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Feeding habits of the Water mongoose (*Atilax paludinosus*)

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Abstract

Water mongooses are solitary, nocturnal herpestines that are found mainly in close proximity to water. The diet of free-living mongooses was assessed through scat analysis. Results show crabs to be the most important component, followed by amphibians and small mammals. Food tests on captive *Atilax* indicated a preference for rodent and amphibian prey. Methods of prey capture are described and the efficiency with which a variety of prey types are handled is discussed. Factors allowing coexistence with other herpestines and also other carnivores are mentioned. It is suggested that the dietary flexibility of *Atilax* resembles that of the ancestral herpestines, and represents the dietary preadaptations that were required by sociable herpestines for their shift towards group life.

Introduction

Details concerning the diet of *Atilax paludinosus* are provided by ROWE-ROWE (1978), DU TOIT (1980), WHITFIELD and BLABER (1980), LOUW and NEL (1986) and MACDONALD and NEL (1986). Feeding habits are mentioned only in general references (SMITHERS 1971; 1983; EWER 1973; ROSEVEAR 1974; STUART 1981). In the present report details of diet of both captive and free-living mongooses, as well as food preferences and prey-catching behaviour of captive animals, are given. In addition an attempt is made to show the significance of the diet of this herpestine against the background of its solitary, nocturnal nature.

Material and methods

Eight mongooses were housed in enclosures measuring $1,5 \times 3 \times 1,2$ m. Their origins and capture information are reported in BAKER (1987) and BAKER and MEESTER (1986). Animals were maintained on a diet of day-old chicks, rats and *Xenopus* (clawed toads). On occasion crabs (*Potamonautes* sp.), chicken's eggs, Orthoptera and oxheart were provided. Each enclosure was supplied with a galvanised iron bath which served as both a pond and a continuous water supply.

In food preference tests the mongooses were offered a choice of two freshly-killed prey items. Prey was killed using carbon dioxide rather than ether, to avoid selection owing to an unfamiliar odour. The items were killed to prevent a biased choice owing to differences in movement or sound patterns. Those used in the tests included insects, crustaceans, amphibians, birds, chicken's eggs and rodents. Each choice test was replicated five times. In each case the item that was taken first by the animal was presumed to represent the preferred food.

In order to observe prey-catching behaviour live prey was introduced into the mongoose enclosures. Time elapsed from detection of prey until attack, and from initiation of the attack until the prey was dispatched, was recorded.

Details of prey-catching behaviour varied slightly from one prey type to another. However, several elements were common to all sequences. Prey-catching was divided up into two components:

1. Sighting. This was inferred from the stance of the mongoose, which included erection of ear pinnae, tautening of the body and, on occasion, piloerection.
2. Attack. The attack commenced when the mongoose started to stalk or chase the prey, and terminated when the prey had been killed. Death was deduced from the prey's lack of movement.

Several components of the attack were recognised, namely the stalk, the pounce and the kill. For each prey type the behaviour patterns used to catch and kill the prey were noted.

Details of the diet of free-living water mongooses were obtained by scat analysis. Monthly samples of scats were collected from Kenneth Stainbank Nature Reserve in Durban from May 1984 until

Table 1. Results of food preference tests

Choice	Preference	Percentage
day-old chick	3	12
amphibian	22	88
	n = 25	
day-old chick	1	4
chicken's egg	24	96
	n = 25	
day-old chick	23	92
crab	2	8
	n = 25	
day-old chick	0	0
rodent	25	100
	n = 25	
amphibian	11	44
rodent	14	56
	n = 25	
chicken's egg	7	41
rodent	10	59
	n = 17	
crab	2	13
rodent	13	87
	n = 15	
amphibian	7	28
chicken's egg	18	72
	n = 25	
amphibian	11	79
crab	3	21
	n = 14	
insect	2	20
crab	8	80
	n = 10	
insect	0	0
amphibian	10	100
	n = 10	
insect	0	0
rodent	10	100
	n = 10	

the water and dealt with on the ground. This involved pinning the crab down and biting it. Most commonly the claws were removed first, presumably to prevent injury to the mongoose. Occasionally the crab was tossed aside and then retrieved before being eaten. ROWE-ROWE (1978) suggests that this may serve to stun and temporarily disorient prey, thus facilitating killing. Occasionally also it was picked up between the forefeet and thrown on to the ground to facilitate its fragmentation and death. The entire crab was usually consumed, although in particularly large specimens parts of the carapace were often discarded.

