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PREDATION BY MONGOOSES, RODENTS AND SNAILS ON *SITALA JENYNSI* (PFR.), *ACHATINA FULICA* BOWDICH AND OTHER LAND SNAILS IN COASTAL TANZANIA.

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SUMMARY

The broken shells of *Sitala jenynsi, Achatina fulica* and other land snails were collected from two sites near Dar es Salaam, Tanzania. Observations in both field and laboratory suggested that most of the shell damage was the result of predation by a snail (*Edentulina obesa*), the Banded Mongoose (*Mungos mungo*), rodents and (perhaps) birds. *E. obesa* was shown to eat some snail species readily, yet neglect others. Details of its predatory behaviour were obtained and there is some evidence that it prefers smaller specimens of *A. fulica*. Field observations of mongooses revealed that they have a number of different ways of breaking snail shells and these methods differ from those used by captive rodents. Birds of an undetected species may use yet another method.

Some idea of the relative numbers of *S. jenynsi* eaten by these four groups of predators was obtained by first clearing the empty shells from an area of ground and then removing the shells that accumulated over each of four successive two or four-monthly intervals. The relative population sizes of the living snails over this period were also estimated. Forty to one hundred percent of the snails eaten by shell-damaging predators was ascribed to *E. obesa* and there are indications that the proportion of the population that was destroyed differed between the four samples.

INTRODUCTION

The dead shells of tropical African land snails have received some attention from collectors and taxonomists, but the ecology of the living animals is still poorly known. We have been studying the land snails inhabiting the scrubland around Dar es Salaam, Tanzania, and in this paper provide information on the identity, behaviour and relative importance of some of their predators. For practical reasons we have concentrated on the commoner molluscs and on those predators that damage the shell in some way.

METHODS

Field Sites

The snail populations studied were in and around the grounds of the main campus of the University of Dar es Salaam and at Wazo Hill, respectively 10 and 17 kilometres north-west of the city of Dar es Salaam.

The two areas have a similar altitude (University: 60 - 110m above sea level, Wazo: 80 - 110 m above sea level). The vegetation in both places consists of thick scrub (shrubs, small trees and climbers of various species) except for areas where herbs and grasses predominate after the land

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had been cleared for agriculture at some time in the past (Kasigwa, 1975). One important geological difference is that whereas the University site is on the edge of a clay-bound sand plateau, Wazo Hill is topped by a raised Pleistocene coral reef (Temple, 1970). The presence of the limestone at Wazo Hill is reflected not only by the pH of the soil (Wazo: 7.0, University: 6.0), but also by the greater mean weight of the shells of the Wazo snails (Kasigwa, 1975). The annual climate at both sites is dominated by the occurrence of two rainy seasons (roughly, March to May and October to December), the second one being the less predictable. Bargman (1970) gives more information on the climate of the region.

Prey

We concentrated our attention on *Sitala jenynsi* (Pfr.) (Pulmonata: Urocyclidae) (Fig. 1). This was the most accessible snail at the two sites and occurred at quite high densities (approx.3 m^{-1}; Kasigwa, 1975) and in discrete populations. During the day, and whatever the season, the snails remain on the leaves and branches of the vegetation (particularly shrubs and trees). *S. jenynsi* is an 'annual' species; the snails are usually born at the onset of the first rainy season and rarely live beyond 14 months (Kasigwa, 1975).

