogaster clariventris* Mayr.	Formicidae: Hymenoptera	This study
	b. *D. theobroma*	Miridae: Heteroptera	Collingwood, 1971

activity is observed when the bug is feeding on a stinkbug and the latter directs some of its pungent secretion onto the wings of its predator. If the hind legs are cut off and the acid is applied to the wings, the bug tosses itself around in an attempt to get the acid off.

In this work, the feeding behavior of three subfamilies of Reduviidae was studied. The details are as follows:

Emesinae: The sequence of prey capture in this subfamily differs from the other two subfamilies considered below. It is admirably described by Gillet (1957) in the case of *Bagauda gilleti* (Miller). My observations are in close agreement with his findings. At Legon, the specimens of *Eugubinus annulatus* were fed on mosquitoes. As a first step, the fine tip of one of the antennae of the bug makes contact with a resting mosquito. The other antenna is at once brought across the body of the mosquito, which is gently stroked by the tip of both antennae. This does not seem to disturb the mosquito, possibly due to the excessive fineness of the tip of each antenna. The bug then turns around until the prey is directly ahead. It leans forward to bring the prey within striking distance of its extremely long legs. The bug now raises its raptorial forelegs above the head and darts them forwards to capture the mosquito which is drawn towards the bug's mouth parts and sucked dry within 20-40 min. The prey is throughout held by the forelegs between the femora and the tibiae.

Reduviinae: The larvae of *Acanthaspis vitticollis* feed almost exclusively on ants. On seeing an ant, the larva moves closer to it. It starts stalking the prey by means of a series of short and abrupt movements. On coming within striking distance, the predator suddenly pounces on the prey, grabbing it with the aid of adhesive pads on its fore- and mid-tibiae. The precise way in which the bug pounces is very difficult to see since the movements at this stage are very rapid. It is clear, however, that during this act the proboscis is extended and brought against the surface of the prey. The grip of the fore- and mid-legs is maintained until the prey becomes motionless. Feeding on a single ant in the laboratory, it took a bug, on the average, about 2 hr and then the empty corpse would be added to the material piled on its back. Unlike the harpactorines (*see* below), the sequence of prey capture by reduviine larvae is rather stereotyped. The above observations are broadly in agreement with those of Odhiambo (1958) on *Acanthaspis petax,* Immel (1955) and others on *Reduvius personatus.*

Harpactorinae: The sequence of events involved in the response to prey was essentially similar for all the nine species, both larvae and adults, whose life histories have been followed. First, the antennae are straightened out in front of the head and directed towards the prey. The bug then moves in the direction of the prey with the forelegs raised and proboscis extended forward. On coming closer to the prey, it pounces upon it and grabs it with the forelegs or occasionally the middle legs. The prey is usually probed with the tip of the proboscis before a puncture is made and the contents sucked out. When the prey struggles violently, as is sometimes the case, the reduviid releases its grasp with its legs but retains the animal on the tip of the rostrum which may be violently shaken about until the struggle ceases. In the case of soft-bodied larvae, such as the immature stages of cocoa capsids, the bugs make no attempt to use their legs. The beak is simply pushed inside the body of the larva and the contents sucked out. In several instances it was noticed that when the prey was within a reasonable distance, the bug quickly oriented itself to face the prey and assumed a waiting stance. In this posture the forelegs are raised sharply upwards, with the femora almost vertical and the tibiae protracted. The entire body is raised in front, lowered behind. Once within the reach of the forelegs, the bug jumps forward to secure the prey.

The responses of harpactorine reduviids are slower towards less active prey but more rapid towards active ones. The sequence of events described above, as already noted, is not always rigidly observed. At times the proboscis is extended forward before the bug starts to move towards the prey. Many variations were observed in the raising of the forelegs and possibly this is a defensive response. No particular part of the body of the prey appeared to be especially favored as the site of puncture, though it was observed to be at a place where the cuticle is fairly thin. The position of puncture varies, even in different individuals of the same species, but once the puncture is made, it is used throughout the duration of feeding. The essential features of harpactorine feeding behavior as described above are in agreement with the observations of Parker (1969), Edwards (1962) and Schowerbel (1956) on *Rhinocoris* species.

