

Feeding and ovipositional behaviour in some reduviids (Insecta-Heteroptera)

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Abstract. Feeding behavioural studies of many exclusively predatory species exhibit clearcut stimuli-response mediated sequences and these can be categorised into distinct sub-units like: search and location of prey → approach and attack of prey → immobilisation of prey → transportation of prey to safe place → consumption of prey. These feeding behavioural activities differ among reduviids particularly with respect to prey types. These bugs are endowed with many structural, physiological and behavioural adaptations for efficient predation.

The ovipositional behaviour of reduviids in different habitats also shows considerable variation and their reproductive strategies include selection of suitable sites to assure successful emergence and development of young ones and so far very few egg predators and egg parasites have been reported for these terrestrial insects.

Keywords. Feeding behaviour; ovipositional behaviour; reduviids.

1. Introduction

The family Reduviidae is one of the terrestrial groups of bugs well represented in tropical and subtropical regions of the world. They are known to colonise a wide variety of habitats, such as from under stones, on low herbage or lower foliage or on trees, to the most unusual ones like ant-hills, termitaria, cobwebs, bird nests, rat holes and human dwellings. Naturally, they exhibit a wide range of structural, physiological and behavioural adaptations for an exclusive predatory habit, feeding on a variety of arthropods, including millipedes, termites, bugs, beetles, caterpillars, ants, bees etc. Members of the Triatominae alone have specialised for haematophagy, engorging the blood of birds and mammals.

2. Feeding behaviour

Feeding behaviour of reduviids, as it is true for several other predatory insects, shows many distinct events, and these stimuli-response mediated sequences can be conveniently divided into: location of prey → approach and pounce on prey → immobilisation of prey → transportation of prey to safe place → feeding.

2.1 Location

Being exclusive predators, visual stimuli appear to be of primary importance to these and with the possession of well-developed compound eyes and ocelli they easily locate

and capture various prey types. Visual stimuli from the moving prey initiate subsequent predator-prey interactions. The importance of visual stimuli for predatory reduviids has been well documented (Odhiambo 1958a; Edwards 1962; Parker 1969, 1971, 1972; Livingstone and Ambrose 1978a; Louis 1974; Haridass and Ananthakrishnan 1980a). Species like *Haematorrhophus nigroviolaceus* (Reuter), *Guionius nigripennis* (Fabr.) and *Ectrychotes pilicornis* (Fabr.) as well as other members of the subfamily *Ectrichodiinae* feed exclusively on millipedes (Cachan 1952; Miller 1971; Haridass 1978) and these predators are aroused from a state of akinesis only after receiving the stimuli from the moving millipedes. Even artificial baits like paper, rolled like millipedes, or dead and dried millipedes, also initiated feeding responses in them. Artificial objects or dead bodies of their prey dragged in front of piratine species like *Pirates affinis* Serville, *Ectomocoris tibialis* Distant, *E. ochropterus* Stal, and *Catamiarus brevipennis* Serville, elicited similar responses. Arousal of feeding responses by optic stimuli has also been noticed in several other reduviids, including termite feeding *Rhaphidosoma atkinsoni* Bergroth (figure 1F) and ant feeding *Acanthaspis pedestris*, Stal (figure 1D) *A. siva* Distant, and caterpillar feeding *Sycanus collaris* Fabr (figure 1E), *Rhinocoris marginatus* Fabr and *Sphedanolestes rubicola* Distant. Exceptions to this are the members of *Triatominae*, majority of which have taken to haematophagy and in forms like *Triatoma rubrofasciata* De geer (figures 1G, H), *Linschcosteus costalis* Ghouri (Haridass 1978; Haridass and Ananthakrishnan 1980a) and *Rhodnius prolixus* Stal (Friend and Smith 1977), it is the temperature gradient from the vertebrate hosts that aroused the starved insects. Blinding of their eyes does not deter them from locating their correct hosts and in these haematophagous insects the antenna are the primary sense organs.