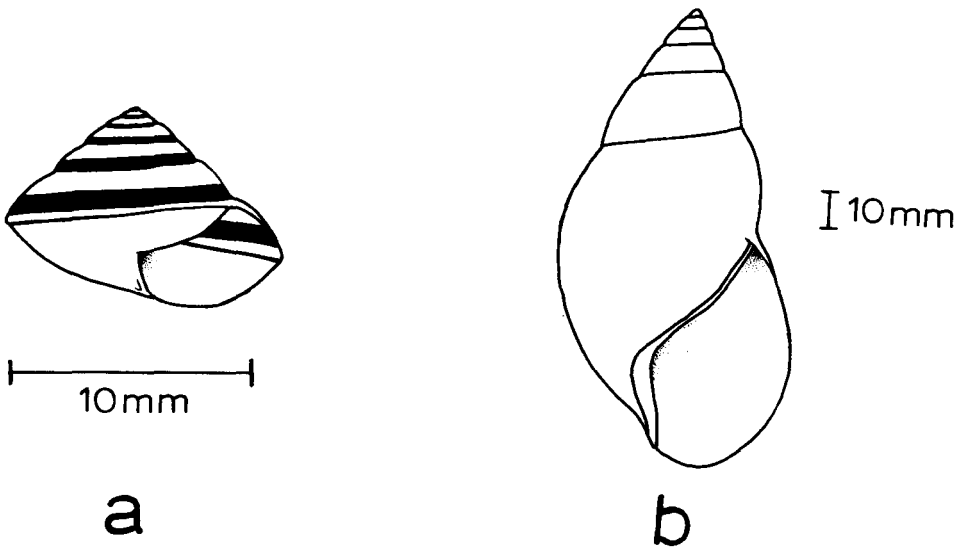

Fig. 1. (a) *Sitala jenynsi,* (b) *Achatina fulica.*

The next most studied species was *Achatina fulica* (Bowdich) (Pulmonata: Achatinidae), the Giant African Snail of Mead (1961) (Fig. 1). This species aestivates below ground in response to prolonged dry conditions and is therefore most obvious during the rainy seasons. Even when active, in our study areas it tends to remain close to the ground. Eight other species featured less prominently in our work, mainly because they were uncommon and/or very seasonal. These were: *Edentulina obesa* (Gibbons) and *Gulella laevigata* (Dohrn) (Streptaxidae); *Edouardia alycaeoides* (Verdcourt), *E. tumida* (Taylor), *Rachis punctata* (Anthon), *Rachistia mozambicensis* (Pfeiffer) and *Rachadina braunsi* (von Martens) (Enidae); and *Tropidophora letourneuxi* (Bgt.) (Pomatiasidae).

Identification of predators

Broken and unbroken empty shells were collected from the ground at the two sites in 1971 and 1972. These were first sorted according to the pattern of shell breakage (if any) and we then attempted to identify the predator responsible for each category of damage. Four groups emerged. Later these were associated (with differing degrees of confidence) with four classes of predator: the streptaxid snail *Edentulina obesa* (also one of the prey species), the Banded Mongoose *Mungos mungo* (Gmelin), rodents (probably of at least two species) and, possibly, birds of unidentified species. Some broken shells could not be ascribed to any of the four categories with any degree of certainty — this applied to all the broken *T. letourneuxi* and to about 10 per cent of the *S. jenynsi*. We were unable to discover the cause of death of unbroken shells, but suspect senescence for the older (age >11 months) *S. jenynsi*.

Two of the agents (*E. obesa* and *M. mungo*) were identified through direct observation in the study areas. The rodents were implicated from the nature of the damage to snails when offered to captive rats, while the evidence for bird predation is circumstantial and rests mainly on the presence of beak-shaped marks on some of the shells.

Behaviour of predators

E. obesa Information on the behaviour of *E. obesa* was obtained from observing the snail in both field and laboratory. In the laboratory twelve adult snails were housed, usually individually, in transparent plastic sandwich boxes (volume approx.0.001m^3) lined with tissue paper. The paper was kept moist and was replaced frequently.

Some experiments were designed simply to test the acceptability of different snail species to *E. obesa*. A single individual of a potential prey species was introduced and the box was then checked periodically for evidence of predation. Snails that were still alive after 48 hours were defined as 'safe'. No more than one snail per day was offered to each *E. obesa* and the sequence in which different prey species were offered was randomized. It was quite clear that some species were eaten avidly while others were neglected. This sort of design was also used to obtain details of the sequence of events when *E. obesa* successfully attacks a snail, except that observations were more thorough, and were continuous during the early stages of predation.

In a series of experiments designed to test whether *E. obesa* selects different size classes of *A. fulica*, two *E. obesa* were housed in separate glass tanks (150mm x 150mm x 130mm). Six 'small' (shell height approximately 15mm, range 13 - 17mm) and six 'large' (shell height approx. 25mm, range 22 – 27mm) *A. fulica* were added to each tank. The containers were checked frequently and each eaten snail was replaced by another of the same size-class to keep the 1:1 ratio constant.