Rodent prey was located by either sight or sound. An initial hesitation usually occurred after detection and was followed by a quick dash and pounce. The killing bite was administered to the head region and commonly spanned the antero-dorsal part of the cranium. "Repeat biting" was not commonly observed in adults although it was occasionally exhibited by juveniles. After the killing bite had been administered the prey was often

February 1985. After collection the scats were frozen until they were prepared for analysis. Preparation included thawing, oven-drying at 50 °C for at least five days and then sorting by dissection microscope into taxonomic categories. Vertebrate prey was identified by the presence of hair (mammal), feathers (bird), scales (fish or reptile) or skeletal elements (amphibians). The distinction between different kinds of invertebrate prey (crab and insects) was easily made as crab exoskeleton is particularly distinctive. Within the Insecta identification to order was made whenever possible. Fruits were identified by their seed types. For the present study no attempt was made to determine proportions of the various food items and only relative percentage frequency of occurrence is reported. This statistic was calculated by totalling all occurrences (ie, presence or absence in each scat) and expressing actual occurrence of each item as a percentage of the total.

Results

Results of food preference tests are presented in Table 1, and of scat analysis in Table 2 and 3. Details regarding prey capture are presented in Table 4.

When crabs were introduced into the ponds, detection occurred only when the mongooses either swam in or walked past the water. Once the prey had been sighted the mongooses systematically began to "feel" over the base of the pond to locate the prey. Their heads were never immersed during this part of the search and only when the crab was located did they duck their heads under the water to catch the prey. Thus the feet were used in prey location and the mouth in grabbing. The orientation of the bite varied but as soon as the prey was firmly held it was removed from

Table 2. Occurrence of food items in 34 scats

Food item	Occurrence	Relative % freq of occurrence
Crustacea	26	22
Insecta	25	21,1
Amphibia	22	18,6
Small mammal	12	10,1
Aves	11	9,3
Reptilia	4	3,3
Diplopoda	4	3,3
Pisces	2	1,6
Chilopoda	2	1,6
Fruit	2	1,6
Mollusca	1	0,8
Miscellaneous	7	5,9

Table 3. Occurrence of various insects in 25 scats

Insecta	Occurrence	Relative % frequency Occurrence
Insecta unidentified	5	10,6
Orthoptera	14	29,7
Coleoptera	17	36,1
Lepidoptera	6	12,7
Dermaptera	2	4,2
Isoptera	1	2,1
Odonata	1	2,1
Diptera	1	2,1

“shaken to death”. It was usually consumed from the anterior end, although on occasion the tail was eaten or the throat opened first. In the case of large white rats the head was often mauled and then discarded. Some of the mongooses (one male and two females) often took their dead rodent prey into the ponds and played with them there (throwing them into the air, “drowning” them and nudging them) before consuming them out of the water.

Killing of amphibian prey varied depending on whether it was *Xenopus* or *Bufo* sp. *Xenopus* was located in the ponds by either sight or touch and treated in the same way as crab prey during the search. Only when the prey was located did the mongoose immerse its head in order to grab it. This prey is slippery and more elusive than crab prey and several misses usually occurred. When the amphibian was caught it was removed from the water, killed by a head bite and then kneaded on the ground. This behaviour was assumed to be aimed at removing the mucous body covering. In the case of *Bufo* sp. the prey was located by sight and killed by a head bite. Again these amphibians were palpated on the ground, presumably to remove any noxious substances. Occasionally “shaking to death” was recorded. When it had finished eating the mongoose cleaned its mouth by wiping it with the forefeet. This removed any mucous that had adhered to the vibrissae, lips and chin. *Bufo* sp. were not eaten as readily as *Xenopus* and in the field, in summer when *Bufo* congregate to mate, evidence was found of random killing. In one pond approximately ten dead frogs were found, each one decapitated and partially eaten. This was attributed to water mongoose as the sandy surrounds were covered with *Atilax* tracks.

Insect prey was usually located visually or aurally and was approached relatively casually. If the prey remained immobile the mongoose held it down with the forefeet and picked it up in the mouth. If the prey moved, however, the mongoose accelerated their attack. When within pouncing distance the prey was either caught in mid-air or pinned down by the forefeet and consumed immediately. Insect prey offered to the mongooses included orthopterans, isopteran, dictyopterans and coleopterans.

