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).
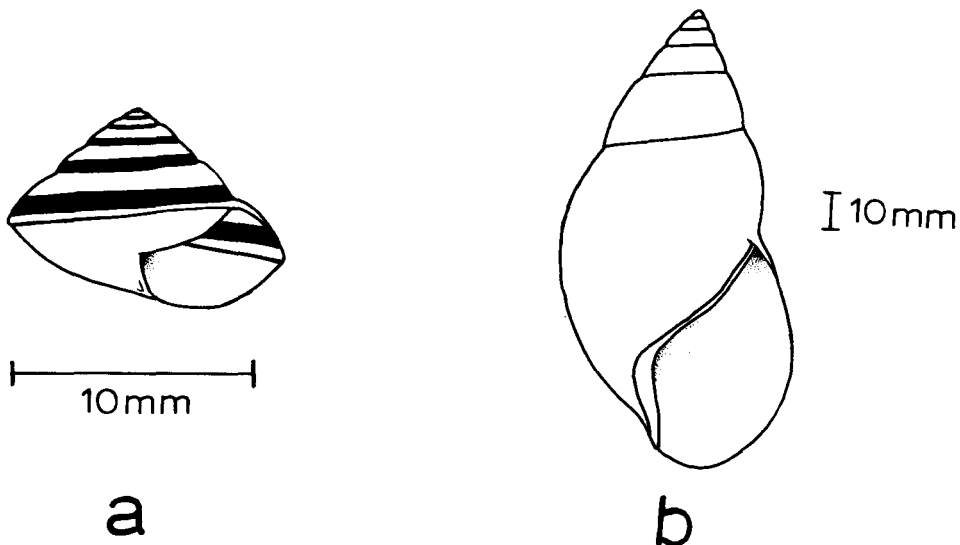

Fig. 1. (a) *Sitala jenynsi*,   (b) *Achatina fulica*.

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 m². 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).
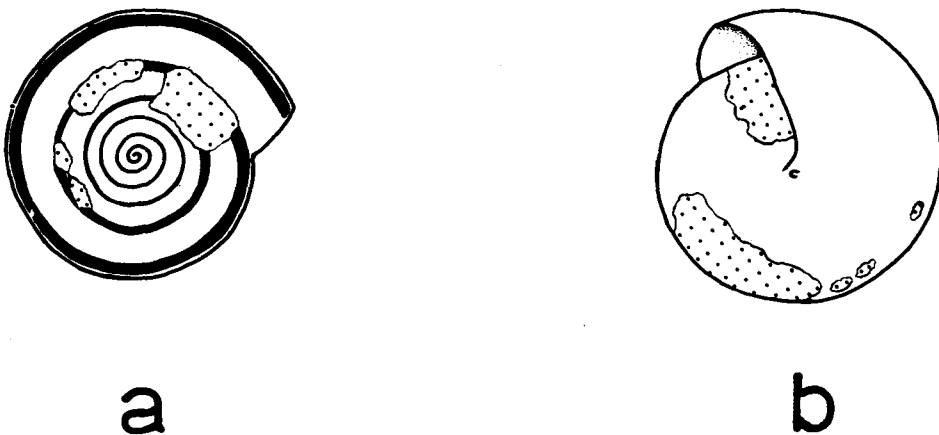

a   **b**

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	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.

a **b**

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).
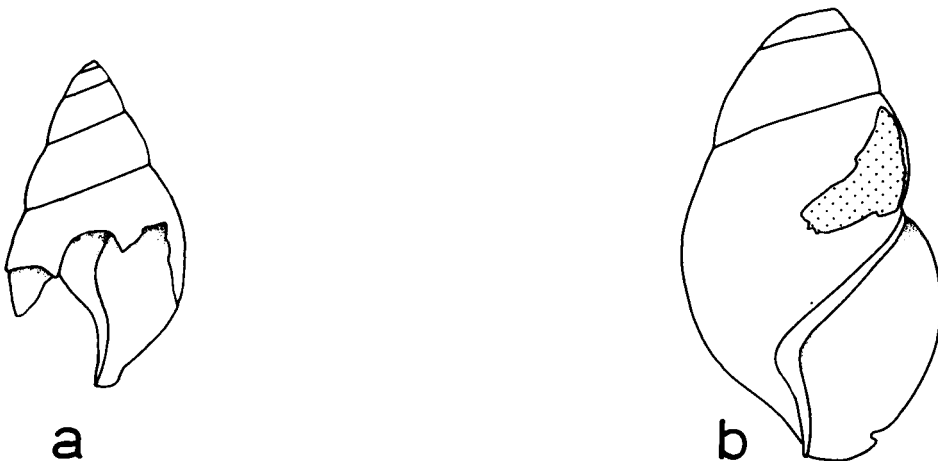

a **b**

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.)

4. Larger, more resistant *A. fulica* are broken against rocks or trèe-trunks. For this operation the mongoose assumes the spectacular postures described by Hinton and Dunn (1967) and Eisner and Davis (1967). The animal holds the prey in both forepaws and stands bipedally on its hind legs with its back to the 'target object'. It then swings its forelegs back-and-forth beneath itself for a number of times (normally 2-4) before throwing the snail under its body; at this point the hindlegs leap into the air, above the snail *en route* to the target. This operation is repeated until the soft parts become accessible, usually because of a crack in the middle of the whorls (Fig.4).