Feeding behavior and the morphology of the legs: The differences in the feeding behavior of the three subfamilies noted above are reflected in the morphological structure used in prey capture. The varied form of leg structure throughout the Reduviidae appears to be correlated with the degree and type of prey specificity. Thus, in the case of harpactorines, the pads of bristles at the tips of the fore- and midtibiae seem to be well suited for the capture of soft-bodied or hairy prey. The tibial adhesive pads of Reduviinae, on the other hand, are most effective on smooth surfaces such as the cuticle of ants and beetles. A particularly striking example of such a successful adaptation may be seen in the case of *Platymeris rhadamanthus* Gerst., which is capable of keeping in its grip the powerful beetles of the genus *Oryctes* (Vanderplank, 1958). These pads were observed to play an important role in the life of the larvae of *Acanthaspis vitticollis*, studied in this work. Any bugs devoid of tibial pads were unable to capture ants. Similar pads have been observed on the fore- and midtibiae of adult Ectrichodiinae, Piratinae and Holoptilinae. The members of these subfamilies are known to feed on arthropods possessing smooth cuticular surfaces (Miller, 1953; Musgrave, 1938, and personal observations). Emesine bugs which lack such pads have well-developed, raptorial forelegs which enable them to hold their prey firmly.

DEFENSE MECHANISMS

Features such as coloration and mimicry contribute greatly to the primary defenses of Reduviidae. In addition, the bugs possess a variety of scent glands which may be of defensive importance against predators. These glands are developed to varying degrees in different subfamilies, and the following are the principal types of glands found in Reduviidae:

1. *Brindley's glands situated at the base of the abdomen under first abdominal tergite:* these glands were found to be absent in *Tribelocephala* sp. (Tribelocephalinae), *Eugubinus annulatus* (Emesinae), *Oncocephalus subspinosus, Pygolampis* sp., *Pygolampis satanas, Oncocephalus* sp., *Sastrapada* sp. and *Thodelmus addahensis* (all Stenopodinae). These glands are, however, present and well-developed in the following groups: *Ectrichodia barbicornis* (Ectrichodiinae), they produce the smell of acetic acid; *Nularda nobilata* (Ectrichodiinae), their secretion has a pungent smell; *Rhaphidosoma occidentalis* (Rhaphidosominae), their secretion has a repelling smell; *Lisarda vandenplasi* (Salyavatinae), their secretion has the smell of ripe bananas.

These glands produce a pungent secretion in the following reduviids, where they are of fair size in Piratinae and Reduviinae but of very small size in Harpactorinae: *Ectomocoris maculicrus, Androclus pictus* (both Piratinae); *Acanthaspis petax, Leptacanthaspis decorsei, Plynoides benoiti* (all Reduviinae); *Vestula lineaticeps, Rhinocoris loratus, Harpagocoris joveri* and *Phonoctonus* sp.

2. *Dorsal abdominal glands, found on the posterior border of fourth abdominal tergite and ventral glands situated at the junction of the thorax and abdomen:* these glands were found to be absent in all the species of Reduviidae under Brindley's glands (*see* above).

3. *Metasternal glands:* These glands were found to be present and of yellow color in the following families (the species examined are the same as listed under Brindley's gland, *see* above): Ectrichodiinae, Stenopodinae, Salyavatinae, Reduviinae and Harpactorinae.

The main organ of secondary defense in reduviid bugs is obviously the generally curved rostrum which is used in inflicting painful stab wounds on any aggressor. The defense mechanisms in various subfamilies are discussed below:

Emesinae: Some of the Emesinae are known to mimic mantids (Villiers, 1948). The canopy-inhabiting emesines of cocoa farms are yellowish to light brown in color and would be difficult to detect amongst cocoa leaves. *Eugubinus annulatus,* which inhabits spider webs, is of a dirty brown color which matches well with that of the spider web. Being quite slender, the bugs can most easily be mistaken for the threads of a spider web. Also when disturbed they hardly exhibit any movement. The bug uses its rostrum as a secondary defense.

Ectrichodiinae: The members of this subfamily live in leaf litter in the cocoa farms. They are, on the whole, dark colored. Thus, *Ectrichodia barbicornis* has a black abdomen and a reddish-brown prothorax. *Santosia erythrocephala* is also blackish while *Microstemma* *atrocyanea* has a black abdomen but a shiny metallic purple thorax. The general dark coloration of these bugs matches that of the habitat they live in and thus affords them protection. All these bugs possess well-developed scent glands producing a very pungent secretion.

