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Feeding habits of *Chicoreus capucinus* (Neogastropoda: Muricidae) in a Singapore mangrove

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KEY WORDS: Indo-Pacific, mangrove, ecology, feeding habit, Mollusca, Crustacea.

ABSTRACT Molluscs form a substantial component of the resident fauna in tropical mangroves. While the majority of them are either herbivorous gastropods or filter-feeding bivalves, predatory gastropods can be common and may therefore exert considerable influence on mangrove biotic structure. One well-known, common predator in Indo-Pacific mangroves is the muricid gastropod *Chicoreus capucinus*. Despite its large size and common occurrence, its biology and feeding habits are poorly known, when compared to its rapanine counterparts. In this study, detailed field observations were made in a disturbed mangrove fringing the West Johor Straits in Singapore. A total of 15 bivalve species, 7 gastropod species and 2 crustacean species were recorded from 341 occurrences of predation in the field. Bivalves constituted 83% of total prey consumed, most of which were drilled. Infaunal lantern shells (*Laternula* cf. *boschasina, L. truncata*), and epifaunal mussels (*Modiolus* cf. *metcalfei*) comprised 37% and 22% of prey drilled, respectively. Gastropods drilled and preyed upon were mainly small, consisting of rissooidean and cerithioidean species. The main crustacean prey was the barnacle *Balanus amphitrite*, although the wood-boring isopod *Sphaeroma* sp. was also consumed. Analysis of gut contents did not reveal additional prey species. The results show that *C. capucinus* is a versatile predator of molluscs and crustaceans, seeking, attacking and consuming a wide variety of prey from different components of the mangrove habitat.

RIASSUNTO I molluschi sono una componente molto importante della fauna residente nelle comunità tropicali delle mangrovie. Per la maggior parte si tratta di gasteropodi erbivori o bivalvi filtratori; ciononostante gasteropodi predatori sono frequentemente comuni e possono in tal caso avere una influenza considerevole sulla struttura biotica del mangrovieto. Un predatore ben noto e realtivamente comune in Indo-Pacifico è *Chicoreus capucinus* (Gastropoda, Muricidae). Nonostante le grandi dimensioni e la relativa frequenza, la sua biologia e le abitudini alimentari sono poco note, soprattutto se in confronto con le controparti Rapaninae. In questo studio sono riportate le osservazioni dettagliate sul campo in mangrovie disturbate nel West Johor Straits di Singapore. Un totale in specie di 15 bivalvi, 7 gasteropodi e 2 crostacei sono stati rinvenuti in 341 casi di predazione nel campo. I bivalvi, per la maggior parte perforati, costituiscono l'83% del totale delle prede consumate. I Laternulidae dell'infauna (*Laternula* cf. *boschasina, L. truncata*), e i mitilidi epifaunali (*Modiolus* cf. *metcalfei*) rapprenentano rispettivamente il 37% e il 22% delle prede perforate. I gasteropodi perforati e predati erano principalmente di piccola taglia, con specie di rissooidei e cerithioidei. I principali crostacei erano balani (*Balanus amphitrite*), benché anche l'isopode xilofago *Sphaeroma* sp. fosse presente nella dieta. L'Analisi del contenuto stomacale non ha rivelato ulteriori specie tra le prede. I risultati mostrano che *C. capucinus* è un predatore versatile di molluschi e crostacei, che ricerca, attacca e consuma un'ampia varietà di prede tra i differenti componenti dell'habitat delle mangrovie.

