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Predation behaviour of land planarians

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Abstract

Predatory behaviour of land planarians is seldom observed or reported. Aspects reported are (1) finding prey; (2) attack behaviour; (3) capture using adhesive mucus, pharyngeal action, poisonous secretions, physical embrace; (4) feeding by extension of pharynx, releasing copious digestive fluid. The species *Bipalium kewense, B. adventitium* and *B. pennsylvanicum* attack earthworms, immobilizing them by physical holding, digesting by pharyngeal secretions and then ingesting the treated tissue. Group attacks on giant African land snails involving chemotactic tracking, occur in *Platydemus manokwari* and *Endeavouria septemlineata.* Specialized capture methods are used by some species; *Rhynchodemus sylvaticus* uses an expanded cephalic hood to capture small insects and in Africa, termites are captured by the elongated anterior of *Microplana termitophaga* as planarians wait within the colony air shaft openings to ensnare the workers in sticky mucus. The result of extensive predation by land planarians may seriously reduce the prey, e.g., providing effective population control of giant land snails by introduced *Platydemus manokwari*, or causing serious depletion of desirable earthworm populations by the exotic *Artioposthia triangulata* in North Ireland.

Introduction

Relatively few published observations exist describing the predatory behaviour of land planarians. One reason is that this behaviour is seldom observed, collectors being more interested in planarians as preserved taxonomic specimens than as subjects for behavioral studies. Moreover, land planarians perish so easily that preservation becomes a first priority. The earliest account of land planarian predatory behaviour is found in ancient Oriental literature written by Chinese and/or Japanese. These accounts from the prescientific age in China and Japan (*ca* 860), found in various manuscripts, woodcut prints and so-called 'Materia Medica', are reviewed by Kawakatsu (1969), Kawakatsu & Lue (1984) and Lue & Kawakatsu (1986). An early summary of habitats and feeding was provided by Moseley (1875), then by von Graff ((1899) and under the heading of ecology and nutrition (von Graff, 1917: 3347). A summary for Australian land planarians is given by Steel (1901). A brief summary by Barker (1989) reviews selected literature of land planarian predation and describes attack on terrestrial slugs in New Zealand. Predatory behaviour includes: A. accidental finding of prey, B. oriented predatory activities with use of tactile and chemical signals, C. capture specializations, e.g., anterior adhesive structures, toxic secretions, physical embrace, D. pharyngeal activities. The present review brings published accounts together. For a full account of the taxonomy (and synonymies) of species reported here see Ogren *et al.*, (1992) and references therein.

Accidental finding of prey

Planarians moving across surfaces with side to side swinging of the anterior end may stop when the food source is accidentally encountered. A classic example of predator behaviour shown by *Bipalium adventitium* Hyman is described by Dindal (1970), and for *Bipalium pennsylvanicum* Ogren by Ogren & Sheldon (1991). Once encountered accidentally the prey are captured and fed upon. Lehnert (1891) briefly described how *Bipalium kewense* Moseley encountered and fed on living earthworms. The Chinese observer 'Yn-Yang Tsa-Tsu' about 860 PE writing of the presumed bipaliid land planarian (Doko), describes how it chases and captures earthworms (Kawakatsu & Lue, 1984; Lue & Kawakatsu, 1986). In the case of *Microplana terrestris* (Müller), prey are found by chance contact through random movements, followed by quick capture (Jennings, 1959). *Rhynchodemus sylvaticus* employs random discovery for capture of small springtails (Wallner, 1937) and small flies placed nearby in its environment (Arndt, 1938; Schremmer, 1955). In nature *B. adventitium, B. kewense, B. pennsylvanicum* individuals are found on the soil beneath stones or logs, presumably quiescent between meals with live earthworms nearby (Chandler, 1976; Neck, 1987; Ogren, 1986; Ogren & Sheldon, 1991). If contact with food is made, and the planarian ready to feed, arousal and predatory behaviour will occur (Neck, 1987). Pfitzner (1958) using *Dolichoplana feildeni* von Graff demonstrated, and illustrated with photographs, the capture of earthworms (*Lumbricus sp.*). Planarians placed in a petri dish with one earthworm, made physical contact, moving over and around the earthworm. After 25 min several, but not all the planarians were coiled around the prey, pressed against its body with extended pharynges. In 45 min the prey was motionless and the planarians were busy feeding. E.M. Froehlich (in Litt., letter of 4 July, 1987) mentions that Rodriques (1972) observed *Geoplana burmeisteri* Schulz & Müller under laboratory conditions capture and feed on garden snails.