Salyavatinae: *Lisarda vandenplasi,* which belongs to this family, frequents the trunks of cocoa trees and its dark brown color matches well with that of the trunk. That this cryptic coloration is effective is clear from the careful inspection of the trees necessary to detect the bug. The secretion from the scent glands smells like that of ripe bananas. While this may have a possible defensive function, the scent might serve to attract prey, *e.g.,* flies such as *Drosophila.*

Reduviinae: The larvae of Reduviinae cover their backs with camouflage material which, in their natural habitat, makes them resemble lumps of dirt. They can only be detected while in motion and employ short and abrupt movements during walking. When one tries to collect the bug, it readily sheds the camouflage material and escapes. The larvae of *Cethera musiva* and *Cethera maculipennis* camouflage themselves with fine wood dust which matches the bark of dead trees on which they live. *Tetroxia nigrispinosa* piles wood dust, bits of dried bark, pieces of leaves, small twigs and soil particles on its back in a manner essentially similar to that of *Reduvius personatus* as reported by Villiers (1948) and Immel (1955). In *Acanthaspis vitticollis* the camouflage material consists mainly of insect corpses along with wood chips, pieces of dry bark, dry leaves and soil particles. *Acanthaspis sulcipes* (Villiers, 1948) and *Acanthaspis petax* (Odhiambo, 1959) use material of an essentially similar nature for their camouflage. Details of the insect species utilized in the camouflage material are lacking for these two species.

Method of sticking material to the dorsal surface: The piling of insect corpses on the back of the bug is carried out with the help of the hind legs which lift the material and push it onto the back. As more and more insects are added, the ones which are placed first at the tip of the abdomen are pushed forward towards the head. Gradually the entire dorsum is covered, although secretory glands assisting in this process of sticking camouflage material are absent from the head and thorax. As more and more insects are added, the earlier ones become so compressed that they appear like small, round balls. On molting, the old pile of corpses and other material are again added by the newly molted animal to its back. The secretion used for sticking the camouflage material to the back exudes through hairs on the dorsum and is produced by glands which are situated at the base of the hairs on the underside of the abdominal dorsum. In *Acanthaspis vitticollis* the arrangement of these glands is as follows (Fig. 2): first segment: secretory glands absent; second segment: bears two glands on each median plate (*i.e.,* four glands); third segment: possesses four glands on each median plate, one gland each on plates lateral to the median plates, many glands on marginal plates; fourth segment: same as in third segment; fifth segment: same as in third segment; sixth segment:

bears five glands on each median plate as well as on the marginal plates; seventh segment: possesses two glands on each median plate, two on the marginal plates.

These glands are minute, globular, transparent structures. From each gland arises a single hair (Fig. 3). The hairs are arranged in a transverse straight line except on the marginal plates where they are

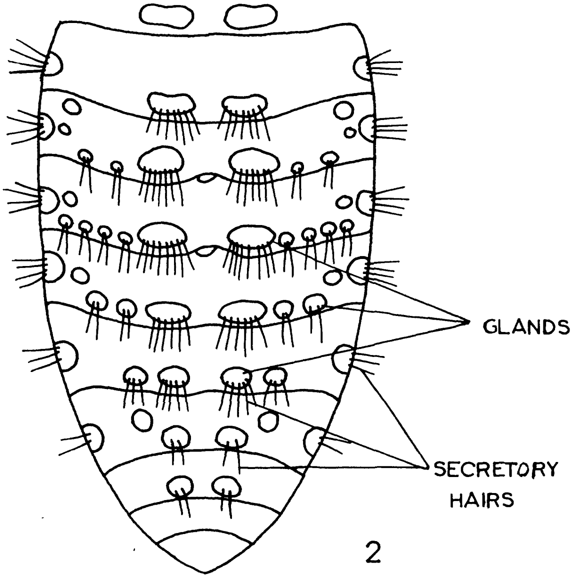

Fig. 2.—Arrangement of secretory hairs on the dorsum of *Acanthaspis vitticollis* Reuter