Banded Mongoose All observations on *M. mungo* were made in the field. Binoculars were usually used and the observer hid behind vegetation for cover.

Rodents In order to test whether rodents prey on *S. jenynsi*, live snails of this species were left overnight on three different occasions in eight cages each containing a single rodent which had been caught on the University site. The rodents were three *Praomys (Mastomys) natalensis* (A. Smith), three *Mus musculus* L., one *Acomys* sp. and one *Praomys (Praomys)* sp. Each animal was offered six snails at a time and was also provided with water and commercial rat pellets. The snails were examined the following day for evidence of predation.

Birds (?) No data on the behaviour of presumed avian predators were obtained.

Relative importance of predators of *S. jenynsi*

An attempt was made to assess the relative importance of the four groups of predators in the mortality of *S. jenynsi*. In mid-April 1973 a small (10m x 12m) area of ground in one particular sampling site ('Hall 6 locality') at the University was cleared of all dead *S. jenynsi* shells. This plot was then checked in November 1973, March 1974 and May 1974. On each occasion all the dead shells were collected and the number destroyed by each predatory agent was noted. At the same time we also recorded the total number of live *S. jenynsi* seen on a set route walked through the Hall 6 locality. The shrubs and trees on this route were thoroughly searched and the numbers of *S. jenynsi* counted. This method of 'counting heads' is quite efficient, and accounts for over 60 per cent of the population in the area sampled (Kasigwa, 1975). It provided a measure of *relative* population size in the Hall 6 locality over the 10 month period.

RESULTS AND OBSERVATIONS

Predation by *E. obesa*

Casual observations suggest that *E. obesa* occurs at a density appreciably less than one per 100 m^2. When active (in the rainy seasons) it appears to confine itself to shrubs and trees, existing on a diet of other arboreal molluscs. Of these, *S. jenynsi* is usually the most widespread and abundant and is likely to form the major dietary component.

Attacks by *E. obesa* on *S. jenynsi* have been witnessed on at least 20 occasions in the field, and in plastic boxes in the laboratory on many more. There is no evidence that *S. jenynsi* perceives its aggressor when beyond a range of about 4cm; that is, virtually until just before tactile contact. The predator often appears to 'strike' in a fast movement from a distance of 1-2 cm, with its front end fully extended. The response of the prey, if it is not already retracted, is to withdraw rapidly into the shell. In the field this often results in *S. jenynsi* rolling from its position, usually into the undergrowth below. It is tempting to suggest that this behaviour is adaptive, for should *E. obesa* make firm contact with its prey predation nearly always follows.

Observations on captive snails have revealed the sequence of events in the feeding behaviour of *E. obesa*. After a successful 'strike' the front end of the body is inserted into the aperture of the shell and grips the body of the prey, which in response attempts to withdraw into the upper whorls. As the predator extends into the distal regions of the prey, the two shells come to touch one another, aperture facing aperture. *E. obesa* then retracts its tail end, and the bodies of both snails become scarcely visible. This position may be maintained for up to 12 hours, with the predator occasionally moving its shell from side to side (presumably as it delves deeper into the prey, or as the mouth alters its grip). During this operation copious amounts of mucus are produced (by the predator?), securely anchoring the shell of the prey to the substratum. Lastly, the predator relaxes its hold, withdraws its head end into its own shell, and then thrusts the posterior part of its body into the aperture of the prey. In this position it falls into a 'dormancy' lasting several hours before it finally abandons the prey. A shell which has just been attacked by *E. obesa* is identifiable not only by the dried mucus attaching it to its resting site but also by the pale brown *E. obesa* faecal matter on or near it.

Predation by *E. obesa* is often so thorough that none of the soft tissues of the prey remain. In addition, the interior of the shell itself becomes corroded, particularly the columella and the internal surfaces of the whorls (Fig. 2). Commonly all that is left is a translucent 'ghost', consisting mainly of the outer proteinaceous periostracum. Shells attacked by *E. obesa* are readily identified among recently dead shells on the ground. Other streptaxids, such as *E. affinis* Boetger are also known to attack the calcified layers of the shell (Williams, 1951).