An especially interesting and successful opportunistic predator on earthworms is the geoplanid *Artioposthia triangulata* (Dendy). When ready to feed it captures, by encirclement, an earthworm encountered in its environment, extends the pharynx releasing digestive fluids and feeds, often consuming the entire worm (Willis & Edwards, 1977; Blackshaw, 1990, 1991, 1992; Blackshaw & Stewart, 1992: 212). There is no evidence that *A. triangulata* aggressively tracks the earthworm prey (Blackshaw & Stewart, 1992: 212).

Oriented predatory activities

Tactile and chemical sensations in planarians are important in orienting toward prey, recognizing food and capturing prey (Hyman, 1951: 200). The anterior end is important for this behaviour. Ogren (1957) showed that *Rhynchodemus sylvaticus* (Leidy) was attracted to biological fluids such as beef liver juice. The worms moving randomly in a dish, stopped and began feeding on the first liver juice available rather than searching for a larger sample, which was near by. Prey may be tracked by chemical signals, e.g., from mucus trails of snails, or tissue exudates from injured prey as examplified by the planarians *Platydemus manokwari* de Beauchamp and *Endeavouria septemlineata* (Hyman). Once the food signal is sensed, the planarian moves toward the source. A similar feeding orientation, possibly mediated by surface diffusion, was observed for *Bipalium pennsylvanicum* which stopped to feed on mashed and torn slugs (Ogren & Sheldon, 1991). Sensitivity of various regions of the body to nutritive material was tested by Ogren (1957) for *R. sylvaticus* and revealed that all parts of body (pre-eye, post-eye, pre-pharynx, post- pharynx) stimulated the planarian to move its body near the stimulus and extend the pharynx.

Certain Geoplanidae show very aggressive oriented behaviour. *E. septemlineata* follow and capture the giant African land snail. Mead (1963: 306) described how the anterior is moved in a searching manner apparently sensing the snail's slime trail. One or several planarians overtake the snail, crawl upon the body and attack it. It is known that the rhynchodemid *P. manokwari* also effectively preys on the large African land snail and is used to control its populations (Muniappan, 1987, 1990; Kawakatsu *et al.*, 1992; 1993). It is reported that *P. manokwari* uses chemical and tactile senses to locate prey (Kaneda, *et al.*, 1990). Other such effective predations on snails and earthworms are given for geoplanid species by Froehlich (1955b).

Prey preference was demonstrated by Sheldon in Ogren & Sheldon (1991) who showed *B. pennsylvanicum* preferred live earthworms over slugs. In Africa the land planarian, *Microplana termitophage* Jones *et al.*, 1990, uses worker termites as prey but avoids soldier termites. Prey preferences are suggested by the following: *R. sylvaticus* feeding on earthworms (Lehnert, 1891), feeding on small snails, slugs, arthropods and beef liver (Ogren, 1955), *Microplana scharffi* (von Graff) feeding on earthworms (Garnett, 1928), and *Caenoplana coerulea vaga* (Hyman) feeding on isopods (Olewine, 1972). With *Artioposthia triangulata* earthworms of several species are accepted as food. There is no evidence the planarians prefer one earthworm species (Blackshaw & Stewart, 1992: 213), but availability of an earthworm species is important. Isopods are common prey for *Parakontikia ventrolineata* (Dendy) (olim *Geoplana*) according to Barker (1989: 76). However, individual *P. ventrolineata* also attack the slug *Deroceras panormitanum* (Lessona & Pollonera). Feeding follows massive attack by as many as 7 planarians.