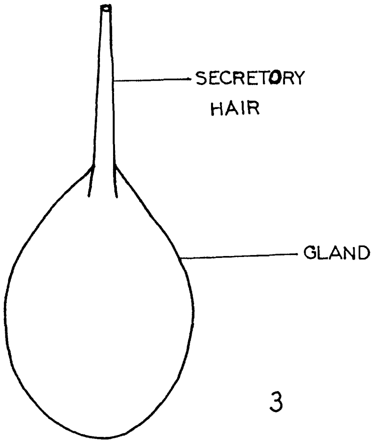

Fig. 3.—A gland showing a single hair

clustered. This association of glands with hairs needs further study. In the cocoa capsids, where the hairs on the larvae exude a secretion, no glands of any kind have been found at the base of the hairs (Aryeetey and Kumar, 1973). Dissections have shown that in the Reduviidae only one simple gland opens at the base of each hollow hair. All the abdominal plates have, as a rule, more hairs than glands. It thus seems that the hairs without glands merely assist in supporting the fine threadlike processes formed from the exudate coming out of hairs provided with glands. That the secretion helping to anchor the camouflage material comes out through the hairs has been reported previously by Immel (1955), Miller (1956) and Odhiambo (1959). The exudate is elastic when fresh, and not very brittle when dry. Actually the secretory material forms a complex web in which new corpses can be easily pushed with the aid of hind legs.

The adults of this subfamily generally tend to have a dark abdomen and brightly colored striped or spotted elytra. Whatever be the value of the coloration in the defense of adult Reduviinae, the most important role is played by the scent glands, which produce a pungent secretion, similar in *Plynoides benoiti* to that of acetic acid.

Harpactorinae: In this subfamily both larvae and adults exhibit a variety of defense mechanisms.

Larvae: First and 2nd instar larvae of *Hediocoris tibialis, Rhinocoris bicolor, R. carmelita, R. loratus* and *Vestula lineaticeps* mimic smaller species of ants such as *Pheidole* and *Anochetus.* The earlier instars of *Pisilus tipuliformis* and *Sphedanolestes leucocephalus* do not mimic ants, but their orange color is likely to act as a warning coloration. All the species, in the 3rd to 5th instars, develop a rich variety of color patterns which are detailed elsewhere (Louis, 1973). The color patterns described for the different instars are likely to play an important role in their defense. However, without any experimentation, one cannot be but speculative. Attention should also be paid to the fact that when disturbed, the harpactorine larvae tend to disappear into the leaf litter which, as said earlier, acts as a shelter habitat.

Adults: Adult arboreal harpactorines have colorations which match their habitat. *Authenta fulvipennis* and *Nagusta punctaticollis* are dark brown in color, *Odontogonus dimensis* is light brown, while *Margasus afzelli* and *Margasus impiger* are dark metallic green. These colors match the leaves of twigs of the cocoa canopy where these bugs live.

Those found in herbs include *Rhinocoris carmelita* and *Harpagocoris joveri.* The former is dull brown, while the latter is black with yellow-tipped wings. In this case, coloration does not seem to match the surroundings, but on the other hand they have other means of defense, *e.g., Rhinocoris carmelita* adopts a cataleptic or death-feigning behavior when disturbed (Edwards, 1962, and personal observations), while *Harpagocoris joveri* mimics a braconid wasp (Villiers, 1948, and personal observations).

The majority of bugs living at the shrub level are conspicuously colored; thus, *Pisilus tipuliformis* is largely orange in color, *Rhinocoris* *bicolor* is black with either red, yellow or dull white prothorax. *Rhinocoris loratus* is black with a white prothorax. *Rhinocoris rapax* is yellowish and *Sphedanolestes leucocephalus* is orange. In the case of *Vestula lineaticeps* the general color is light to dark brown or black. Although the color is dull, during flight the yellow color of the abdomen is conspicuous. One of the functions of these colors might be to prevent reduviid species from feeding on one another. But the flying behavior of almost all harpactorines in cocoa farms is characterized by swift, jerky, running movements carried on simultaneously with rapid vibrations of the wings which are held high over the body. Such a behavior pattern is highly suggestive of certain wasps. The blend of coloration of thorax, abdomen and wings tends to give the harpactorines the appearance of an aculeate wasp. A well-known case of mimicry is shown by *Phonoctonus* species, which mimic *Dysdercus* species. This has been a subject of investigation by several workers. The present author is of the view that the mimetism enables *Phonoctonus* to gain entry into the colonies of pyrrhocorids on which they feed. Thus, mimetism enables them not only to have an easy access to their food but also to gain protection, at least of the same degree as is available to pyrrhocorids.

