The ecology of western Indian Ocean carnivorous land snails

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Abstract: The carnivorous snails of the western Indian Ocean are discussed in terms of their predatory behaviour and ecological relationships with their prey. Data are presented for the introduced *Euglandina rosea* (Oleacinidae), *Gonaxis quadrilateralis* (Streptaxidae) and the native streptaxids *Edentulina dussumieri*, *Imperturbatia constans*, *Careoradula perelegans* and *Gulella poutrini*.

Introduction

The western Indian Ocean islands support exceptionally diverse and abundant endemic radiations of carnivorous land snails (Bruggen 1967; Gerlach & Bruggen 1999). In addition a small number of alien species have been introduced, either accidentally (*Gulella bicolor* (Hutton 1834)) or deliberately during biological control programmes (*Gonaxis quadrilateralis* (Preston 1910) and *Euglandina rosea* (Férussac, 1821). With both native and alien carnivores forming a significant proportion of the molluscan fauna it would be expected that these snails would have a significant role in the region's ecology. There is only one published account of an ecological aspect of this fauna (Gerlach & Bruggen 1999), this details adaptations to carrion feeding in the Seychelles streptaxid *Careoradula perelegans* (Martens, 1898). A study of the ecology of the oleacinid *E. rosea* (Gerlach 1994) included data from Seychelles and the Mascarenes and presented brief studies of the Mauritian streptaxid *Gulella poutrini* (German). The present paper summarises available data for carnivorous snails of Seychelles and Mauritius.

Methods

Carnivorous snails of Seychelles have been studied in the field continuously since 1986. Field data for Mauritius and Réunion are derived from surveys carried out in 1996. During field studies molluscs have been collected from a wide range of sites by hand searching, sieving and Winkler extraction. In most sites 10 haphazardly located 1m² quadrats have been used to estimate population densities.

The behaviour of the different species was studied in laboratory conditions. The large streptaxid species from Seychelles, *Edentulina dussumieri* (Dufo, 1840), and the commonest small species, *Imperturbatia constans* (Martens, 1898), were used in feeding trials as was the commonest Mauritian species *Gulella poutrini*. In addition the alien species *Gonaxis quadrilateralis* and the oleacidnid *Euglandina rosea* were studied. These were kept in individual plastic boxes measuring 18×10×6cm and kept damp. Lighting was on a fixed 12:12 hour light:dark cycle. Any individuals that were not being used in experiments were provided with suitably sized prey ad libitum. Prey were either wild collected from gardens (Helicidae) or captive bred (Subulinidae and *Liardeita* spp.).

Prey species were maintained under the same conditions but using a variety of containers

zes; prey were not kept individually. Decomposing leaves were fed to herbivorous species and small subulinids to carnivorous species.

Results

Morphology

Dissections of specimens in this study showed that the digestive anatomy of *E. osea* exhibits several specialisations for carnivory. The buccal mass is contained within an extensible rostrum allowing the radula to be projected beyond the mouth and into the prey. The radula is adapted to carnivory by its large size and the specialisation of the teeth into elongated cones. The salivary glands are large and the intestine short, features that in other molluscs have been suggested to be adaptations to carnivory (Tillier 1989). An elastic crop is present, which stores the food mass prior to digestion (pers. obs.). In association with this the digestive gland (hepatopancreas) is large. The chemosensory lips at the front of the mouth are also specialised for predatory behaviour. They are greatly elongated, maximising the area they cover when used in detecting mucus trails deposited on the substrate by their prey (Cook 1985). These lips are also present in other carnivorous families of mollusc (Watson 1934; Gerlach 1994). Of the streptaxids studied here they are only apparent in *Edentulina dussumieri*