Coexistance and orientation of predator and prey in the same habitat is important to capture, making more certain the discovery of preferred food. Land planarians are part of the soil ecosystem (Dendy, 1890b; Ogren, 1955; Ogren & Sheldon, 1991; Ball & Sluys, 1990), belonging to the soil 'heterotrophic microcommunity' of Dindal (1990: 8). Land planarians also have specialized physiological adaptations that assure their success in precarious terrestrial environments (Little, 1983).

Habitat relationships between predator and prey are described by Sheppe (1970: 214; Jones *et al.*; Darlington & Newson, 1990; Jones, 1993) for *M. termitophaga* which places its body purposively within earth openings to capture worker termites. The red geoplanids *Geobia subterranea* (Schultz & Müller) live within numerous burrow passages in the soil habitat of the earthworm *Lumbricus corethrurus* which are attacked. While the planarian body restrains the prey, its extruded pharynx sucks earthworm blood for food (Shultz & Müller, 1857; Schultz, 1857). An interesting ecological study of vertical distribution of 5 species of earthworm prey available to *Artioposthia triangulata* has revealed that surface active species were more frequently used as food (Blackshaw & Stewart, 1992: 214).

Capture techniques

Techniques may include anterior specialization, entrapment in sticky mucus, activity of the pharynx and physical immobilization by holding, finally subduing the live prey. Anterior features such as head musculature, mucoid glands, chemical and tactile receptors are of fundamental importance for capturing prey. The capture of snails by geoplanid species is described by Froehlich (1955b; 267). The planarian adhers to the snail's shell by its anterior end, eventually surrounding the prey, then extending the pharynx beneath the shell to begin feeding. If the head of *Bipalium kewense, B. adventitium* or *B. pennsylvanicum*, successfully contacts the earthworm prey, the planarian usually adhers to the epithelium, then moves onto the earthworm and glides its head along the body of its prey (Barnwell *et al.*, 1965; Dindal, 1970; Neck, 1987; Ogren & Sheldon, 1991). In examining the role of the head in behaviour of *B. kewense*, Barnwell (1966) revealed that the head is important for detection of prey, but not for capture and ingestion. Head ablation experiments were performed followed by regeneration and feeding experiments. The planarians did not attack when the head region was incompletely regenerated. Capture and ingestion of prey, however, did not require an intact head but was possible by action of the intact pharynx.

In his biological studies of land planarians, Froehlich (1955b) observed *Rhynchodemus* sp. using its expansive cephalic hood to capture prey, e.g., small springtails (Collembola). I can confirm capture of Collembola with the cephalic hood by *R. sylvaticus* from my unpublished field notes (1956) as also observed by Wallner (1937). E.M. Froehlich (in litt.) mentions that the geoplanid *Pasipha pasipha* (Marcus) captures isopods with its cephalic musculo-glandular organ. In a taxonomic paper, Froehlich (1955a) stated that the capture of prey may be the function for the anterior glandulo-muscular organs found in *Choeradoplana* von Graff (e.g., *C. marthae* C.G. Froehlich) and *Issoca* Froehlich (e.g., *I. piranga* C.G. Froehlich). Winsor (1991) described *Pimea monticola* Winsor from New Caldonia which possesses an anterior ventral pad of glandular-muscular organs with possible adhesive functions involved in capture of prey and also in holding to a substrate.