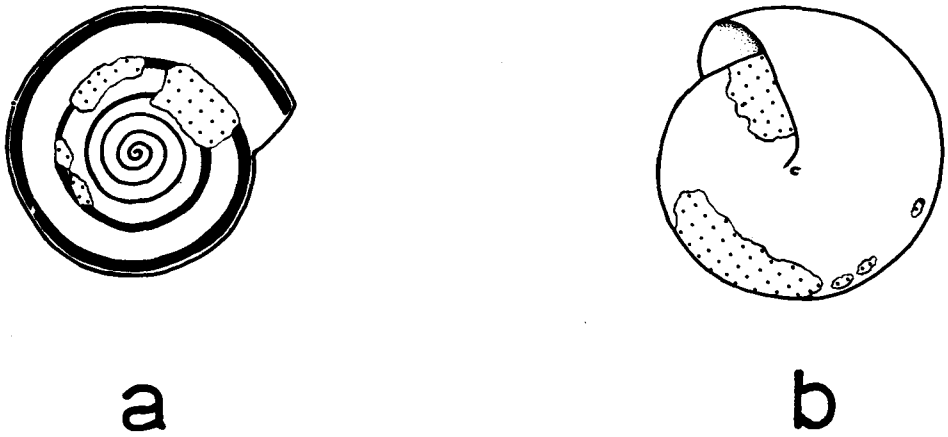

Fig. 2. Predation by the snail *Edentulina obesa* on two specimens ((a) and (b)) of *S. jenynsi*. Stippling indicates areas of shell corrosion. (Drawn from photographs by Kasigwa, 1975.)

E. obesa will prey on other snail species when available. In the field we have observed it feeding on *A. fulica* (small juveniles only), *Edouardia* spp., *Rachis punctata*, *Rachistia mozambicensis* and *Rachadina braunsi*. The last four of these, like *S. jenynsi*, have a pronounced tendency to climb and are therefore likely to be encountered by *E. obesa*. The only climbing snail we have never seen being eaten is the prosobranch *Tropidophora letourneuxi*. Laboratory observations on two *E. obesa* showed that they would actually attack *T. letourneuxi* when out of its shell, but would desist after it had retracted and closed its operture with its operculum. Williams (1951) makes a similar observation for another prosobranch, *Maizania magilensis* (Craven) when attacked by *E. affinis*.

Other snails which live close to the ground, such as *Gulella laevigata* and *Pseudopeas* sp. were never seen to fall prey to *E. obesa* in the field. In part this may be due to the difficulties of us finding snails in the dense vegetation at ground level. However, we have tested the acceptability of two of these species to captive *E. obesa* and one of them, *Gulella laevigata*, appears to be resistant to predation. This species, like *T. letourneuxi*, attracted attention when mobile, but after it retracted it was soon neglected. Undoubtedly this was partly due to the small size of the aperture of this small snail (shell 8mm x 4mm), but the teeth projecting from the sides towards the centre of the aperture may also have made it difficult for the predator to gain entry. Further evidence for this is that *Gulella usugarica* Crosse (a larger species with a larger aperture) and *G. alleni* Verdcourt (similar in size to *G. laevigata*), both from the West Usambara mountains in Tanzania and both 'toothed', were also safe from predation.

We also presented single *Achatina fulica* snails to *E. obesa*, and these were readily accepted when they were below a certain size. Not surprisingly, large snails (shells over 100mm x 50mm) were disregarded. (This vacant niche for such a molluscan predator is perhaps filled elsewhere in East Africa by *Edentulina affinis* a snail about twice the size of its congener (Williams, 1951).) However, young snails (shell height < 5mm) were readily accepted. There is also evidence from choice experiments that *E. obesa* prefers the smaller of two juvenile size-classes of *A. fulica*. The total numbers of the two size-classes eaten by a pair of snails are given in Table 1. Each snail took a statistically significantly higher proportion of the smaller prey. We suspect, therefore, that selection varies with the size (and therefore age?) of the prey, but the full details of the response will only come from further experiments.