Predatory behaviour

Previous studies have defined discrete categories of feeding behaviours in *Euglandina rosea* (Cook 1983, 1989 a&b). These are summarised in Fig. 1. The behavioural sequences are notably different between the oleacinids and the streptaxids. Whilst *E. rosea* behaves as a generalist predator attacking all items identified as prey (including streptaxids), the streptaxids were more selective. This selectivity, expressed as a tendency to attack only relatively small prey that were either inactive or moving away, may be largely a consequence of specific size differences. In this respect it is worth noting that the smallest streptaxid observed (*Imperturbatia constans*) would only attack very small prey from behind, the larger species (*Gulella poutrini* and *Edentulina dussumieri*) would attack larger prey moving nearby but avoided prey heading towards the predator, whilst the largest (*Gonaxis quadrilateralis*) would attempt to attack all prey. Thus these behavioural differences may be expressed only as a consequence of size differences; the larger streptaxid species may be equally as effective predators as the oleacinid *Euglandina* species. If larger taxa are highly aggressive predators, the largest streptaxids may be able to consume smaller individuals of *E. rosea*. The extreme rarity of the larger streptaxids means that relevant data are not available but the presence of a subadult shell of *E. rosea* in the vicinity of a population of the large Mauritian streptaxid *Gonodomus pagodus* may possibly represent the outcome of one such interaction.

In *Edentulina dussumieri* no attempt was made to restrain prey during attack and if the first strike was not successful the prey always escaped. Pursuit was not attempted. In four cases of predation on *Liardetia sculpta* prey was consumed whole.

Predation by *G. poutrini* was found to be simple, involving a strike at the prey shortly after contact (on average 6.6 seconds). The *Omphalatropis* spp. responded by retracting into the shell on all occasions when attacked, blocking the aperture with the

operculum. Once the prey had retracted the predator was unable to penetrate the operculum. *G. poutrini* consume *Omphalatropis* when they are able to cause serious physical damage with their first strike, the limited experimental data suggest that successful strikes occur on fewer than 20% of occasions. In a natural environment where the complex structure of the leaf litter may impede movement in some directions a higher success rate may be possible.
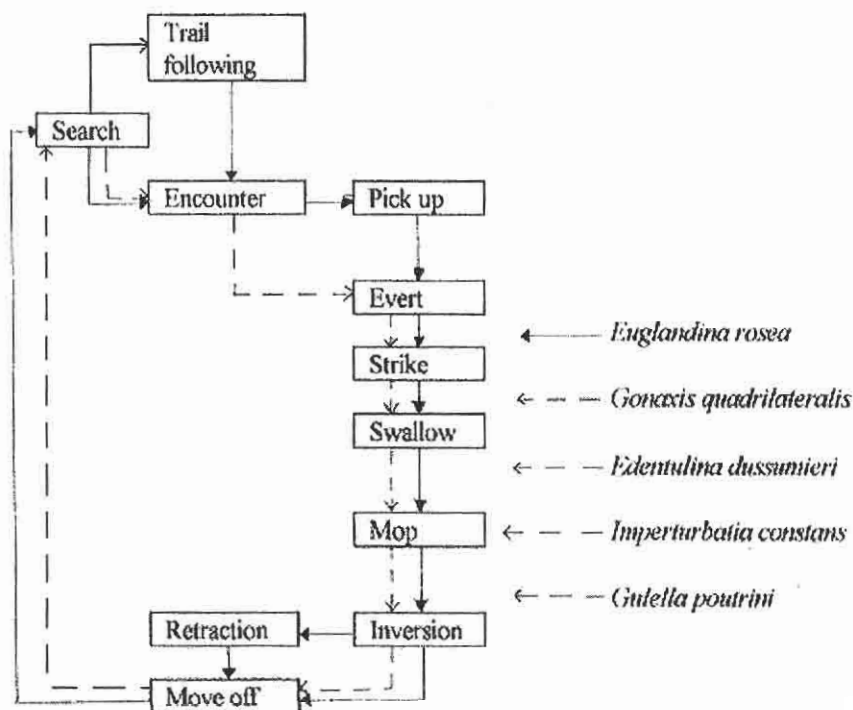

Fig. 1. Predatory behaviour in carnivorous snails.

Diet

Euglandina rosea preys exclusively on molluscs (Gerlach 1994). The diet of Euglandina rosea is known to include a wide variety of mollusc species. Studies prior to and during its use in biological control concentrated on the question of whether or not it would prey on A. fulica (Mead 1961; Muragaki & Deguchi 1987). In addition a wide range of pantropical species have been recorded as prey (Pilsbry 1948; Cook 1983, 1989a; Tillier & Clarke 1983; Clarke et al. 1984; Kinzie 1992; Lee pers. comm.). It has been reported that 83% of E. rosea dissected in Mauritius contain the remains of indigenous molluscs (Griffiths 1987); the detailed data of dietary analysis in the Mascarenes suggest that E. rosea is a generalist mollusc predator preferring small terrestrial prey species (Griffiths et al. 1993). It is also reported to be rarely cannibalistic (Gerlach 1994).