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INTRODUCTION

Chicoreus capucinus (Lamarck, 1822) is a relatively large (up to 125 mm shell height but typically up to 50 mm) intertidal muricine neogastropod that is common and often abundant in mangroves of Southeast Asia (Berry, 1963; Brandt, 1974; Sasekumar, 1974; Frith, Tantanasiriwong & Bhatia, 1976; Wong, Charles & Khoo, 1984; Houart, 1992; Wong & Ahmad, 1996; Middlefart, 1997). In Singapore, *C. capucinus* is found in pockets of highly disturbed mangroves along the East and West Johor Straits, a narrow estuarine channel separating Singapore Island from peninsular Malaysia. The species occupies a broad zone covering the landward edge to the seaward fringe (Berry, 1972) and occurs in a wide variety of habitats ranging from mangrove tree trunks (Morton, 1976a as *C. adustus*), algal mats to muddy sandbanks, as well as artificial substrates such as jetty pilings and monsoon drain walls. Its common occurrence in the mangroves, however, belies our knowledge of the biological role in this increasingly threatened tropical ecosystem. Several studies have examined its basic biology at Phuket Island in Thailand (e.g., Nielsen, 1976; Middlefart, 1996; Aungtonya & Vongpanich, 1997; Gribsholt, 1997) and development of imposex (Swennen et al., 1996; Tan, 1999) but, in general, molluscan predator-prey relationships in the mangroves are poorly understood. *Chicoreus capucinus* is exceptional amongst members of the Muricinae because of its estuarine distribution. At the same time, it is also one of a few gastropod predators present in substantial numbers in the mangal. This study aims to investigate, through field and laboratory observations, the feeding biology of *C. capucinus* in the mangroves of Singapore. The natural diet was determined by examining the stomach and rectal contents of individuals collected from the mangroves. Direct observations in the field and feeding experiments in aquaria were also carried out to determine feeding techniques.

MATERIALS AND METHODS

Field observations

Field observations were made over a period of five weeks, during September-October 1999 and again in February 2000, in a small area of disturbed mangrove (1° 26.8'N, 103° 44.1'E) near Sungei Buloh Nature Park on the northwest coast of Singapore fronting the West Johor Strait. An area about 1.5 ha in size adjacent to the Nature Park was selected as the study site. Each visit lasted about three hours in daylight at low tide, during which the mangrove floor was searched thoroughly for *Chicoreus capucinus*. A total of ten visits was made. For each individual found in the process of attacking/consuming prey, the size and identity of the item were recorded as was the size of the predator. Density of individuals were determined by randomly throwing 50cm x 50cm quadrats in the area sampled. Location and size of drill holes on individual prey were determined in the laboratory. Similar observations were also made on *C. capucinus* preying upon barnacles on mangrove tree trunks.

Laboratory and aquarium observations

Chicoreus capucinus individuals from the same locality were dissected and examined for stomach and rectal contents. They were cracked and fixed immediately in 4% seawater formaldehyde after collection. After fixing for 48 hours, they were washed in tap water and stored in 80% ethanol. Gut contents were removed and mounted on slides in Aquamount (TAYLOR, 1984). These were examined under the microscope and compared with intact prey specimens obtained from the same habitat. To observe and document feeding in aquaria, 20 *C. capucinus* were starved for one month, after which they were kept singly in perforated vials submerged in aerated seawater and prey introduced in turn to them. The following two gastropods and six bivalves were provided as prey items: *Littoraria vespacea* (Littorinidae), *Xenostrobus* cf. *atratus* (Mytilidae), *Brachidontes* sp. (Mytilidae), *Perna viridis* (Mytilidae), *Isognomon ephippium* (Isognomonidae), *Saccostrea cucullata* (Ostreidae) and *Enigmonia aenigmatica* (Anomiidae). All of these occur in the same habitat as *C. capucinus*. The prey items in the vials were examined carefully for evidence of predation after five days.

RESULTS

Of a total of 2097 *Chicoreus capucinus* individuals located on the mangrove floor, 341 (16.2%) were found in association with prey. In the majority of cases, each predator was associated with a single prey item, and prey sharing was observed on only a few occasions. Individuals were well spaced apart, with a mean density of 0.9±1.0 individuals per 2500 cm^2 (n=200 quadrats; range between 0 and 5 individuals). The size of *C. capucinus* with prey ranged between 10.8 and 51.7 mm in shell height. A total of 24 prey species was identified, comprising 15 bivalve species, seven gastropod species and two species of crustaceans (Table 1). Bivalve prey items ranged from juvenile mussels 1.4 mm in shell length to adult *Laternula truncata* with a shell length of 44.3 mm. Gastropod prey ranged between 2.8 mm in shell height (*Iravadia* sp.) to 18.4 mm (juvenile *Cerithidea obtusa*). Bivalves constituted 83% of the total prey items identified. These included the epifaunal mussels *Modiolus* cf. *metcalfei* Hanley and *Brachidontes* sp. which are byssally attached to and found amongst strands of the densely matted *Chaetomorpha gracilis*, as well as the infaunal bivalves green alga *Diplodonta* sp., *Dosinia* sp., *Marcia marmorata*, *Geloina erosa, Tellina* sp., *Glauconome virens, Laternula* cf. *boschasina* and *L. truncata.* Gastropods comprised less than 10% of the total prey consumed, and most of these were either *Iravadia* sp. (12 observations) or *Cerithidea obtusa* (8 observations). Other gastropods eaten included juvenile *Nerita*, *Telescopium,* onchidiids and *Salinator.* The remaining 7% were two crustaceans: the barnacle *Balanus amphitrite amphitrite* (29 observations) and the wood-boring isopod *Sphaeroma* sp. (5 observations).