Table 4. Sighting and attack times in prey-killing behaviour

Prey item	Time taken to sight prey		Time taken to attack prey		Total attacks
	range	\bar{x}	range	\bar{x}	
Rodent	23–35s	21s	1–5s	3s	n = 5
Amphibia	25–279s	161,2s	45–56s	50,6s	n = 5
Crustacea	120–300s	204s	25–80s	49s	n = 5
Orthoptera	12–40s	23,4s	1–5s	3s	n = 5

The only live bird prey given to the mongooses were young chickens. These were located by sound, pursued and killed by a head bite. The entire prey was consumed. When dead adult pigeons were given to the mongooses the primary wing feathers and some tail feathers were usually discarded, as were the head and bill.

Chicken's eggs were broken by throwing them on the ground. This was accomplished by rearing up on the hind limbs and throwing the egg vertically downwards. In some cases when the eggs were particularly small the mongooses took the whole egg into the mouth and simply broke it open with the canines. The entire contents were eaten and in some cases even the shell was consumed.

Discussion

Scat analysis showed a preponderance of crab, insect and small mammal prey with amphibians and birds forming a significant part of the diet. While insects were frequently found in scats of free-living mongooses they formed a negligible portion of the bulk of the diet when compared with other food items. In food tests they were not a preferred food item. Two factors may account for this apparent lack of interest. Firstly, the prey given during food tests was dead and movement of insects seems to be an important stimulus for capture. Secondly, prey offered at the same time as insects during food choice tests was always larger, energetically more rewarding, and thus more attractive to the mongooses. However, the tendency of small carnivores to exploit a variety of prey items should not be ignored, and in their natural habitat mongooses are likely to examine and consume any moving object provided that the effort expended in capture is not too great.

Food tests indicated a preference for rodent and amphibian prey. If only those tests in which naturally occurring items were considered (thus excluding choices containing chicken's eggs and day-old chicks) rodents were most frequently selected (44 % of the time) followed by amphibians (38 %), crabs (15.4 %) and finally insects (2.3 %). These results are particularly interesting when seen in the light of scat analysis results which reveal crabs to be the most abundant prey item. This suggests that while *Atilax* might prefer rodents, circumstances in the natural environment are not conducive to their exploitation. *Atilax* is a relatively large, solitary herpestine whose preferred habitat includes watercourses and nearby dense vegetation. The significance of this choice of habitat lies in the solitary nature of the mongooses and the associated need for cover from potential predators. For these reasons the most commonly encountered prey item is crabs, one which is furthermore under-utilized by any other co-existing species (MACDONALD and NEL 1986). Further, the well-defined digits of *Atilax* are particularly well adapted to seeking out crabs that may be hidden beneath rocks and in crevices. RADINSKY (1975) has shown that neocortical sulcal patterns in *Atilax* suggest increased tactile sensitivity and muscular control of the hands. It appears that these characteristics preadapt the water mongoose to its particular niche. In the field evidence of searching for prey in holes and crevices is exhibited by a concentration of tracks and footprints in the vicinity of crab holes in the mud along river banks.

The abundance of alternate food sources, such as amphibians and water-nesting birds, amongst the riverine vegetation provides an important secondary dietary component, and reduces the need to venture into the savannahs in search of prey. However, *Atilax* is not entirely restricted to stream areas. At Giant's Castle Nature Reserve (pers. obs.) and at Vernon Crookes Nature Reserve (MADDOCK, pers. comm.) *Atilax* moves from one stream bed to another across relatively open grassland. During these trips any terrestrial prey that is encountered may be taken, which may account for the relatively high occurrence of rodents in the scats, and illustrates the obvious preference for rodent prey. The only hazard in open country is lack of adequate cover for this large solitary herpestine.

Prey-catching tests reveal rodents to be the most rapidly noticed and dispatched food

items, while crabs offer more resistance during sighting and attack. While these results are consistent with the food preferences of *Atilax*, the abundance of crabs and the security offered by the sheltered environment within which crab-hunting occurs, must have survival implications for *Atilax* which are of greater consequence than the preference for rodents.

