CHAPTER 5

ECOLOGY

FOOD

One aim of the present study was first to determine how many individuals and how much biomass was contributed to the ecosystem by the reptiles and amphibians. Secondly, how do these animals interact with other facets of this ecosystem. One of the most fundamental interactions is their diet.

The Burkea africana - Eragrostis pallens savanna has a wide diversity of species but is depauparate in numbers (see Chapter 4). This feature is shown by the mammals, birds, reptiles, amphibians and insects. Such a wide diversity of species leads to a wide feeding spectrum and, therefore, also to a number of specialists. Most species feed on a variety of food items, but some prefer one group of prey, while another prefers other prey, but there are a few, which are specialists or stenophagous. This is a dangerous practice as the species is likely to be in dire straits if its prey should exhibit large scale population fluctuations, a feature common to the savannas of the world, due to climatic variation.

All the reptiles and amphibians present in the savanna ecosystem at Nylsvley belong to the secondary and tertiary levels of the trophic chain. They are, therefore, all predators. None appear to feed on vegetation.

Snakes

The snakes are among the largest of the reptilian and amphibian predators. They are certainly the most diverse. They therefore feed on a large variety of prey (Table 13). Snakes can be divided into various categories depending on what they feed on. It can be seen that there are few species of invertebrate feeders although food appears to be freely available. Those snakes that do feed on invertebrates are chiefly dependent on termites (Isoptera) and centipedes (Chilopoda). In addition, the young of some of the sand snakes have been recorded as feeding on grasshoppers, FitzSimons (1962), and possibly even other arthropods.

Of the remaining 26 species, six (23%) are exclusively batracophagous or prefer amphibian prey as opposed to 11 (42%) feeding mainly on lizards while six (23%) are mammalian predators, two are snake eaters and one feeds exclusively on birds' eggs. It is remarkable that there are few snakes which show a preference for birds. Perhaps this is due to the low density of avifauna in the Study Area, as well as the difficulty in capturing them. In spite of the name bird snake applied to <u>Thelotornis capensis</u>, this species feeds, at least at Nylsvley, more on amphibians and lizards, although also recorded feeding on the eggs of birds.

Table 13. Food of snakes on the Nylsvley Nature Reserve. Occasional prey (+), preferred (++), exclusive (+++).

	Invertebrates	Amphibians	Lizards	Snakes	Birds	Birds' eggs	Mammals
Leptotyphlops distanti	+++						
Aparallactus capensis	+++						
Typhlops bibroni	+++						
Philothamnus semivariegatus		+++					
Causus defilippii		+++					
Crotaphopeltis hotamboeia		+++					
Psammophylax tritaeniatus		+++					
Thelotornis capensis		++	+	+		+	
Philothamnus hoplogaster		+++					
Dispholidus typus			++		+	+	
Psammophis jallae			+++				
Psammophis sibilans			++				+
Psammophis angolensis			+++				
Telescopus semiannulatus			++		+		+
Mehelya nyassae			+++				
Lycophidion capense			+++				
Boaedon fuliginosus			++				+
Prosymna sundevallii			+++				
Amblyodipsas polylepis			++	+			
Xenocalamus bicolor			++	+			
Bitis arietans		+					++
Dendroaspis polylepis					+		++
Python sebae							+++
Naja haje annulifera		+		+	+	+	++
Naja mossambica		+					++
Pseudaspis cana			+				
Mehelya capensis		+	+	++			
Atractaspis bibronii			+	++			+
Dasypeltis scabra						+++	

The largest group (53,29%) are mainly lizard feeders, termed by Barbault (1971), sauriphages. With few exceptions, they feed almost exclusively on lizards, and of those that do include other groups in their diet, the juveniles feed exclusively on lizards until they reach a size where other prey such as mice, snakes or birds can be overpowered.

There are, however, more noctural saurophagous snakes than diurnal species while there are only three or four nocturnal lizard species. Nocturnal saurophagous snakes are, therefore, able to locate resting diurnal lizards in their hiding places, a deduction supported by stomach content analysis. Nocturnal lizards, with the possible exception of Lygosoma sundevallii, are not common, as the results of the trapping show. All nocturnal snakes are relatively slow-moving, which indicates that they capture their prey by locating them in their burrows or hiding places, or else trap them unawares (Table 14). The preponderance of lizard feeders, both terrestrial and fossorial, is a reflection of the variety of lizards found on the reserve and in the Study Area in particular. Barbault (1971), reported that five species of snake were saurophagous at Lamto. This situation fits in with the relatively poor diversity of lizards in that savanna. In contrast, he lists eight species feeding almost exclusively on batrachians, while several other species include amphibians in their diet. This accounts for 27,58% of the serpents at Lamto. Similarly, at Nylsvley, the batracophages account for 20,69% of all species, but only 20,98% in numbers captured.