Gut-contents analysis of 44 specimens of *Chicoreus capucinus* from the mangroves revealed that 29.5% of predators had barnacle exoskeletons (*Balanus amphitrite*) while 31.8% contained unidentifiable soft tissue.

In the aquarium, juvenile neritid (*Nerita* sp.) and adult littorinid gastropods (*Littoraria vespacea*) were preyed upon and eaten. *Nerita* sp. was mostly drilled either through the shell (50.0% of the cases) or at the edge of the calcareous operculum (33.3% of cases). The rest were consumed without any evidence of drilling. For the littorinid *L. vespacea*, about half were drilled through the edge of the operculum, whilst the remainder were either drilled through the shell at the suture between the last and penultimate whorls, or were attacked and consumed with no drill marks. Of the bivalves, *Xenostrobus* cf. *atratus*, *Brachidontes* sp., *Perna viridis*, *Isognomon ephippium*, *Saccostrea cuccullata* and *Enigmonia aenigmatica* supplied to the predators, three (*Brachidontes, Saccostrea* and *Enigmonia*) were all drilled and eaten, while *Xenostrobus, Perna* and *Isognomon* were neither drilled nor consumed by *C. capucinus* during the course of the experiments (Table 2).

Most prey was attacked by boring. Drill holes were present in the majority of prey items (78.8% of total) observed in the mangroves. Both bivalve and gastropod prey were drilled. Typically, the drill hole was a circular perforation between 0.4 and 1.5 mm in diameter surrounded by an irregular corroded region. In general the diameter of the drill holes made correlated with predator size (r=0.365, P<0.01 [n=105] for drill holes on *Laternula* cf *boschasina*; r=0.692, P<0.01 [n=69] on *Modiolus* cf. *metcalfei*). *Chicoreus capucinus* overwhelmingly preferred to drill the posterior regions of both bivalves (Figure 1). Despite the infaunal habits of *Laternula* and its permanent shell gape, the drill holes were concentrated on the posterior half of either valve.

These observations also show that *C. capucinus* is capable of attacking and consuming prey by other, as yet undetermined, methods. The method of attack seems to differ for different prey. Whilst 79% and 89% of *Laternula* cf. *boschasina* and *Modiolus* cf. *metcalfei* were drilled, 52% of *Laternula truncata* and 44% of *Marcia marmorata* were consumed with no evidence of drilling by *C. capucinus* (Table 1). Nearly 90% of barnacles consumed by *C. capucinus* were not drilled. About 30% of Iravadia sp. and *Cerithidea obtusa* appear to have been attacked and consumed without drilling. One method employed by *C. capucinus* when feeding on gastropods is access via the operculum. *Littoraria vespacea* was drilled through their operculum in many cases (see above).

The anomalodesmatan bivalve *Laternula* cf. *boschasina* and an epifaunal mussel *Modiolus* cf. *metcalfei* were the two major prey items of *C. capucinus* on the mangrove floor. They comprised 37.1% and 21.5% of the total prey items eaten, accounting for nearly half of the predatory activities of *C. capucinus*. There was, however, a significant difference in the mean size of *C. capucinus* feeding on *L.* cf *boschasina* and those feeding on *Modiolus* cf. *metcalfei* (t-statistic=14.11, df=105, P<0.001). Those feeding on *Laternula* were significantly larger than those preying on *Modiolus*. The mean shell height of *C. capucinus* individuals preying upon *L.* cf *boschasina* was 37.7±5.1mm (n=126), while the mean size of those preying upon *Modiolus* was 22.7±8.2mm (n=73). The average shell length of *L.* cf *boschasina* was 16.7±4.0mm

Table 1. Bivalves, gastropods and crustaceans preyed upon by *Chicoreus capucinus* on the mangrove floor at Sungei Buloh Nature Park, West Johor Strait, Singapore based on field observations.