The strong preference for chicken's eggs in food tests may result from the apparent satisfaction that the mongooses derive from breaking them open. In a controlled captive environment with reduced stimulation, *Atilax* may approach egg-breaking more eagerly, simply as an activity to relieve boredom, rather than because eggs are a preferred food item. Evidence in support of this is shown by the frequent occurrence of stone throwing in captivity. Any small, hard object is investigated and thrown onto the ground. Because the behaviour persists beyond the time that would be required to open any food item, it is perceived (by the observer) as a "game" or as an energy releasing mechanism. While evidence for egg consumption from scat analysis is absent unless the shell is also consumed, bird's eggs may form an important part of the diet of free-living *Atilax*, albeit an irregular and unreliable one.

While *Atilax* relied on the interaction of several senses to capture prey, it appeared that sound and touch played the most important roles. Searching for aquatic prey was almost entirely a tactile exercise as visibility below water level was often reduced by turbulence, while detection of terrestrial prey was facilitated by audition. During live food tests the mongooses discerned the whereabouts of hidden terrestrial prey by standing still and listening for movement, evidenced by erect pinnae and slight alterations in head position. As soon as visual contact was made the attack commenced. Clearly sense of touch and hearing were detection mechanisms while vision played a follow-up role.

Variation in prey-catching methods is clearly related to the shape, activity and habitat of the different prey items. In the smaller herpestines (*Helogale undulata rufula*: RASA 1973; *Galerella sanguinea*: BAKER 1980) the killing bite for rodents is carefully directed at the eye and ear cavities. This is necessary for these small carnivores, as without a specifically oriented bite it would be difficult to penetrate the skull of the prey. In *Atilax*, however, the larger size of the jaws and teeth as well as the more powerful jaw action easily damages the skull, and so obviates the need for a well-oriented killing bite. This was evident also from the scats of free-living mongooses, in which complete or semi-complete skulls of vertebrate prey were never found.

EISENBERG and LEYHAUSEN (1972) regard a precisely aimed killing bite as a recent advance in predatory behaviour whereas an undifferentiated bite with associated tossing or shaking is thought to be primitive. *Atilax* exhibits both an undifferentiated killing bite and "shaking to death", indicating that as far as prey-killing is concerned it should be considered a primitive herpestine. "Shaking to death" was not, however, an invariable behaviour pattern and was thought to be associated with the degree of hunger. When less hungry the mongooses were more inclined to play with their food, and in these circumstances "shaking to death" was frequently recorded.

"Food-washing" was often exhibited by several of the mongooses. LYALL-WATSON (1963) discusses the function of this activity and suggests that it is a response to captivity. This behaviour was more common if the food given to the mongooses was not completely thawed, or if it was covered by sand and debris, thus suggesting a direct causal relationship between food condition and food manipulation.

The method of egg-breaking employed by *Atilax* is different from that of many other herpestines, which tend to throw the egg backwards between the hind limbs. EWER (1973) discusses the evolution of these throwing patterns, and suggests that they have developed as a result of the animal's normal foraging patterns. Thus the "backward throwers" are usually those herpestines that scratch about for insects using a backward directed scratch, while the "vertical throwers" such as *Atilax* have dexterous "fingers" and are more likely to

succeed in holding the egg between the forefeet and to bite at it. In frustration they may rear up and drop the egg onto the ground, so initiating the tendency to throw downwards (EWER 1973). Observations on young mongooses confirm this pattern; the earliest response to eggs was always an attempt at biting, and only later was the mature behaviour pattern learnt.

SHEPPEY and BERNARD (1984) and GITTLEMAN (1986) demonstrate that relative brain size appears to be related to feeding efficiency in carnivores. When comparing the

Table 5. Percentage relative occurrence of food items in the diet of *Atilax*

Food item	WHITFIELD	ROWE-	SMITHERS	BAKER	LOUW and NEL (1986)			MACDONALD and NEL (1986)
	and BLABER (1980)	ROWE (1978)	(1983)	present study	Kobee Valley	Betty's Bay	Highland state For	
Crustacea	54,2	43	23,6	22	44,7	54,3	23,7	36,5
Amphibia	14,4	14	29	18,6	5,2	2,5	7,5	—
Mammalia	1,3	14	23,6	10,1	5,2	1,7	10	8,9
Aves	—	14	—	9,3	1,3	1,5	6,2	19,5
Reptilia	—	1	—	3,3	—	—	—	—
Pisces	7,2	2	4,5	1,6	26,3	2	5	10,6
Insecta	16,2	2	19	21,1	14,4	12,6	17,5	7,6
Mollusca	—	—	—	0,8	—	10,7	—	2,9
Myriapoda	—	—	—	5	—	—	—	1,7
Vertebrata unidentified	—	—	—	—	—	—	—	8,9
Plant	3,1	2	—	1,6	2,6	11,5	20	—
Carrion	—	5	—	—	—	—	—	—
Unidentified	3,1	3	—	5,9	—	2,5	10	2,9