The number and biomass of amphibians are greater than those of lizards, and show a range in size from the tiny caco to the large bullfrog, yet there are only a few amphibian predators at Nylsvley. Moreover, amphibians are basically available during the season of the year when the snakes are also highly active. Lack of predators may be due to the fact that the amphibians are largely dependent on rainfall to become active, and therefore avoid the crucial time of the year when the snakes emerge from hibernation. However, this does not explain the same phenomenon at Lamto where the snakes and amphibians are active all year round.

There are very few mammophages in the Study Area, which is a reflection of the low density of rodents and other small mammals here. On the Reserve, there are six mammal eaters (20,69%), which contribute only 12,47% in number of all snake species. They feed mostly on mammals, particularly when adult

(Table 14).A seventh species, Boaedon f. fuliginosus, feeds almost exclusively on lizards when young, but inclines more towards small mammals when it matures. Only the two cobra species, Naja mossambica and Naja h. annulifera are occasionally seen in the Study Area, while the other species could be considered rare.

Table 14. Feeding records of snakes on the Nylsvley Nature Reserve and environs.

Snake	
Lycophidion capense	Ichnotropis capensis (1)
Mehelya nyassae	Ichnotropis capensis (1)
Philothamnus semivariegatus	Phrynobatrachus natalensis (1)
Crotaphopeltis hotamboeia	Kassina senegalensis (3)
Crotaphopeltis hotamboeia	Bufo garmani (juv.) (1)
Psammophylax tritaeniatus	Tomopterna cryptotis (1)
Psammophylax tritaeniatus	Ptychadena anchietae (1)
Psammophis sibilans brevirostris	Mabuya s. punctatissimus (1)
Psammophis sibilans brevirostris	Dendromus melanotis (1)
Thelotornis capensis	Breviceps adspersus (1)
Thelotornis capensis	Streptopelia semitorquata eggs (2)
Thelotornis capensis	Ichnotropis capensis (1)
Thelotornis capensis	Lygodactylus capensis (1)
Thelotornis capensis	Panaspis wahlbergi (1)
Thelotornis capensis	Lizard (unid.) (2)
Naja haje annulifera	Bitis arietans (1)
Naja haje annulifera	Ploceus sp. (1)
Naja haje annulifera (juv.)	Bufo gutturalis (1)
Naje haje annulifera	Turnix sp (1)
Naja mossambica (juv.)	Kassina senegalensis (1)
Naja mossambica (ad.)	Muridae (1)
Dendroaspis p. polylepis	Muridae (1)
Bitis arietans	Otomys angoniensis (2)
Atractaspis b. bibronii	Leptotyphlops distantii (2)

( ) number of records

Snakes such as the puff adder (Bitis arietans), are important rodent feeders and live along the ecotone between woodland and grassland, where cover and food such as Praomys natalensis, Otomys angoniensis and Rhabdomys pumilio are available, but within the Study Area, the puff adder is rare, The Mozambique spitting cobra tends to live close to rocky outcrops, again possibly because Aethomys namaquensis as well as shelter are readily available. Similarly, Naja haje annulifera tends to prefer the more densely vegetated savanna towards the western end of Paddock 1, as opposed to the more open eastern part of the Study Area. For instance, the Egyptian cobra was trapped on 17 occasions in 12 out of 21 traps (61,90%), as opposed to 10 times in nine out of 28 traps (32,14%). The more heavily grassed area being more suitable to rodents such as were mentioned previously and which very rarely enter the Study Area. The Egyptian cobra is, however, relatively euryphagous, feeding on mammals, snakes and toads, as well as birds which makes the abovementioned anomaly even more significant. On account of the fact that no snakes were sacrificed for stomach contents analysis, it was only possible to obtain a few feeding records. Snakes which were captured and showed that they had recently fed, were forced to regurgitate by palpation. Table 14 gives the feeding records of such snakes as well as those of road kills around the Nylsvley Nature Reserve.