Williams (1951) reports that a Black-legged Mongoose in Zanzibar, *Bdeogale tenuis* (Thomas and Wroughton), also feeds on *A. fulica* but makes no mention of the methods described above. Instead he describes a fifth behaviour: 'The animal holds the mollusk between its paws and strikes it rapidly against some hard object until the shell is broken'. Mead (1961) provided indirect evidence for similar behaviour by the mongoose *Herpestes edwardsi* Geoffroy when preying on *A. fulica* in Ceylon (Sri Lanka).

Predation by Rodents

Empty *S. jenynsi* shells lacking the top 3 or 4 whorls were commonly found on the ground in the study area. Rodents were suspected as candidates for such predation and this hypothesis was tested by experiments with eight captive animals: of these, only the single *Acomys* and the three *P.(M.) natalensis* accepted the snails, which they did on all three nights. They apparently treated the snails in the same way, removing the tops of the spires and leaving an empty shell similar to those found in the field. We were unable to observe the predators in action but deduce that the rodent holds the snail in its teeth (and forepaws?) with the apex within its mouth, bites through both sides of whorls 3 and/or 4, swallows the apical portion (including the shell) and then pulls out the soft parts. The lower whorls are therefore left clean but with a characteristically ragged edge where the snail has been cracked by the teeth (Fig.5). Similar evidence for rodent predation has not been obtained for other snail species. It is interesting to note that the captive rodents did not use the method of breaking successive pieces off the aperture, as European rodents apparently sometimes do when feeding on helicids (Kerney and Cameron, 1979) and as we have recorded occasionally for mongooses. European rodents have also been recorded as using the same method as their African relatives (Bang and Dahlstrom, 1974; JAA, personal observations).

a   b

Fig. 5. Predation by rodents on two specimens ((a) and (b)) of *S. jenynsi*. Stippling indicates external areas of the shell that have been removed. (Drawn from photographs by Kasigwa, 1975.)

Predation by birds (?)

The marks on some dead and living *S. jenynsi* snails suggested to us that they might have been attacked by birds, but we never witnessed such an event. Such specimens are similar to those eaten by rodents in that the tip has been nipped off, but the cut is cleaner and closer to the apex (i.e. at about the 3rd whorl). Snails which have recently been killed in this way sometimes have

the bulk of the body remaining in the lower whorls. Some live *S. jenynsi* and *E. obesa* have been found with two V-shaped (beak?) indentations on the tip of the shell in the position expected from the appearance of the de-tipped shells. These marks could result when the snails slip out of the bird's grip during predation. The bird which is our prime suspect is the White-browed Coucal, *Centropus superciliosus* Hemprich and Ehrenberg, a species which frequents the study areas, feeds occasionally on slugs (Moreau, 1935) and although not reported as eating snails, is generally omnivorous (Mackworth-Praed and Grant, 1957). It also has a beak corresponding in size to the marks found on some shells. Mead (1961) observed the related species *C. chlororhynchus* Blyth pecking holes in the shells of live *A. fulica* in Ceylon.

Relative importance of predators of *S. jenynsi*

Table 2 gives the numbers eaten by each class of predator for the four sampling occasions in 1973/74, along with the number of live *S. jenynsi* observed in the whole of the Hall 6 locality. The data all refer to the same cohort, which was born in March and April, 1973.

TABLE 2

Recorded predation on the 1973/74 generation of S. jenynsi *at a site in the Hall 6 locality, University of Dar es Salaam.* —

Month of sample	Age (months)	Total number live snails counted in Hall 6	Numbers eaten in small site by:					No. of empty but unpredated shells
			E.obesa	*M.mungo*	Rodents	Birds?	All	
July 1973	4	1099	17	–	–	–	17	11
November 1973	8	651	23	14	5	–	42	9
March 1974	12	461	42	10	7	9	68	74
May 1974	14	93	5	4	3	–	12	41

By May 1974 the numbers in the 73/74 generation had declined to below 10 per cent of their July 1973 value. Throughout this period *E. obesa* was clearly the most prominent of the four groups of predators, taking 40 to 100 per cent of the total recorded predation. It is clear that *E. obesa* did not feed in direct proportion to the density of *S. jenynsi*: the numbers taken on the four occasions differ statistically significantly from an expectation based on the relative population sizes (goodness-of-fit $X^2_{(3)} = 49.92$, $p < 0.001$). Disproportionately very few snails were taken in July 1973 and disproportionately many more taken in March 1974. A number of factors probably contributed to this effect. The July snails were small and we might have been more likely to overlook them when the ground was searched. They were probably more liable to be destroyed totally by *E. obesa* (and the same applies to the other predators, none of which was recorded for July). If the results for July are ignored there is still appreciable overpredation for March and underpredation for November ($X^2_{(2)} = 14.49$, p. < 0.001). The March data cover the start of the main rainy season, when there is a corresponding increase in the activity of *E. obesa*. The snail breeds at this time and if each individual feeds more and if there are more snails feeding (because of births) there will be increased predation. The data for predation by *M. mungo* and rodents during the last three sampling intervals do not differ statistically significantly from an expectation based on the availability of *S. jenynsi* ($X^2_{(2)} = 1.70$ and $X^2_{(2)} = 4.39$, respectively) on the three occasions when data were collected.