Prey items	Total no. of observations	% drilled	Prey size range (mm)	Predator size range (mm)
Bivalves				
Barbatia sp. (Arcidae)	2	100.0	9.2 and 12.5	33.5 and 51.0
Brachidontes sp. (Mytilidae)	5	100.0	6.3–13.5	15.5–29.4
Modiolus cf. *metcalfei Hanley* (Mytilidae)	73	89.0	1.4–12.4	10.8–39.9
Musculista senhousia (Benson in Cantor) (Mytilidae)	21	100.0	4.4–14.7	13.9–39.1
Undet. Mytilidae	1	100	15.9	42.4
Diplodonta sp. (Ungulinidae)	6	66.7	6.4–21.3	33.7–51.7
Marcia sp. (Veneridae)	9	55.6	5.3–25.0	19.2–39.1
Dosinia sp. (Veneridae)	1	100	11.8	44.4
Undet. Veneridae	2	0	5.3 and 5.6	26.2 and 42.2
Geloina erosa (Solander) (Corbiculidae)	7	100.0	4.9–15.3	24.7–39.1
Undet. Tellinidae	4	25.0	11.9–29.2	30.0–35.7
Glauconome virens (L.) (Glauconomidae)	1	100	14.0	33.9
Laternula cf. *boschasina* (Valenciennes in Reeve) (Laternulidae)	126	79.4	7.8–30.4	26.4–49.3
Laternula truncata (Lamarck) (Laternulidae)	21	47.6	8.9–44.3	27.7–48.3
Martesia striata (L.) (Pholadidae)	2	100.0	not measured	not measured
Gastropods				
Nerita sp. (Neritidae)	2	100.0	not measured	not measured
Iravadia sp. (Iravadiidae)	12	66.7	2.8–4.1	9.5–16.9
Fairbankia sp. (Iravadiidae)	1	0	3.3	17.7
Cerithidea obtusa (Lamarck) (Potamididae)	8	62.5	6.9–18.4	32.2–37.7
Telescopium telescopium (L.) (Potamididae)	1	100	11.0	40.5
Onchidium sp. (Onchidiidae)	1	0	6.1	28.3
Salinator cf. *burmana* (Blanford) (Amphibolidae)	1	100	6.3	40.4
Crustaceans				
Balanus amphitrite Darwin (Cirripedia)	29	20	not measured	not measured
Sphaeroma sp. (Isopoda)	5	0	not measured	not measured

Table 2. Gastropod and bivalve prey items consumed by *Chicoreus capucinus* in perforated vials submerged in aquaria. All prey items are found in the mangroves. Each vial contained one predator and one prey item (n=20). The prey were examined after five days. (*) denotes drill holes through the shell or the operculum.

Molluscan prey item presented to *Chicoreus capucinus*	No of prey presented	No of prey eaten after five days	No of prey drilled	No of prey eaten without drill holes
Nerita sp. (Neritidae)	20	12	10	2
Littoraria vespacea Reid (Littorinidae)	20	20	14*	6
Xenostrobus cf. *atratus* (Lischke) (Mytilidae)	20	0	0	0
Brachidontes sp. (Mytilidae)	20	20	20	0
Perna viridis (L.) (Mytilidae)	20	0	0	0
Isognomon ephippium (L.) (Isognomonidae)	20	0	0	0
Saccostrea cucullata (Born) (Ostreidae)	20	20	20	0
Enigmonia aenigmatica (Holten) (Anomiidae)	20	20	20	0