Feeding trials for Edentulina dussumieri demonstrate that it preys upon the following molluscs (maximum sizes of consumed prey are given in parentheses): Pachnodus niger×velutinus (7.8×6.7mm), Achatina spp. (8.7×5.8mm), Subulinidae (4.9×1.9mm), Liardetia sculpta (2.6×2.8mm) and Leptichnoides verdcourti (12mm long). Helicina theobaldiana were not attacked (10 trials).In the field predation was observed on Pachnodus kantilali (juvenile), Leptichnoides verdcourti and, on one occasion, on a fully grown nemertine worm (Geonemertes pelaensis). In the latter observation the nemertine (approximately 100mm in length) was being swallowed whole from the anterior end, peristaltic movements of the worm's body were detectable but there were no obvious responses to the predation. Two other nemertines were moving away from the site rapidly (Gerlach 1998). In addition E. dussumieri was frequently observed feeding on resin flowing out of the leaf blades of palm species (Nephrosperma vanhouettana and Phoenicophorium borsigianum).

Imperturbatia constans attacked and consumed Liardetia sculpta below 1.9mm in diameter. These were all investigated prior to attack, which would only occur if the prey was encountered from behind; head contact led to avoidance of the prey. None of the four prey consumed were swallowed whole. No larger prey were consumed and no field observations of predation were made

Gulella poutrini consumed. Liardetia sculpta, Omphalatropis expansilabris, O. rubens, O. desjardinisi and juvenile Macrochlamys indica. Meghimatium bilineatum was not eaten. Although the range and numbers of prey offered was insufficient to demonstrate any significant preferences the initial feeding trial does show that G. poutrini is able to prey upon smaller molluscs, including the operculate Omphalatropis spp.

Trail following behaviour

As the following of prey mucus trails is a significant component of the predatory behaviour of Euglandina rosea (Cook 1985) this was investigated in order to determine if any preferences were being expressed in hunting and whether or not streptaxids exhibit the same behaviour.

Predator preferences for specific prey were studied by comparison of the frequency of predators following trails left by different prey species. This was carried out by allowing prey ('markers') free movement on a sheet of squared paper (squares measuring 4×4mm) and recording which squares were crossed (squares labeled by numerical and alphabetical coordinates). The predator ('follower') was subsequently placed near the trail and also allowed

free movement, the squares it crossed were also recorded. Trail following was determined having occurred when trails overlapped for at least 5 consecutive squares. For a trial to recorded trails must have crossed at least once. The frequency of overlap in the absence trail following was determined by using the same method as above for two 'followe individuals of different herbivorous species, *Helix aspersa* and *Cepaea nemoralis*, (eliminati trail following for predation or for mating purposes as the two individuals were not congeneric This allowed comparison of the frequency and significance of trail following for each pre species.

The effects of size differences on the frequency of trail following were investigate by using a series of artificial trails. These were formed by allowing one individual *Achatin fulica* to move over a sheet of paper in which the form of a linear template of a specific wid had been cut to form straight trails with precisely controlled widths, all with identical chemic cues (due to their all being laid by the same 'marker' individual). A 'follower' predator wa allowed free movement near the trails, investigative behaviour and direct turns onto the tra were noted once the trail had been contacted. Each trial was repeated 10 times, the sam marker and two different followers being used on each trail. The same followers were use for all trail sizes to ensure comparability of results. In all cases illumination was overhea and uniform, eliminating any lighting influence on the direction taken by the follower.

The data on trail width show that the proportion of trails investigated and followe increases with increasing width (Fig 2.). The regression slopes are not significantly differen and the two data sets have a partial correlation coefficient of 0.893 (P=0.001), showing tha trail investigation and following are dependent on trail width.
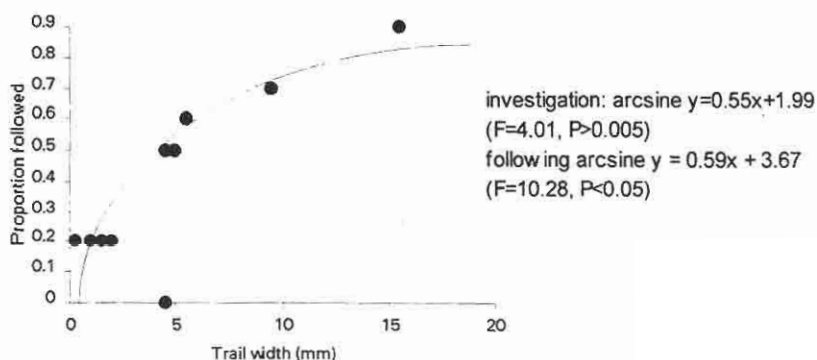