Most adult harpactorines possess scent glands that produce pungent secretions. These might prove distasteful to predators such as birds. The adults of all the harpactorines appeared distasteful to me. However, mantid predators in the cocoa farms have been observed to feed on several harpactorines investigated in this work, *e.g.*, *Sphodromantis lineola* on *Vestula lineaticeps* and *Harpagocoris joveri*.

COURTSHIP, MATING AND OVIPOSITION

Courtship.—Courtship in adults was often observed in the laboratory cultures. In all the 10 species of Harpactorinae reared, the details of the behavior are essentially similar.

The male approaches the female with the antennae and rostrum extended, an attitude very similar to the initial steps in prey-capture by both sexes. The female usually responds by performing similar movements in the direction of the male. When the two sexes come near each other, they make mutual contacts with the antennae. Usually the male also touches various parts of the female with the tips of his antennae and later explores her body with his proboscis. Next he gets behind her and either jumps or climbs onto her back. In the process of mounting, the male performs quick agitated movements involving a shaking and shivering of the entire body. These movements cease once the male has settled in the precopulatory riding position during which his proboscis rests on the front of the female's pronotum or at times on her neck. His entire body is above and parallel to the thorax and abdomen of the female (Fig. 4). His fore- and midlegs grip her thorax and the hind legs hold the abdomen. Generally the female is receptive to the above advances by the male but at times she may raise her forelegs when the first contact is made. In such cases the male moves away but comes back to make periodic attempts to approach the female. He usually succeeds in mounting her. The riding position of the male may last from a few seconds to several hours. Parker (1969) reports that in one instance, *Rhinocoris tropicus* continued the precopulatory riding position for as long as 7.5 hr.

Mating.—When attempting to copulate, the male slips either to the right or to the left side of the female while still holding her with some or all the legs, and attempts to bring the tip of his abdomen underneath hers. At the same time the male tries to engage his genital capsule with that of the female. Initially, he is usually unsuccessful, in which case the riding posture is assumed again, but once the male and female genitalia are engaged firmly the male retracts his proboscis — though in some cases the contact is usually maintained with the pronotum. Copulation was observed to last from 15-40 min. In the case of *Hediocoris tibialis,* however, it took more than 2 hr.

Rhinocoris bicolor has three color forms: red, white and yellow. Attempts to mate the different color forms with one another failed as the female either killed the male or the male never approached the different colored females. In laboratory cultures, it was observed that a particular color form produced progeny of a particular color only. The color forms and their significance are discussed in detail elsewhere (Louis, 1973).

Oviposition.—Animal food appears essential for oviposition as females fed on sugar solution failed to oviposit. Both fertilized and virgin females lay eggs though the latter fail to hatch. The unfertilized eggs are normal when laid but shrink after a week or so. In the breeding cages the eggs were usually laid on the covers, sometimes on the sides, and in one or two cases on vegetation or other support pro-

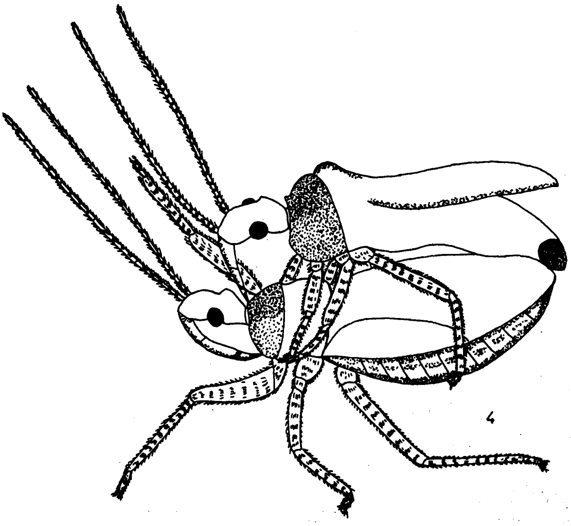

Fig. 4.—Precopulatory riding position in Harpactorinae

vided in the cage. *Rhinocoris carmelita*, however, always laid its eggs on the filter paper covering the floor of the plastic container. On no occasions were the eggs seen on the sides of the container. In the field, the egg masses of *Pisilus tipuliformis* were found on the upper side of cocoa leaves, and on the underside of a fern leaf (Davalliaceae) and of *Datura suaveoleus* (Solanaceae). The eggs of *Rhinocoris carmelita* and *Pisilus tipuliformis* were noted to be guarded by the female till the 1st instar larvae had hatched out.