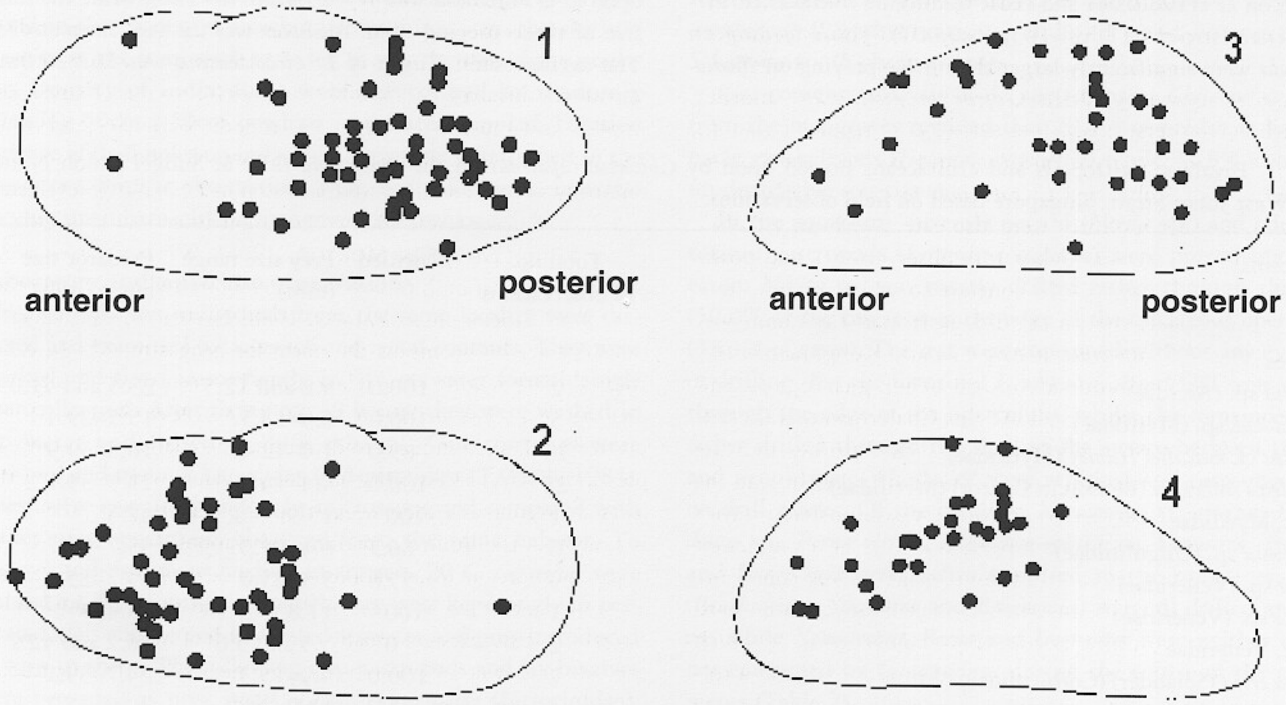

Figure 1. Location of drill holes on left (top row) and right (bottom row) shells of (1, 2) *Laternula* cf. *boschasina* and (3, 4) *Modiolus* cf. *metcalfei* from a total of 199 observations of predation on the two bivalve species by *Chicoreus capucinus* at Sungei Buloh mangroves. In *Laternula,* a total of 52 left valves and 48 right valves were drilled. In the case of *Modiolus,* a total of 36 left valves and 29 right valves were drilled. In all cases, one drill hole was associated with each valve

and that of *Modiolus* was 6.7±2.3mm. Size correlation between predator and prey size was evident within each prey type. A weak but significant relationship ($r=0.196$, $P<0.05$, $n=126$) was detected for *C. capucinus* preying upon *Laternula,* while a stronger significant correlation was determined between *C. capucinus* and *Modiolus* ($r=0.357$, $P<0.01$, $n=73$). Significant positive correlation was observed between mean sizes of predator and prey ($r=0.694$, $P<0.01$, $n=11$) (Figure 2), i.e., predators generally preyed upon bivalves and gastropods that were in proportion to their size on the mangrove floor.

On mangrove tree trunks, the predominant prey was *Balanus amphitrite*. Again, prey-sharing was not observed, although the abundance of prey on the trees may account for the high densities of *C. capucinus* on barnacle colonies. Of a total of 200 observations, 76 individuals (38%) were seen attacking or feeding on barnacles. The mean size of *C. capucinus* preying upon these was 32.4±5.4mm (n=76) and the mean barnacle size (apertural length) was 2.9±0.9mm (n=76). Only eight of 76 barnacles being attacked/consumed had drill holes on their opercular plates. No drill holes were present on the external wall plates. The majority of barnacles attacked did not show any sign of drilling and, presumably, *C. capucinus* had forced its proboscis between the plates to gain access to the animal beneath.