investigation: arcsine y=0.55x+1.99
(F=4.01, P>0.005)
following arcsine y = 0.59x + 3.67
(F=10.28, P<0.05)

Fig. 2. The effect of trail width on trail following frequency

The sensory lips used in trail following cover approximately 15mm when fully extended (a greater area is covered in searching when the head is moved from side to side but little head movement occurs during following) beyond a trail width corresponding to this 15mm no discrimination would be expected to occur. In accordance with this 100% of trails are followed at a width of 16mm, no further increase is possible so the leveling out of the relationship does occur as expected due simply to the area covered by the sensory appendages of *E. rosea*.

Comparing the data for following trails of different species from the trials described above demonstrates that there is no clear preference for any species (the range of expectations given are calculated from the standard error of ±0.11 of the slope of the above regression):

In *Edentulina dussumieri* none of the species tested was followed more frequently than the random non-predatory model predicts. This shows that trail following is not a component of predatory behaviour in *E. dussumieri*. In this context it is worth noting that although there are extensions to the lips in *Edentulina dussumieri* these are not as pronounced as in *E. rosea*, and are presumably of limited use as chemoreceptors. None of the other streptaxid species encountered in the field localities possessed significantly elongated lips, suggesting that their trail following ability was no more developed than that investigated above. Absence of trail following was also demonstrated in *Gonaxis quadrilateralis*. The primary mode of predation in streptaxids would thus appear to be essentially random search.

For *Euglandina rosea* the data demonstrate that there is no expression of species preference in trail following that is not explicable solely by size variation, with the exception of the slug *Meghimatium bilineatum* which is followed less frequently than would be expected due to the production of a copious white mucus on provocation. The mucus caused *E. rosea* to move away in all trials of the slug and of palatable prey artificially coated with the mucus. This presumably distasteful mucus would be expected to be detectable in the mucus trail left during locomotion. It has been hypothesised (Cook 1985, 1989a) that avoidance of such mucus accounts for the low frequency of trail following recorded in the case of the philomycid slug *Philomycus carolinianus*, an explanation which is probably also valid for the confamiliar *M. bilineatum*.

Table 1. Number of trails of different species followed (10 trials)

Predator	Species	trail width (mm)	followed	expected
Euglandina rosea				
	Helicina theobaldiana	1	2	1.6-1.8
	Tropidophora pulchra	5	3	3.3-4.4
	Omphalatropis rubens	3	3	2.5-3.1
	Vaginula seychellensis	10	8	5.4-10
	Edentulina dussumieri	5	4	3.3-4.4
	Stylodonta unidentata	10	7	5.4-10
	Macrochlamys indica	5	4	3.3-4.4
	Leptichnoides verdcourti	3	3	2.5-3.1
	Meghimatium bilineatum	3	1	2.5-3.1
Edentulina dussumieri			Mean overlap	Random overlap
	Helicina theobaldiana		1	1.8
	Stylodonta unidentata		10	2.3
	Subulinidae		2	2.3
	Leptichnoides verdcourti		3	1.7

Selection

The influence of prey size on predation efficiency was studied by feeding tria using prey lacking chemical or mechanical defences (*Helix aspersa*) (measuring 5-35mr and juvenile Subulinidae (1.2-5mm long). The results are shown in Table 2.

Speeds of movement

The speeds of a variety of prey species were compared to those of hatchling, juveni and adult predators to determine whether rapid locomotion was an effective anti-predatc defence in some species. Speed was compared by placing an individual of each species on sheet of squared paper (4×4mm squares) and recording the time taken to cover 30 squarε (120mm). For *E. rosea* a prey trail was provided to induce predatory behaviour, the prε were periodically disturbed from behind with the tip of a pair of forceps to induce avoidanc behaviour. The followers were fed 2 small prey in the 24 hours prior to the trial, the prε number resulting in the maximum speed. By these means it was ensured that hunting an escaping speeds were being recorded. 10 trials were used for each taxon.