There are two snakes which feed almost exclusively on other snakes. The one species, Mehelya capensis or Cape file snake, is a non-venomous reptile, killing its prey by biting rapidly along the length of its prey, these include poisonous as well as non-poisonous species. Atractaspis bibroni is a burrowing species not often seen above ground except during the rains. It feeds largely on blind (Typhlops spp.) and thread snakes (Leptotyphlops spp.), which appear to be abundant in certain parts of the Reserve. Together these snakes represent 1,45% by number of the species in the Study Area. These are, therefore, highly stenophagous species.

An even more stenophagous species is the common eggeater (Dasypeltis scabra), which contributes 6,74% by number of the terrestrial snakes captured (see Chapter 4). As far as can be ascertained, these reptiles feed exclusively on birds eggs. Tarboton (1980), recorded a high loss of eggs from bird nests in the Study Area. This loss, however, cannot be accounted for by the reptiles alone, of which four snake species are the main culprits (see Table 14).

The biomass of these groups are of great importance. For instance, the terrestrial batracophagous snakes have a percentage biomass of only 5,49 which is equivalent to 4,47g/ha, which in turn are sustained by a mean amphibian biomass of 355,38g/ha. Including the batracophagous vine snake (Thelotornis capensis) with a mean biomass of 56,49 g/ha, then 6,29g/ha of amphibians are available to maintain 1g/ha of batracophagous snake.

Similarly, the saurophagous snakes contribute 25,53% of the biomass of all terrestrial snakes, which is equivalent to 20,8g/ha. The mean lizard biomass which sustains this biomass of snakes is 22,49g/ha, exclusive of the arboreal Cape dwarf gecko, which contributes another 41,87g/ha, which totals 64,36g/ha. Therefore, in order to sustain 1g/ha of saurophagous snake, there are 3,09g/ha of lizard.

The mammophagous snakes represent the greatest imput of biomass and account for 65,5% or 53,37g/ha. However, prey species density was extremely low, although diversity is high. Temby (1977), was unable to establish density or biomass for the small mammals of the Study Area. During my trapping censusses for reptiles, a variety of small mammals were trapped over a period of 22 months. A mean of 2,04g/ha were recorded from this. This figure would, therefore, represent a minimum biomass figure of rodents and insectivores, with the exclusion of bats, mole rats and golden moles. Temby (loc.cit.) records that on a nearby farm a density of two squirrels (*Paraxerus cepapi*) per hectare were recorded whose biomass would be 432,0g /ha, bringing the total biomass per hectare to approximately 434,04g/ha. Therefore, a minimum small mammal biomass of 8,13g/ha would be available to sustain 1,0g/ha of mammophagous snake. Bauerle (1972), at the Pawnee site of the Grassland Biome Study, determined that for each gram of snake there were 3,8g of prey. He showed that this was equivalent to $2493,66 \times 10^3$ J day and found that the combined mammophagous snakes on the site used a minimum input of $7,08 \times 10^3$ J/day, therefore only taking in a very small proportion of the available energy. He ascribed this to behavioural and physiological adaptations. At least one snake shows a remarkable degree of energy conservation. This is the vine snake, but it would not be amiss to include the other snake species on the Reserve as being no different from that of Bauerle's study.

Lizards

The lizards of the Study Area number 16 species, some of which are rare. All except three species are diurnal. This means during the day 13 different species forage about looking for food. From capture results it can be seen that only four species combine to make up almost 96% of the numbers of lizards found in the Study Area (Figure 14). Two of these are skinks, one is a gecko, the other is a lacertid. They feed on remarkably similar food (Figure 31), but because there are size differences as well as feeding strategies, competition is largely avoided. This last feature