2.2 Approach and pounce on prey

Successful location is followed by the quick approach to the prey located and pouncing on them for subsequent immobilisation. Several species exhibit a definite preference for a particular prey type. *Ectrichodiinae* show a preference for spirostreptid millipedes (figure 1A) and never attempt predation on polydesmid species. Similarly *P. affinis* prefers carabid *Omphora pilosa* Klug and *O. atrata* Klug than any other ground beetles and *E. tibialis* and *E. ochropterus* prefer gryllids to any other insects (figure 1C). Fast runners like *Piratinae*, *Ectrichodiinae*, *Acanthaspidinae*, *Reduviinae* etc., quickly reach the prey and pounce on them gripping them tightly with tibial pads (figures 1A, B). The presence of tibial pads on the fore- and/or mid-tibiae is a characteristic feature of this family (Gillette and Wigglesworth 1932; Miller 1942; Edwards 1962; Bahadur 1963; Haridass and Ananthakrishnan 1980b). These tibial pads with their oil secreting tenet hairs, enable the predators to increase the gripping efficiency during prey capture. The tibial pads enable the insects to withstand static tension, on rough and smooth surfaces to an extent of 20–27 g (Haridass and Ananthakrishnan 1980b). In contrast to the fast running habits, members of *Harpactorinae*, *Emesinae*, and *Rhaphidosomatinae* exhibit slow gait and use the long legs and rostrum to reach the prey and gripping of the latter is never involved (figures 1G, H). Some reduviids like the species of *Apiomerinae* and *Ectinoderinae* make use of the resin coated legs to capture prey like fly-paper (Miller 1971). The fore-legs of the thread-legged emesine bugs are also raptorial (Wygodzinsky 1966). The camouflaging of the body surfaces with particles of mud and debris as seen in

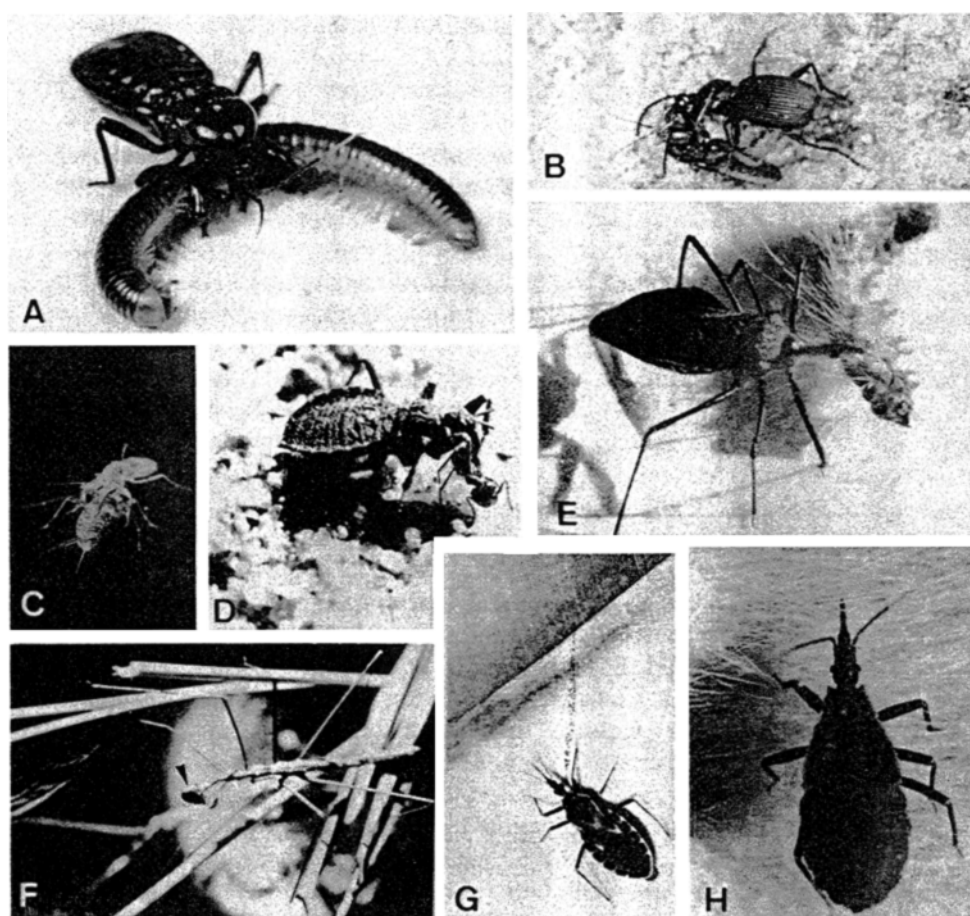


Figure 1. Feeding behaviour in some reduviids. **A.** *Haematorrhophus nigroviolaceus* feeding on millipede prey. **B.** *Pirates affinis* (5th nymph) immobilising carabid beetle. **C.** *Ectomocoris tibialis* feeding the gryllid prey. **D.** *Acanthaspis pedestris* feeding the camponotine ant. **E.** *Sycanus collaris* dragging the immobilised caterpillar prey. **F.** *Rhaphidosoma atkinsoni* with termite worker (arrow) hanging from the rostral tip. **G.** *Triatoma rubrofasciata* adult orienting towards the hand of a sleeping person. **H.** *Triatoma rubrofasciata* 5th nymph engorging blood from the body of a dog.

many Acanthaspidinae and Triatominae (Odhiambo 1958b; Livingstone and Ambrose 1978a, b; Zeledon *et al* 1973), the cryptic body colouration and mimicking dry twigs and grass stems as in Rhaphidosomatinae and Emesinae are some of the other adaptations of this family for efficient predation.