DISCUSSION

Not surprisingly, the different species of predator have different ways of getting to the soft parts of snails. *E. obesa* differs from the other three groups in that the shell damage is caused *after* the snail has entered the aperture and eaten most of the body. Furthermore, the damage occurs from the inside, to the extent that the presence of the undigested periostracum is often the only factor preventing local collapse. It is not certain whether all *Edentulina*-attacked snails suffer in this way—a certain fraction could be killed without noticeable shell damage. The adaptive significance of shell corrosion is clear: by first dissolving the prey's shell and then absorbing the mineral salts *E. obesa* obtains a ready supply of ions for its own shell. Mongooses and rodents were sometimes recorded eating pieces of shell, but this behaviour may be due more to accident than design.

The strategy adopted by a given predator when attempting to eat a snail will presumably depend, at least in part, on the size, strength and shape of the shell. These properties (which are not necessarily independent of one another) will clearly vary from species to species. It is for this reason, perhaps, that *M. mungo* employs a number of methods to crack *A. fulica* shells that it does not use on the much smaller *S. jenynsi*.

There is also considerable variation in shell properties *within* species and this is manifest in two ways. First, within populations there is variation that will depend partly on the different ages of the individuals and partly on the different external (environmental) and internal (genetic) factors that act on them. Thus populations of *A. fulica* show considerable variation in shell size in common with populations elsewhere (Mead, 1961). Our choice experiments suggest that *E. obesa* prey selectively on these snails, tending to take the smaller of the two size-classes presented. Life table analysis of *A. fulica* populations in Hawaii also provides evidence that other streptaxids (*Gonaxis quadrilaterilis* (Preston), *G. kibweziensis* (E.A. Smith) and *Euglandina rosea* (Ferussac)) preferentially attack smaller snails (Nishida and Napompeth, 1975). It seems likely that this behaviour is more related to some characteristic of the soft parts of the prey rather than to the size or strength of the shell *per se*. The properties of the shell also vary between populations of a given species. For example, the shells of Wazo Hill *S. jenynsi* tend to be larger, of a different shape, and heavier than those of their University counterparts. Although too few data are available to make an accurate comparison of the behaviour of predators at the two sites, we suspect that the choice of method used by *M. mungo* is related to the strength (= thickness?) of the shell.

Compared with the other predators, *E. obesa* appears consistently to take more *S. jenynsi* throughout the year, at least in the area that was sampled. It is probable that *E. obesa* depends entirely on molluscan prey and, at least in our study areas, on *S. jenynsi* in particular. Both the Banded Mongoose, *M. mungo*, and one of the rodents, *P. (M.) natalensis*, are renowned as opportunistic omnivores (Delany and Happold, 1979) and the importance of snails in their diet is unknown.

ACKNOWLEDGEMENTS

REFERENCES

BANG, P. & DAHLSTRON, P. (1974). Animal Tracks and Signs. Collins, London.
BARGMAN, D.J. (1970). The climate of Dar es Salaam. Tanzania Notes and Records 71: 55 – 64.
DELANY, M.J. & HAPPOLD, D.C.D. (1979). Ecology of African mammals. Longman, London.
EISNER, T. & DAVIS, J.A. (1967). Mongoose throwing and smashing millipedes. Science 155: 577 – 579.
HINTON, H.E. & DUNN, A.M.S. (1967). Mongooses: their natural history and behaviour. Oliver and Boyd, Edinburgh.
KASIGWA, P.F. (1975). Studies on the ecological genetics of the land snail *Sitala jenynsi* (Pfr.). M.Sc. thesis, University of Dar es Salaam.
KERNEY, M.P. & CAMERON, R.A.D. (1979). A Field Guide to the Land Snails of Britain and North-West Europe. Collins, London.
MACKWORTH-PRAED, C.W. & GRANT, C.H.B. (1957). African Handbook of Birds. Series 2. Birds of Eastern Africa Vol. 1. Longmans, London.
MEAD, A.R. (1961). The Giant African Snail: a problem in economic malacology. University of Chicago Press.
MOREAU, R.E. (935). A synecological study of Usambara, Tanganyika Territory, with particular reference to birds. J. Ecol. 23:1–43.
NISHIDA, T. & NAPOMPETH, B. (1975). Effect of age-specific predation on age distribution and survival of the Giant African Snail, *Achatina fulica.* Proc. Hawaii. ent. Soc. 22: 119–123.
TEMPLE, P.H. (1970). Aspects of the geomorphology of the Dar es Salaam area. Tanzania Notes and Records 71: 21–54.
WILLIAMS, F.X. (1951). Life-history studies of east African *Achatina* snails. Bull. Mus. Comp. zool. Harv. 105: 295–317.

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