Table 6. Food items of major importance in the diet of various herpestines

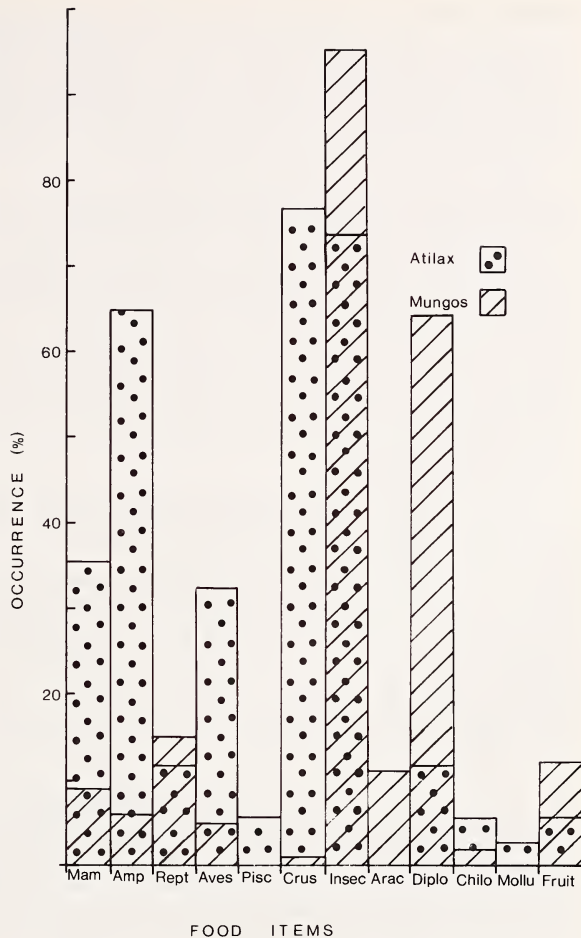
Herpestine	Activity period	Social structure	Food item	Habitat	Source
<i>Ichneumia albicauda</i>	N	Sol.	Insects	Savannah	TAYLOR (1972)
<i>Herpestes ichneumon</i>	D	Sol./Co-op	Rodents	Wide tol./Dense veg.	STUART (1983) DELIBES et al. (1984)
<i>Atilax paludinosus</i>	N	Sol.	Crabs	Dense veg.	Present study
<i>Galerella sanguinea</i>	D	Sol.	Insects	Savannah	BAKER (1980)
<i>Galerella bulverulenta</i>	D	Sol.	Insects	Dense veg./Savannah	MACDONALD and NEL (1986)
<i>Cynictis penicillata</i>	D	Co-op.	Insects	Savannah	MACDONALD and NEL (1986)
<i>Mungos mungo</i>	D	Soc.	Insects	Wide tol.	SADIE (1983)
<i>Suricata suricatta</i>	D	Soc.	Insects	Open/arid	ROBERTS (1981)
<i>Helogale undulata</i>	D	Soc.	Insects	Savannah	RASA (1977) SMITHERS (1983)

N – Nocturnal; D – Diurnal

encephalization quotients of the herpestines it is clear that *Atilax* has the highest relative brain size, providing morphological evidence of its greater feeding efficiency. This is manifested in the variety of prey taken (Table 5) and the flexibility of prey-catching methods. This appears to be characteristic of all herpestines and demonstrates the adaptability that is common amongst small carnivores. However when comparing the food items of major importance in the diets of a sociable herpestine (*Mungos*) and *Atilax* (Fig.) it becomes clear that *Mungos* relies most heavily on grouped prey items, such as insects (Table 6). Solitary animals on the other hand are able to exploit a wider spectrum of prey of both small and large size, because the disturbance of prey caused by a group of foraging animals is not a factor that affects prey selection in solitary animals. Of significance in the diet of *Atilax* however, are the larger and more energetically rich prey items.