TABLE 1

Predation by two E. obesa *when presented with equal numbers of two sizes of* A. fulica

		A. fulica 15 mm No. eaten	*A. fulica* 25 mm No. eaten	$\chi^2_{(1)}$	P
E. obesa	A	11	3	4.57	<0.05
E. obesa	B	21	6	8.33	<0.01

The χ^2 values are based on a 1:1 expectation

We have found, to our cost, that *E. obesa* will eat its own kind if more than one are kept in a container in the absence of alternative food. We have never observed such cannibalism in nature, but it has been recorded for two other streptaxids, *E. affinis* and *Gonaxis kibureziensis* E.A. Smith in coastal Kenya (Williams, 1951).

Predation by the Banded Mongoose

Mungos mungo uses at least four different methods of breaking snails, perhaps depending on the size and strength of the shell.

1. In the case of juvenile *S. jenynsi* (< 4mm diameter), it places the entire animal in its teeth and swallows the soft parts and most of the shell.
2. Adult *S. jenynsi* have a considerably thicker shell and are first held in the forepaws in a vertical position, apex upwards. Then, with its lower incisors against the lower side of the body whorl and its upper incisors on the upper side of one of the spire whorls, the mongoose bites off a portion of the shell and pulls out the body with its teeth, leaving the empty shell characteristically agape on one side (Fig.3). A similar technique is used on *E. obesa* but the position of the bite is more variable. Of eight specimens eaten by mongooses, three were bitten at a perpendicular or oblique angle to the long axis of the shell; the remainder had a portion bitten from one side.

Fig. 3. Two methods of predation by the Banded Mongoose, *Mungos mungo*, on *S. jenynsi:* (a) by biting a piece off the side of the shell (removed area indicated by stippling), (b) by breaking successive pieces from the aperture and along the lower whorls. ((a) Drawn from photograph by Kasigwa (1975); (b) drawn from specimen.)

3. Sometimes *M. mungo* deals with *S. jenynsi* by biting sections off the shell, starting at the aperture and working along the whorls until the withdrawn body is accessible to the teeth. Shells so attacked have the lower portion of the columella characteristically exposed (Fig. 3). *A. fulica* with shells below about 50mm in height are also broken in this way (Fig.4). This method has been recorded for small mammals preying on helicid snails in Europe (Kerney and Cameron, 1979).

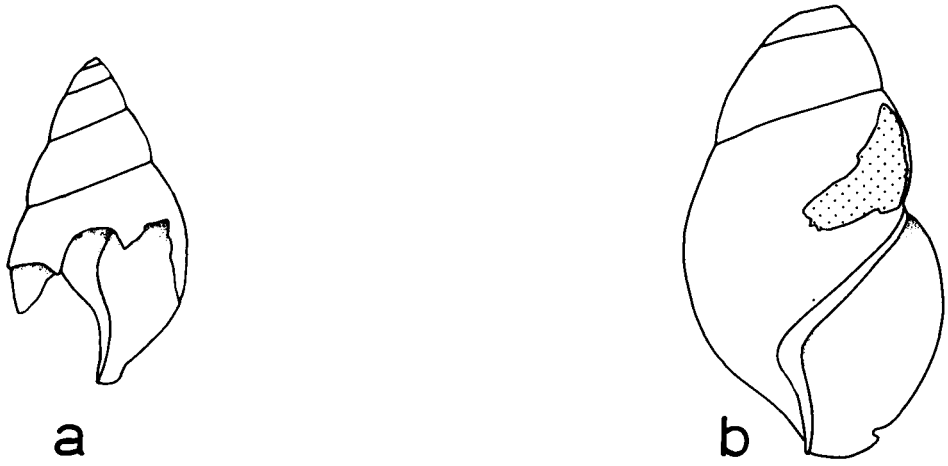

Fig. 4. Two methods of predation by the Banded Mongoose, *M. mungo*, on *A. fulica:* (a) by biting successive pieces from the aperture and along the lower whorls, (b) by breaking the shell (stippled area) by throwing it against a rock. (Drawn from photographs by Kasigwa, 1975.)

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