DISCUSSION

The diets of a number of rocky-shore and coral reef rapanine gastropod species are well investigated. Several species of *Morula* and *Thais* feed on barnacles, polychaetes, sipunculans, chitons, various bivalves as well as other gastropods (TAYLOR, 1978, 1980, 1984; ABE, 1980, 1989; TONG, 1986; HARPER & MORTON, 1997; TAYLOR & GLOVER, 1999). By comparison, data on muricine gastropods are in general lacking (GRAHAM, 1955; RADWIN & D'ATTILIO, 1976; TAYLOR, 1982; PONDER & VOKES, 1988). WELLS (1958) investigated the diet of *Murex fulvescens* Sowerby which comprised oysters, mussels, scallops and tellinids. In Florida, *M. pomum* Gmelin drilled oysters (MENZEL & NICHY, 1958) and *M. florifer* Reeve fed predominantly on the venerid bivalve *Chione* (PAINE, 1963). In Hong Kong, polychaetes, crustaceans, fish remains and unidentified tissue, possibly of molluscan origin, were found in the gut of *M. trapa* Röding, indicating their capacity to feed on a variety of prey and carrion (TAYLOR, 1982). For what little is known about the diet of *Chicoreus* species, most are able to feed on bivalves. Chicoreus *ramosus* (L.) fed on *Anadara granosa, Perna viridis, Modiolus metcalfei, Meretrix meretrix* and *Ruditapes* sp. in aquaria, and were seen to feed on the giant clam *Tridacna crocea* in the field (RUANGCHOY & TANTICHODOK, 1991). Both *C. ramosus* and *C. virgineus* (Röding) can drill the venerid bivalve *Meretrix meretrix*

(Patterson Edward, Raghunanthan & Ayyakkannu, 1992). Taylor (1980) observed that *C. brunneus* and *C. micropyllus* fed principally on bivalves (mostly *Alectryonella plicatula*) and barnacles (*Balanus trigonus*) in Hong Kong. In Singapore, *C. torrefactus* (Sowerby) drills *Gafrarium pectinatum,* another venerid bivalve (pers. obs.). Nielsen (1976) reported that *C. capucinus* fed on *Saccostrea cucullata* and *Balanus amphitrite.* Gribsholt (1997) observed *C. capucinus* feeding mainly on *S. cucullata,* but other molluscs were also eaten, including *Cultellus* sp., *Cerithidea cingulata* (laboratory observations), and possibly shipworms (*Teredo* sp.). In contrast to what amounts to a largely bivalve diet, the potamidid gastropod *Cerithidea* was the main prey of *C. capucinus* at Ang-Sila and Kungkraeban Bay in the Gulf of Thailand, although other gastropods and bivalves were consumed as well (Wells, Chalermwat, Kakkai & Rangubpit, unpublished observations). These studies indicate that it is capable of feeding on a variety of prey, but at the same time they suggest that its dietary composition varies according to the predominant prey available at a particular location. In the Sungei Buloh mangroves, bivalves constitute the main prey type of *C. capucinus*. It is at home both on hard and soft substrata (unlike its counterpart *Thais gradata,* which is confined to mangrove tree trunks and prop roots), and a tolerance for a wide range of salinities as well as an ability to withstand dessication (pers. obs.) are likely factors that allow access to a wide range of prey.

Field observations showed that juveniles may have different diets compared to adults. *Chicoreus capucinus* feeds on a variety of gastropods and bivalves, and possibly switches from a diet of small gastropods and mussels to larger gastropods, barnacles and other bivalves as it grows. Such size-related prey selection and associated versatility in prey handling were also seen in *Thais clavigera* (Küster) and *T. luteostoma* (Holten), two common intertidal muricids in Hong Kong (Taylor & Morton, 1996). While positive prey-predator size relationships have been demonstrated for several other species of Muricidae (e.g., Palmer, 1988; Taylor, 1990) such relationships are by no means the norm for neogastropods. In other studies, there was no clear relationship between predator size and prey size (e.g., Tan & Morton, 1998; Taylor & Glover, 1999). Further studies are in hand to determine the relative importance of prey availability, accessibility and energy value in determining the diets of juvenile and adult neogastropod predators. Nevertheless, it is clear from the limited aquarium observations that a wide variety of potential prey items of various sizes can be exploited by *C. capucinus*. Littorinids such as *Littoraria vespacea,* and the anomiid bivalve *Enigmonia aenigmatica* are usually out of reach of most *C. capucinus* in the field as they occupy non-overlapping niches, but they are readily drilled and eaten when circumstances allow.