Various feeding strategies are available to large solitary herpestines, and strict reliance on large prey items is not the rule. *Ichneumia albicauda* is an herpestine of comparable size to *Atilax* and is also nocturnal. However this solitary animal is unusual in that it relies most heavily on insect prey and moves about mainly in savannahs (SMITHERS 1983). Over large areas within their range *Atilax* and *Ichneumia* co-exist (ROWE-ROWE 1978, SMITHERS 1983), but occupy mainly different habitats, *Ichneumia* occurring in savannah and *Atilax* along watercourses. Thus spatial separation and the associated exploitation of largely different food items are the two most important factors that allow coexistence of these two animals.

Another similar-sized coexisting and solitary herpestine is *Herpestes ichneumon*, whose diet tends towards small mammals (STUART 1983; DELIBES et al. 1984). Whether *H. ichneumon* is strictly solitary or whether it lives in small family parties is uncertain (SMITHERS 1983; BEN-YACCOV et al. 1986). Whatever the circumstances, diurnal activity is unusual for a large mongoose and protection from predators may be afforded by its



Percentage frequency of occurrence of food items in *Atilax* and *Mungos* scats. Data for *Mungos* taken from SADIE (1983). The % occurrence of insect prey for *Mungos* is underestimated due to the fact that SADIE did not record total occurrence, but noted the variety of prey taken

preferred habitat of dense vegetation close to water (SMITHERS 1983). It is, however, not uncommon in open grassland (MADDOCK, pers. comm.) which may account for its tendency towards group-living, in that predation risks would be reduced through increased alertness. Nevertheless, co-existence with *Atilax* and *Ichneumia* appears to be possible primarily as a result of temporal spation, and in addition because a preference for rodent prey precludes any competition.

These three examples illustrate a few of the patterns that result when activity regimen, habitat and diet are varied, and show that flexibility is characteristic of herpestines.

The ability of *Atilax* to exploit a variety of food items allows it to coexist compatibly not only with other herpestines (MACDONALD and NEL 1986) but also with other carnivores that may be more specialised predators, for example *Aonyx capensis* and *Lutra maculicollis* (ROWE-ROWE 1978; VAN DER ZEE 1981). LOUW and NEL (1986) report that virtually no overlap occurred in the diet of *Atilax* and *Aonyx* at Betty's Bay, with *Aonyx* taking prey of mainly marine origin, while *Atilax* utilized shore crabs and other terrestrial species. At St Lucia WHITFIELD and BLABER (1980) have shown that *Atilax* consume penaeid prawns, providing further evidence of dietary flexibility and the resultant occupation of divergent habitats.

Clearly, feeding patterns in *Atilax* are a consequence of several factors, the most important being its solitary mode of life, with habitat selection and availability of prey types being consequent upon this factor. When compared with other herpestines it is obvious that solitary representatives exploit a wider variety of food types (Table 6). If we follow current trends (GORMAN 1979; RASA 1986) and assume that group-living in herpestines is a recent development that was stimulated primarily as an anti-predator response when a shift into open country occurred, then the dietary flexibility of the ancestral, solitary herpestines, of which *Atilax* is a modern representative, preadapted those sociable species for group life, and their consequent shift in feeding patterns.

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Zusammenfassung

Ernährungsgewohnheiten der Wassermanguste (Atilax paludinosus)

Wassermangusten sind einzellebende, nachtaktive Schleichkatzen, die meist am Wasser vorkommen. Die Zusammensetzung ihrer Nahrung im Freiland wurde durch Kotanalysen ermittelt. Die häufigsten Beutetiere waren Krabben, gefolgt von Amphibien und kleinen Säugetieren. Zweifachwahlversuche mit Beutetieren bei Wassermangusten in Gefangenschaft ergaben eine Bevorzugung von Nagetieren und Amphibien. Die Methoden des Beutefangs werden beschrieben, und die Fähigkeit, unterschiedliche Beutetierarten zu erlangen, wird erörtert. Umstände, die das Zusammenleben mit anderen Herpestinen erleichtern, werden erwähnt. Die Vielseitigkeit im Beuteerwerb bei *Atilax* dürfte dem ursprünglichen Zustand bei den Schleichkatzen nahekommen. Sie kann als Präadaptation an die Ausbildung eines differenzierten Gruppenlebens bei Herpestinen angesehen werden.

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