Table 2. Size effects

Species	Percentage of prey killed from each size group (mm), 10 trials						
	1-5	6-10	11-15	16-20	21-25	26-30	31-35
Euglandina rosea	62	100	100	80	60	40	20
Gonaxis quadrilateralis	80	50	20	0	0	0	0
Edentulina dussumieri	80	30	0	0	0	0	0
Imperturbatia constans	60	0	0	0	0	0	0
Gulella poutrini	100	0	0	0	0	0	0

Table 3. Analysis of predator and prey speeds (one-tailed t-test, without assumin homoscedasticity: * = P<0.05; ** = P<0.005; ***=P<0.001)

Taxon	Speed (mm/s)	t value of predation		
		Euglandina (2.177)	*Edentulina* (0.792)	*Gulella* (0.533)
Euglandina rosea - juvenile	1.407	4.88 ***	-8.50 ***	-14.79 ***
hatchling	0.443	7.73 ***	2.55 *	3.01 **
Achatina fulica <20mm	0.670	6.85 ***	1.63	-2.99 **
>20mm	1.240	3.47 **	-6.80 ***	-8.93 ***
Edentulina dussumieri	0.792	9.46 ***	-	-3.42 **
Gulella poutrini	0.532	11.45 ***	2.10	-
Stylodonta unidentata	0.487	8.69 ***	4.06 ***	0.61
Liardetia sculpta	0.211	14.31 ***	9.10 ***	5.56 ***
Macrochlamys indica	1.718	3.13 **	-10.80 ***	-15.37 ***
Leptichnoides verdcourti	3.112	2.78 *	-17.38 ***	-18.23 ***
Deroceras laevis	2.937	2.31 *	-15.10 ***	-16.21 ***
Meghimatium bilineatum	0.772	9.81 ***	-0.33	-3.40 **
Omphalatropis rubens	1.057	7.89 ***	-5.01***	-7.72 ***
Pachnodus kantilali	1.719	3.11 **	-11.00 ***	-11.98 ***
Pachnodus niger×velutinus	1.817	3.22 **	-11.23 ***	-12.31 ***
Bradybaena similaris	1.352	5.92 ***	-7.94 ***	-13.22 ***

Only *Deroceras laevis* and *Leptichnoides verdcourti* move significantly faster than adult *Euglandina rosea* (Table 3) whilst the mean speed of most species is significantly higher than that of the streptaxids, which would only be able to catch very small prey (such as *Liardetia sculpta*) or (for *Edentulina dussumieri*) the slow moving *Achatina fulica* and *Stylodonta unidentata* if pursuit was attempted. The observation that unsuccessful attacks were not followed by any attempt at pursuit is in accordance with these data.

Prey density

In order to obtain more representative data, density effects were studied using the small prey size class which occurs at densities of 0-48.5m^{-2}. Predator efficiency at different densities and with different depths of leaf litter was studied using one predator in a 0.25m^2 container. Small prey (*Liardetia sculpta* and Subulinidae) were supplied at densities of 4, 8, 12, 16 and 20m^{-2} (corresponding to 1, 2, 3, 4 and 5 prey), which encompasses the natural density range. After a 24 hour period the number of prey remaining was recorded. The predators used had been fed only two small prey during the previous 48 hours to maintain them at a consistent hunger level. Leaf litter depths used were 1 and 4cm. Each experimental block was replicated five times.

Predation efficiency of adult *E. rosea* is influenced by leaf litter depth and prey abundance (Table 4); the effects on juveniles and subadults are not significant. Efficiency decreases with increased litter depth and reduced prey density (Fig. 2), this is most apparent in adults as relatively small increases in leaf litter depth cause a large increase in the abundance of small spaces providing safe refugia for small prey. In contrast, the hatchlings and juveniles are small and able to penetrate most spaces in the litter. Similarly, small streptaxids are not affected by litter depth.