2.3 Immobilisation of prey

After prey capture, the behaviour of these bugs is to search for a suitable site for stylet insertion and injection of toxic salivary secretions. The maxillary and mandibular stylets are usually inserted in the pleural membrane of the neck region or at the base of

the anterior legs or at the antennal bases (Haridass and Ananthakrishnan 1980a). When small, like termites and young caterpillars, the prey is lifted off the ground by the rostral tip of the predators to escape the violent encounters with the prey (figure 1F). But in most cases, involving larger prey species like carabid beetles, millipedes and caterpillars, the predation always entails a violent reaction and following unsuccessful salivary injection, the prey often escapes. Under these conditions, predation is attempted quickly for a second time, invariably with success. Often in Ectrichodiinae, improper gripping of the millipede always resulted in the entwining of the prey around the predator, and the latter allows itself to be dragged for long distances. It is noteworthy that a majority of them, particularly those of Ectrichodiinae, Piratinae, Acanthaspidinae and Reduviinae that encounter such violent reactions from their preys are endowed with tough body coverings to withstand the rough treatment meted out to them during predation. In all cases of successful insertion of stylets and injection of salivary toxins, the prey including larger ones like millipedes, caterpillars and beetles, become totally paralysed and killed within 20–30 sec. The caterpillar feeding Harpactorinae immobilise and kill their prey by stabbing the stylets and by injecting the saliva two to three times in quick succession.

The stylet structure of Reduviidae exhibit a wide range of modifications and evolutionary progression, involving elaborate barbs, teeth and tubercles in their mandibular and maxillary stylets (Cobben 1978). The salivary system of reduviids is also very complex (Baptist 1941; Edwards 1961; Southwood 1955; Haridass 1978) and the anterior lobes of the main glands are concerned with the secretion of neurotoxic substances involved in the paralysis and death of the prey (Haridass and Ananthakrishnan 1981b).

While succumbing to death, millipedes, caterpillars, beetles and ants secrete copious secretions of obnoxious, and irritant exudations like formic acid, *p*-benzoquinones, and other phenolic compounds (Eisner *et al* 1962, 1963; Roth and Eisner 1962). When such repellants are secreted, the immobilisation of the prey is followed by a distinct behaviour of the predators, where they spend considerable time in cleaning the body and antennae, using the fore legs and by rubbing the body surfaces on the ground (Haridass and Ananthakrishnan 1981a).

2.4 Transportation of prey

Transporting the immobilised prey to a safe place for consumption is yet another distinct unit of the feeding behaviour. By inserting the stylets at suitable places, usually at the bases of the mouth parts, or antennae or anterior legs, the prey is dragged beneath the body as the predator walks, or by pulling the long bodied prey while the predators move backwards (figure 1E).

2.5 Feeding

Feeding on the immobilised prey is the last unit of the behavioural sequence and it lasts for about 1½ to 2 hr. Since the mouth parts are of the stylet-type, the predigested food from the prey body is flushed out by the watery secretions of the accessory glands, while the posterior lobes of the main glands secrete enzymes for the digestion of the prey

(Miles 1972; Miles and Slowiak 1976; Haridass and Ananthakrishnan 1981b). The salivary glands of haematophagous triatomine bugs secrete anticoagulants to facilitate sucking of large quantity of vertebrate blood without the danger of the blood being clotted (Baptist 1941; Haridass and Ananthakrishnan 1981a, c). While blood feeders engorge from the same feeding site, the predatory forms manipulate the body of the prey with the fore legs and change the feeding sites as and when a particular part of the prey's body contents are emptied (figure 1A) and in this fashion they completely suck out everything leaving behind only the rectal regions and the empty exoskeleton.