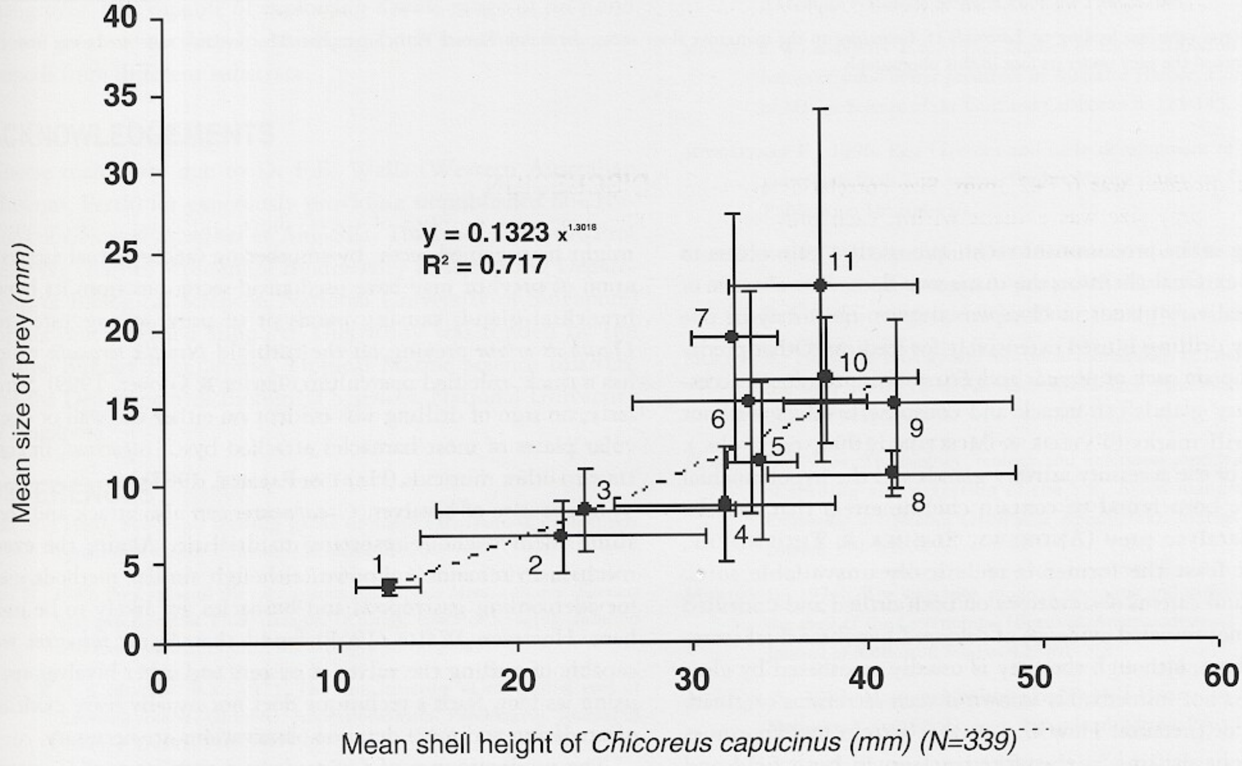

Figure 2. Predator-prey size relationship between *Chicoreus capucinus* and its molluscan prey items at Sungei Buloh mangroves. The mean shell height and standard deviation (±SD) of *C. capucinus* individuals seen feeding upon a particular prey type (nos. 1–11) and the mean size (±SD) of prey are plotted for each of the 11 gastropod and bivalve prey. Prey types: 1–*Iravadia* sp.(n=12); 2–*Modiolus* cf. *metcalfei* (n=73); 3–*Musculista senhousia* (n=21); 4–*Geloina erosa* (n=7); 5–*Cerithidea obtusa* (n=8); 6–*Marcia* sp. (n=9); 7–*Tellina* sp. (n=4); 8–*Barbatia* sp. (n=6); 9–*Diplodonta* sp. (n=6); 10–*Laternula* cf. *boschasina* (n=126); 11–*Laternula truncata* (n=21). Sample sizes with less than four prey items were excluded.