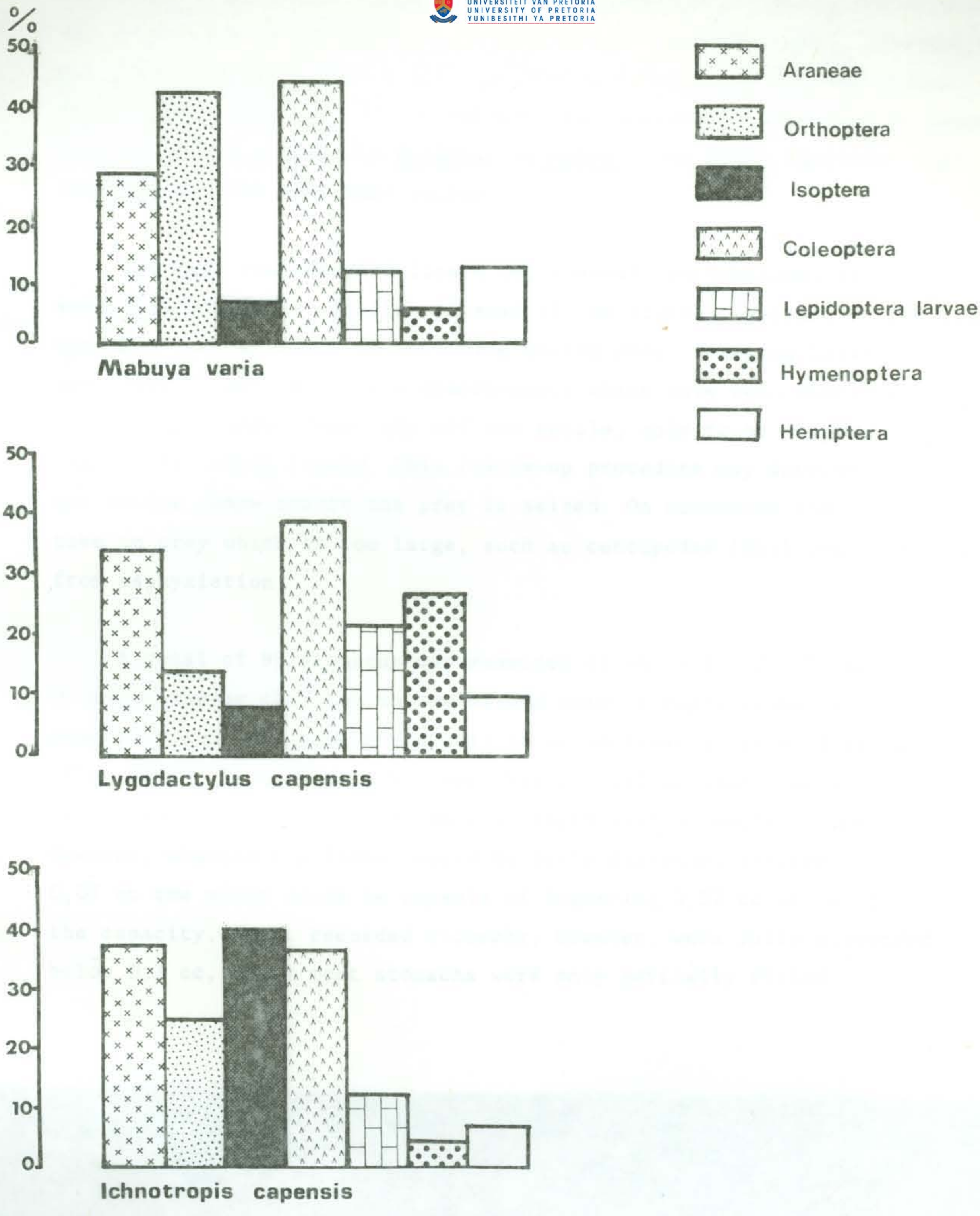

Figure 31. Comparison of main prey of three lizard species in the <u>Burkea africana</u> - <u>Eragrostis pallens</u> Study Area.

is best illustrated by the individual species themselves.

Ichnotropis capensis, the Cape rough-scaled lizard is a small animal rarely reaching 120,0 mm in total length, with a mean mass of 3,38 g when fully adult. It is an active forager, emerging at approximately 07h00 on warm mornings, and starts foraging shortly afterwards. This it does by short bursts of rapid movement followed by walking and the flicking of its tongue in likely places. This tendency is most pronounced around Grewia flavescens shrubs, under which considerable leaf litter accumulates and, therefore, provides suitable food and shelter for many insects, including termites (Isoptera - Family Termitidae). These in fact appear most frequently in the diet (Table 15). It is also seen to actively forage for these insects by scratching about the leaf litter and actually disappears under the leaves on occasion. A measure of its success is the fact that stomachs have been examined containing 90% by volume of these insects. The other main food items, such as spiders, grasshoppers and beetles are also, no doubt, frequently located in the same places (Figure 32). Broadley (1979), records one instance of predation on another lizard, namely a juvenile Panaspis wahlbergi, but is in agreement that termites are the main food source.

The Cape rough-scaled lizard is, however, euryphagous, as can be seen from Table 15. Similar to most of the diurnal lizards, it has acute eyesight when it comes to observing moving prey. Foraging lizards have been seen to actively chase grasshoppers which have been disturbed by the moving lizard. These fly off and settle, only to be snapped up by a rapidly following lizard. This follow-up procedure may involve more than one active chase before the prey is seized. On occasions the lizard may take on prey which is too large, such as centipedes (Chilopoda) and die from asphyxiation.