Sharing of the food is not observed in any of the adults, though smaller nymphal stages of Ectrichodiinae and Harpactorinae not only share the same millipede or the caterpillar respectively, but also jointly attempt predation of larger prey. Cannibalism is very prevalent in reduviids, the males often succumbing to females and small nymphal stages falling victims to large ones. The feeding behaviour of Triatominae is comparatively less complicated and the host location is by the temperature gradients emanating from the vertebrate host (figure 1G). On locating a suitable feeding site, considerable time is spent in probing with rostral tip and in the sampling of blood. The mechano- and chemo-receptors of the rostrum are believed to get signals from nucleotides of the host's blood about the suitability of food source (Pinet 1968; Bernard *et al* 1970; Friend and Smith 1977). Once selection is made feeding continues from the same site and terminates only after satiation, due to the stretching of the abdominal stretch receptors affecting critical abdominal volume (Maddrell 1963; Anuzel 1972). Nymphs of triatomine bugs also exhibit cannibalism, fully fed older nymphs are attacked by younger ones, the latter pierce the swollen blood filled abdomen of the latter and feed. Such victims do not suffer from any ill effects (Ryckman 1951; Haridass and Ananthakrishnan 1981c).

3. Ovipositional behaviour

A wide variety of habitats are colonised by reduviids and an important aspect of their reproductive strategy is the selection of a suitable site for oviposition to ensure successful emergence and development of young ones. Sexually mature females resort to multiple matings, exhibiting either an-end-to-end or a riding type of copulatory posture characteristic of several Heteroptera (figures 2A, E, G, H and K). Ground dwelling piratine species like *P. affinis*, *E. tibialis*, *E. ochropterus*, *E. cordiger* and *C. brevipennis*, deposit their eggs in the soil (Radio 1926; Miller 1953, 1971), using the plate-like ovipositors. The gravid female assumes a slanting posture with raised head and thorax and with the apex of the abdomen alone touching the ground makes side-to-side, twisting, and downward thrusting movements to insert one egg (figure 2D). The exposed part of the egg (figure 2F) is then covered with small particles of sand and mud by the manipulation of the hind legs. Ectrichodiinae like *H. nigroviolaceous*, *Guionius nigripennis* and *Ectrychotes pilicornis* deposit their eggs in clusters. While the latter two species glue the eggs in the crevices of bark of trees (figure 2C), the females of the former dig slanting tunnels (7–8 cm) in the ground to deposit eggs loosely (figure 2B). After oviposition they spend considerable time to refill the tunnel with excavated mud using mid- and hind legs, and finally press the closed tunnel with the abdomen. Unlike the plate-like ovipositors of the species that insert their eggs in the soil or in crevices, these structures of Ectrichodiinae are very much reduced and stublike. Members of