The head is frequently used as grasping organ whose adhesive ventral surface can strongly attach to the prey or substrate or both, and in *Bipalium* species the broad semilunar head encircled by the sensory tract serves as a device for detection and adhesive attachment. In the case of *B. pennsylvanicum* the planarian uses this organ to capture earthworm prey (Ogren & Sheldon, 1991) by first gliding over, then firmly attaching to the body surface with the underside of its head. This was also observed by Neck (1987) for *B. kewense*. According to Dindal (1970), once head contact is made by *B. adventitium* on the earthworm, the planarian crawls onto the prey and extends its pharynx while the body encloses the prey. This planarian behaviour is described in a 9th century Chinese manuscript translated by Lue & Kawakatsu (1986: 318). Sheppe (1970: 214) and Jones, *et al.* (1990) described how in Africa the land planarian *M. termitophaga*, situated at the rim of colony air shafts, actively captures worker termites by extending its head, touching the prey, quickly withdrawing the extended anterior, then crawling over the termite body which becomes entrapped in slime. This was graphically illustrated by Jones (1993). Pfitzner (1958) observed how *Dolichoplana feildeni* captures and feeds on earthworms (*Lumbricus* sp.). Planarians made physical contact by their anterior then moved over and around the earthworm for capture. The head of *Artioposthia triangulata* is the first region to contact and adhere to earthworm prey and is followed by contact by the mouth and coiling of the planarian around the earthworm (Blackshaw & Stewart, 1992: 212).

Entrapment in sticky mucus is important. Observations by Steel (1901) for Australian land planarians indicate they are effective carnivores, capturing annelids, molluscs and arthropods by crawling over the body which then becomes entangled in mucus. Capture of beetles and crustaceans using mucus entrapment and physical force by *Caenoplana spenceri* (Dendy) is related briefly by Spencer (1891). Feeding began when the pharynx penetrated the arthropod's joints (Spencer, 1891: 86). Mucus entrapment has been observed for other geoplanids (Brittlebank, 1888; Dendy, 1890a, b). In Rhynchodemidae, *R. sylvaticus* entraps fruit flies in adhesive mucus (Arndt, 1938) and similarly with other insect prey (Schremmer, 1955). According to Jennings (1959) mucus entrapment does not aid initial prey capture by *M. terrestris* because mucus dries quickly in the habitat. Nevertheless, mucus provides a role later in preventing escape.

Planarian pharyngeal activities and released digestive fluids are of fundamental importance to successful capture and immobilization of prey. For *R. sylvaticus* the importance of the pharynx to predation and feeding is confirmed by Schremmer (1955) and Arndt (1938). Descriptions by Jennings (1959) of predation by *M. terrestris* demonstrate the importance of the cylindrical pharynx being thrust through the body wall quickly without apparent aid of solvent juices. Ogren (1957), for *R. sylvaticus*, revealed that an extension response of the pharynx occurs to nutrients found by the planarian.

The experiments of Barnwell (1966) using *B. kewense* demonstrated that capture and ingestion required the intact pharynx rather than the head. Dindal (1970) reported it was the extended and secreting pharynx of *B. adventitium* contacting the earthworm that provoked violent prey reaction, rather than initial contact by the planarian. Moreover, the released digestive secretions quickly liquefied portions of the earthworm surface. Therefore, the pharynx was of primary importance to successful capture. In *B. adventitium, B. kewense*, and *B. pennsylvanicum* the pharynx is of the collared, or plicate type (Dindal, 1970) which spreads out over the surface forming a strong attachment. The earthworm prey reacts very quickly to escape the contact of the pharynx (Dindal, 1970; Ogren & Sheldon, 1991) but once strong contact is made the planarian's hold is seldom broken.

Physical holding is common, e.g., the capture of snails and slugs by geoplanid species. Froehlich (1955b: 267) described how planaria hold and surround prey and *Bipalium* sp. is known to enclose snail prey for feeding (Miyoshi, 1955). Jennings (1959) described how the prey is held down, by the arched body of *M. terrestris* which attaches to the substrate and by mucus secretion. Physical holding of small prey by *R. sylvaticus* also was shown by Schremmer (1955). Capture of lumbricid earthworms by *B. adventitium, B. Kewense* and *B. pennsylvanicum*, as recorded by Dindal (1970), Neck (1987) and Ogren & Sheldon (1991), and by *Artioposthia triangulata*, as reported by Blackshaw & Stewart (1992: 213), results in the planarian effectively attaching, holding and enclosing the prey.