The eggs are laid either singly or in groups over a period of several days and the numbers vary greatly for each species. The eggs are fixed to a suitable substratum with the aid of a translucent cement probably secreted by the posterior pair of accessory glands of the internal female reproductive organs. Unfertilized eggs, if laid in batches, do not appear to be as tightly held together as are fertilized eggs. It seems that the quantity of cement produced is less in unfertilized females. Various details of the eggs are discussed elsewhere (Louis, 1973).

DISCUSSION

From the foregoing account the following three points worthy of attention emerge:

Significance of the precopulatory riding position. — According to Parker (1969), it serves two purposes. It makes it impossible for the female to feed on the male and it makes it difficult for the female to dislodge the male during copulation. The former explanation sounds implausible since this type of precopulatory position is also seen in many families of nonpredacious Heteroptera.

Parental care.—The first observations on parental care in Harpactorinae seem to be those of Bequaert (1912) on *Rhinocoris albopilosus*, where the male guards the eggs. Odhiambo (1959) confirmed this and found that the males kept watch over the eggs till they hatched and, even if driven off, soon returned to the same egg batch. Present observations on maternal care in *Pisilus tipuliformis* and *Rhinocoris carmelita* are in agreement with those of Edwards (1962) and Parker (1965a, b). Dispons (1965) has reported maternal care in *Rhinocoris erythropus*. The function of the brooding behavior, according to Odhiambo (1959), is to protect the eggs from parasites. His conclusions are based on the observations that in *Rhinocoris albopilosus* the eggs on the periphery of the batch, *i.e.*, the less guarded eggs, were usually parasitized. More direct evidence was furnished by Bequaert (1912), who noticed a brooding *R. albopilosus* male preventing a female peteromalid from ovipositing in the egg masses it was guarding. Thus, it is clear that there is an advantage in having eggs bunched together. Parental care is known in several families of Heteroptera. According to Cobben (1968) and Kumar (1969), the occurrence of maternal care in groups such as Oncomerinae, Natalicolinae, Cydnidae, Scutelleridae and Acanthosomatidae (all belonging to superfamily Pentatomoidea) is a primitive feature. But the paternal and maternal care exhibited in Harpactorinae may, according to Cobben (1968), be a recently evolved character in view of the advanced type of embryogenesis in this group. It is, however, rather difficult to visualize selection pressures which might have caused the evolution of parental care recently in some harpactorine genera only, considering that many species of Harpactorinae which do not display any parental care have survived at least as long an evolutionary period as the ones exhibiting parental care. On the other hand, harpactorines are in some respects (*vide infra*) the most advanced reduviids. Considering their distribution all over the globe and the fact that Harpactorinae contains the largest number of species found in any subfamily of Reduviidae, they are the most successful reduviids. Many reduviids live concealed and lay eggs in well-protected situations. Harpactorines, on the other hand, inhabit relatively exposed situations and lay eggs in places, *e.g.*, leaves of plants, where they are readily accessible to natural enemies. It is possible, therefore, that some harpactorines have evolved parental care only recently, although it could be argued that some harpactorines have lost the primitive parental care as a behavioral feature or evolved it anew. In the present state of our knowledge of reduviid biology, nothing can be said about the relative merits of any of the interpretations considering that the parental care amongst Reduviidae is not known outside Harpactorinae.

Laying of eggs singly or in groups.—Harpactorines lay eggs either singly or in groups. Cobben (1968) has even considered that some Harpactorinae show "an approach to formation of an ootheca in that standing eggs are covered with a sticky substance." Laying of eggs singly or in small groups over a period of several days is obviously advantageous since it provides better survival chances for the eggs. The value of the formation of an ootheca without an adequate protective cover, as seen in Harpactorinae, seems to be doubtful, since it exposes several eggs collectively to the hazards that a single egg might normally encounter. But then it must be admitted that this depends on (a) whether the single eggs ever get covered by the sticky material and (b) what this material does anyway. A parasite has to look further for clumped eggs, even if the final loss is high. But which is better clearly depends upon the behavior of the parasite.

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