Table 4. Analysis of variance of *Euglandina rosea* adult predation efficiency

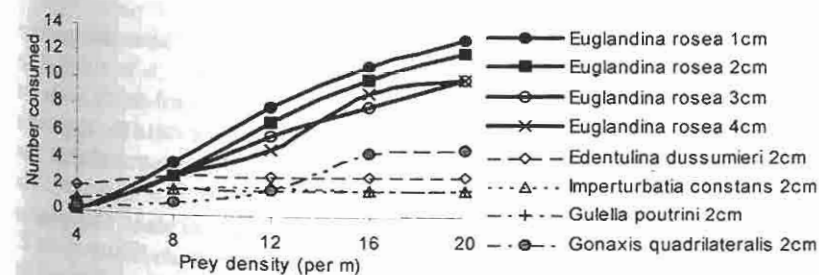| Source of variance	SS	DF	MS	F	P	
Litter (cm)	0.873	1	0.873	21.294	<0.001	***
Prey abundance	0.832	1	0.832	20.297	<0.001	***
Litter & prey	0.319	1	0.319	7.770	0.008	**
Residual	1.476	36	0.041			
Total	3.5	39	0.9			

Fig. 2. Relationship between litter depth and predation efficiency

The sigmoidal curves produced fit the Holling type III functional response with a delay in predation response to increasing prey density (Real 1977) or a delay caused by a search for alternative prey. As predation is non-selective the latter explanation can be discounted. As density exceeds a critical value (in this case over 4 prey m^{-2}) predatory efficiency increases until a maximum is approached. The only significant regression is for *Euglandina rosea*, which takes the form:

$$\text{Number consumed per day} = \frac{18X^2}{10+X+1.44X^2}$$

where X = prey density. R^2=0.89, P<0.001.

Discussion

The diet of *Euglandina rosea* in the wild includes small terrestrial molluscs which are the predominant dietary component due not to any feeding selectivity but to their abundance in leaf litter. Consumption rates are reduced for very small prey (due to detection difficulties) and for large prey. Large prey appeared to be consumed less frequently due to the physical toughness of the flesh as suggested by observations where predators repeatedly struck prey without puncturing the skin. The trail following behaviour expressed during searching is dependent on prey size as larger trails represent a greater area of sensory clues which are easier to detect and follow. This selection of large prey in hunting is offset by the difficulty of consuming the prey, and the greater abundance of smaller alternatives. This situation exists where arboreal prey occur, leaving clear trails on the vegetation. When such prey are present the hunting behaviour of *E. rosea* leads it to follow the trails up the vegetation and into temporary arboreality. With the exception of avoidance of possible distasteful species *E. rosea* shows no ability to discriminate between prey species on the basis of the trail following species that are difficult to eat or inedible (such as species of Veronicellidae) as frequently as edible species of the same size class.

The predatory behaviour of *E. rosea* is such that the prey consumed most frequently will be those species that leave large trails on an open substrate and are large enough to locate easily but small enough to be consumable (effectively 5-30mm long). Such prey are uncommon in the areas studied with the exception of the Seychelles *Pachnodus*.

The above discussions of the factors affecting the success of the introductions and the selection of different prey indicate that all sympatric species are likely to be subject to predation when conditions are suitable for *E. rosea* establishment. Several extinctions of arboreal molluscs have been associated with *E. rosea* introductions, in contrast to the apparent persistence of terrestrial species. This would appear to contradict the demonstrated absence of selectivity in feeding by *E. rosea* but as demonstrated above trail following behaviour would be expected to result in heavy predation on relatively large arboreal taxa. The causes of differential extinction rates of the prey were considered with regard to the efficiency of *E. rosea* predation, the effectiveness of defences possessed by the prey and the effect of *E. rosea* on recruitment to prey populations.

In contrast to *E. rosea*, streptaxids appear to be less efficient hunters although their relatively small size enables them to locate prey in deep leaf litter. All species have lower

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consumption rates than *E. rosea* and are restricted to preying on small snails. Although chemosensory lips are present in streptaxids trail following is not a significant aspect of predation which is basically a random search.

In addition to the systematic study described above the following species of Indian Ocean streptaxid were observed feeding in the wild: *Streptosele acicula* (feeding on small Subulinidae), *Gulella bicolor* (small Subulinidae), *Stereostele nevilli* (*Gonaxis souleyetianus*), *Gonospira callifera* (*Omphalatropis* spp.), *Gonospira* sp. (smaller *Gonospira* sp., *Omphalatropis* spp.) and *Gonodomus pagodus* has been recorded killing and consuming an adult *Machrochlamys indica* (O. Griffiths *pers. comm.*).

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