Plate 1. *Chicoreus capucinus* feeding on *Laternula* cf. *boschasina* on the mangrove floor at Sungei Buloh Nature Park, Singapore. The predator was lifted away from the substrate to reveal the prey under its foot in this photograph.

Drilling is the predominant technique used to gain access to prey with external shells on the mangrove floor. The absence of accessory salivary glands in *C. capucinus* (pers. obs.) may be one reason why drilling is used extensively for feeding. Other predatory gastropods such as *Morula* and *Thais* with prominent accessory salivary glands can attack and consume bivalves without leaving drill marks (TAYLOR & MORTON, 1996; pers. obs.). Secretions of the accessory salivary glands and the hypobranchial gland have been found to contain choline esters that may be used to paralyse prey (ANDREWS, ELPHICK & THORNDYKE, 1991). At least the former is technically unavailable to *C. capucinus,* and careful observations on both drilled and undrilled prey have not revealed evidence of coloured hypobranchial secretions on them, although the prey is usually smothered by clear mucus. It is not immediately known if such secretions originate from prey or predator. How *C. capucinus* attacks and consumes prey without drilling is therefore unclear. In both field and aquarium observations, neritid gastropods were sometimes consumed without drill marks on either the shell or its operculum. This implies that *C. capucinus* was somehow able to insert its proboscis between the operculum and the apertural wall of a *Nerita* shell. It is unclear how this is achieved. *Chicoreus capucinus* might have gained access by smothering (and eventual asphyxiation of prey) or may have used toxic secretions from its hypobranchial gland, causing paralysis of prey, as suggested for *Dicathais orbita* preying on the turbinid *Ninella torquata* which has a thick, calcified operculum (Taylor & Glover, 1999). Similarly, no sign of drilling was evident on either the wall or opercular plates of most barnacles attacked by *C. capucinus*, in contrast to other muricids (HART & PALMER, 1987).

In the case of bivalves, *C. capucinus* can also attack and consume them without resorting to drilling. Again, the exact mechanism remains unknown, although similar methods used for overcoming gastropods and barnacles are likely to be used here. However, WELLS (1958) found that *Murex fulvescens* was capable of pulling the valves of oysters and other bivalves apart using its foot. Such a technique does not usually leave evidence of predation and more detailed observations are necessary.

The predominance of *Laternula* as a prey item of *C. capucinus* is interesting. The predators appear to prey on these lantern shells rather than, for example, the more abundant and conspicuous epibyssate bivalve *Isognomon ephippium,* as observed in the field and in aquaria. Though *Laternula* has a thin shell with a permanent gape and is generally immobile as adults

(MORTON, 1976b; SAVAZZI, 1990), the well camouflaged, sand-encrusted siphons, infaunal habits (they are usually buried at depths of 2 cm or more below the substratum, and are virtually impossible to detect visually on the mud surface) and possession of well-developed, complex siphonal eyes mounted on the tip of siphonal tentacles (ADAL & MORTON, 1973; MORTON, 1973; NILSSON, 1994) are predator defences. In particular, the shadow reflex described by MORTON (1973), i.e., the flicking of siphonal tentacles in response to a shadow, could flick sand grains over its siphons, possibly making it difficult for *C. capucinus* to grasp the siphons as they withdraw on contact, which are themselves likely to be "drill-proofed" by the layer of sand grains attached to them. Nonetheless, *C. capucinus* appears to have little difficulty in detecting, attacking and consuming both small and large *Laternula* individuals. From numerous observations it seems likely that *C. capucinus* extends the anterior region of its foot into the substratum and by wrapping its foot around the posterior region, pulls out *Laternula* from its burrow. It then proceeds to drill the shell on the substratum surface. Drill holes were made on the posterior half of the bivalve, also on the left or right valve (and infrequently at the hinge). The sand-encrusted, tough-skinned siphons were usually left uneaten.

The relatively high frequency of predation by *C. capucinus,* its catholic diet and common occurrence all suggest that this predator plays a significant role in the ecology of Sungei Buloh mangroves. It is capable of exploiting a wide range of prey and shows great versatility in handling both bivalves and gastropods from different substrata.

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