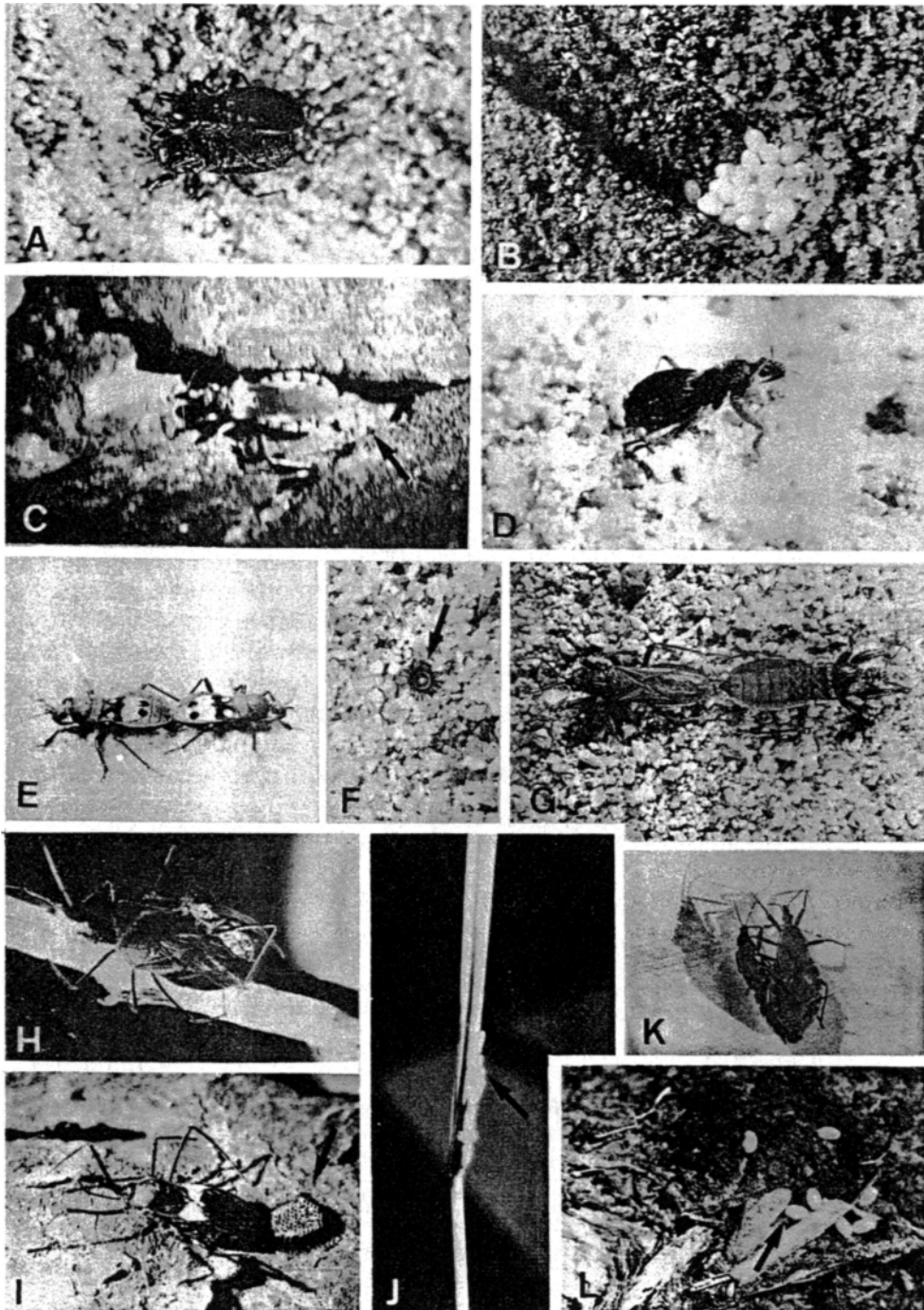


Figure 2. Ovipositional behaviour in some reduviids. A. Copulating adults of *Haematorhophus nigroviolaceus*. B. Loose egg cluster of *H. nigroviolaceus* inside a tunnel excavated in the ground. C. *Guionius nigripennis* attaching eggs to the crevices on tree trunk. D. *Ectomocoris tibialis* inserting single egg into the ground. E. Copulating adults of *Catamiarus brevipennis*. F. Oviposited egg of *Pirates affinis*. G. Copulating adults of *P. affinis*. H. Copulating adults of *Sycannus collaris*. I. Compact egg mass of *S. collaris* glued to the surface of tree trunk. J. Eggs of *Rhaphidosoma atkinsoni* attached to grass stem. K. Copulating adults of *Triatoma rubrofasciata*. L. Eggs of *T. rubrofasciata* inserted into the crevices of dry cow-dung cakes.

Acanthaspidinae like *Acanthaspis siva*, *A. pedestris*, *A. quinquispinosa* (Fab.) and those of Salyavatinae like *Lizarda annulosa* Stal and *Petalochirus indicus* as well as these of Triatominae like *T. rubrofasciata* and *L. costalis* oviposit the spheroidal or sub-ovate eggs loosely scattering them on the ground, under stones or in crevices (figure 2L). *Rhaphidosoma atkinsoni* found usually among grasses, glue the bases of the flask shaped eggs to the stems, the eggs projecting at an angle (figure 2J). This oviposition is very similar to those already described for other Rhaphidosomatinae (Miller 1953).

The most elaborate ovipositional behaviour is exhibited by species of Harpactorinae and this is known for a large number of forms (Kershaw 1909; Muller 1937; Cheriyan and Kylasam 1939; Bose 1951; Wallace 1953; Miller 1953, 1971; Odhiambo 1959; Edwards 1962, 1966; Parker 1969; Nyiira 1970; Swadner and Yonke 1973a, b). The gravid females of *Rhinocoris marginatus*, *Sycanus collaris* and *Sphedanolestes bowringi* Distant attach a cluster of large number of eggs on the under surface of big boulders, or on the stems of trees and plants. While placing the eggs the females work from the margins to the centre of the egg mass always in precise 'chevron' pattern, gluing the eggs in vertical but oblique rows. Each egg is attached to the substratum as well as to the previously laid one giving a polygonal shape to the completed egg mass (figure 2I). The females cover such egg masses with copious secretions from their accessory glands transforming the egg masses into almost an ootheca (Southwood 1956; Miller 1971; Hinton 1981). Though parental care has been reported in many harpactorine bugs (Bequart 1912; Odhiambo 1959; Parker 1965; Miller 1971; Ralston 1977) this has not been noticed in any of the species observed.

The success of the ovipositional behaviour of Reduviidae is evident from the total absence of egg predators for this group as well as from the fact that so far very few egg parasites have been reported for reduviid eggs (Odhiambo 1959; Swadner and Yonke 1973a; Masner 1975; Sankaran and Nagaraja 1975).

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