Immobilization may involve paralysis as well as physical holding for Johri (1952), studying *B. kewense*, observed that following physical contact, the earthworm prey reacted violently to the planarian but was soon paralyzed. The abundant sticky mucus is presumably an important factor in immobilization. In other cases release of digestive fluids, which contain proteolytic enzymes (Jennings, 1959, 1962) and other biochemicals possibly toxic to the prey, is important to immobilization and successful capture. This has been observed in examples above and studied in depth for *M. terrestris* by Jennings (1959, 1962). According to Dindal (1970) *B. adventitium* feeding on earthworms, immobilizes prey while releasing copious digestive fluids. However, immobilization may not always occur. Restudy of predation by *B. pennsylvanicum*, prepared on video tape by Dr Joe Sheldon, revealed that, while physical holding is important to successful capture and restraint, the earthworm may continue to struggle and move while the pharynx is applied and feeding takes place.

Discussion

The above citations provide good evidence that land planarians attack and capture prey much larger than themselves employing different techniques such as physical force, adhesive mucus, pharyngeal action, and very effective digestive secretions poured over the surface of the live prey by the protrusile pharynx. This is followed by active feeding. Land planarians can apparently find food by waiting in ambush for prey to make physical contact, by chance encounter during random locomotion, or by oriented behaviour tracking the prey be sensory cues. Perhaps they can use each of these strategies at various times to acquire food, however, orientated searching may be a more restricted behaviour.

A question related to food preference still not completely answered is: do land planarians prey on each other showing cannibalistic behaviour? A brief summary on cannibalism is provided by von Graff (1917: 3348). Cannibalism in fresh water planarians was observed by Hull (1947) who believed crowding was partly responsible. Although it has not been commonly observed, land planarians can be cannibalistic (Froehlich, 1955b: 268) which may occur as a result of limited food supply.

Other topics are described elsewhere such as feeding behaviour of other Turbellaria (Hyman, 1951: 200–202; Jennings, 1963, 1968), possible toxic effects of planarian secretions on prey and/or on vertebrates by accidental contact or ingestion (Arndt, 1925; Arndt & Manteufel, 1925; Hyman, 1951: 203; Lue & Kawakatsu, 1986: 381 Chinese lit), or possible neurotoxic effects (Blackshaw & Stewart, 1992: 213). Considerations raised by Barnwell *et al.* (1965) are the frequency of predation and the need for food in relation to environmental temperatures. Experimentation on attack rate by *Artioposthia triangulata* by Blackshaw (1991: 690), revealed that planarians attacked earthworms placed in their experimental environment with consumption decreasing over the second and third feeding periods. An average of 1.4 earthworms was consumed per week under experimental conditions. The larger planarians attacked more frequently, thus consumed more prey (Blackshaw, 1991: 692). Toxicity of mucus to prey remains unconfirmed and may not be an important factor (Barnwell *et al.*, 1965, Hyman, 1951: 202) for *B. kewense*. Studies on feeding and digestion, including digestive enzymes such as a collagenase (Landsperger *et al.*, 1981) and external vs internal digestion, have been reviewed and compared for various flatworms by Jennings (1959, 1962, 1963, 1968).

The effects of regular, effective predation on the prey population can have different ecological consequences. Mead (1963, 1979) and Muniappan (1987, 1990) reported planarians have been used to reduce and control giant snail populations. On the other hand, serious depletion of the earthworm populations in Northern Ireland has resulted from the predation by planarians accidentally introduced from New Zealand (Blackshaw, 1990, 1991, 1992; Blackshaw & Stewart, 1992).

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