A total of 99 stomachs was examined of which 21 (21,2%) were empty. It would appear that the volume of and size of empty stomachs do not appear to increase proportionately to an increase in size of animal (Figure 33) as a 20 mm S/V lizard has a total minimum volume of 0,01 cc as opposed to an adult of 50 mm S/V length with an empty volume of 0,04 cc. However, whereas the former would be fully distended between 0,05 and 0,07 cc the adult would be capable of ingesting 0,52 cc or ten times the capacity. Most recorded stomachs, however, were fully distended below 0,3 cc, while most stomachs were only partially filled.

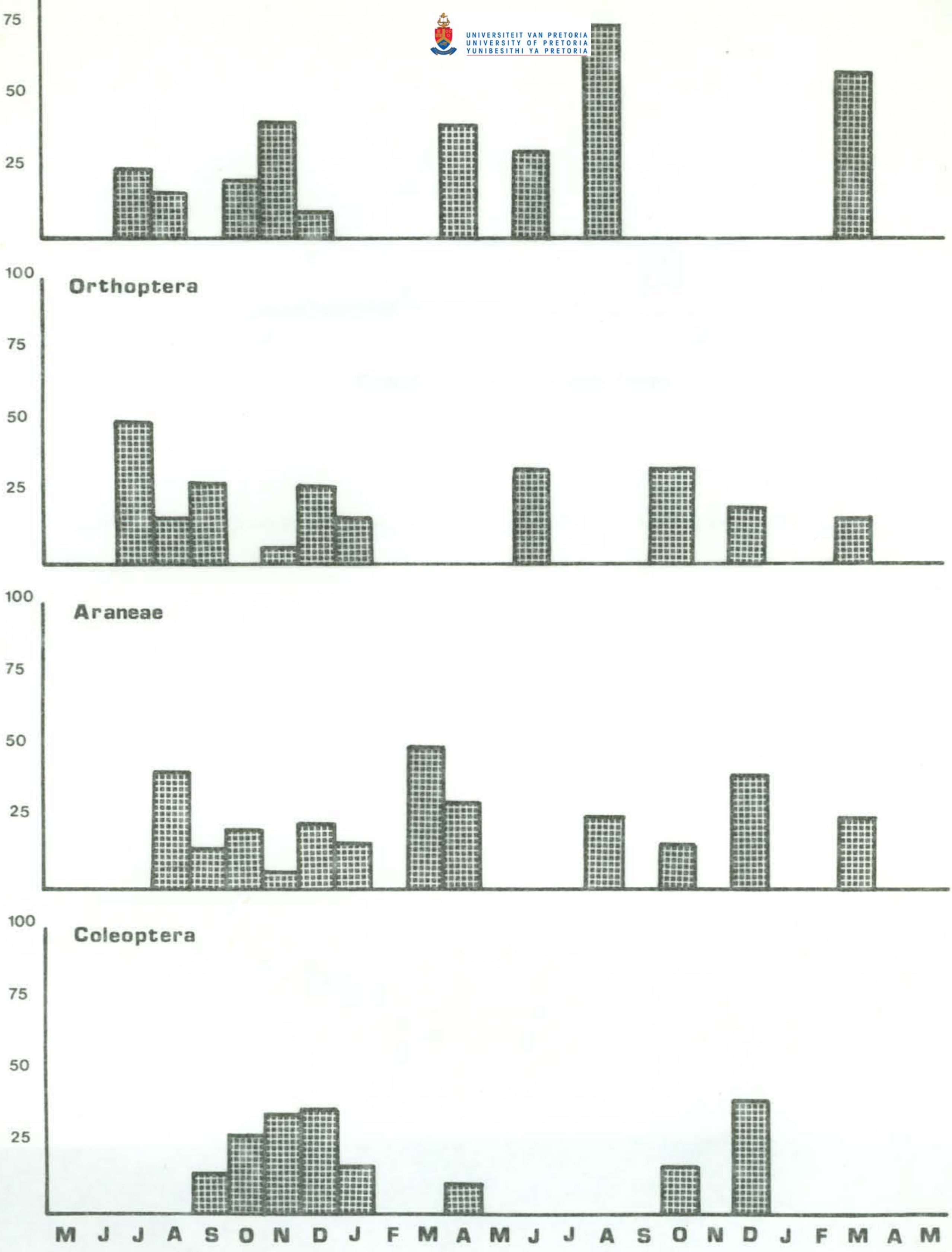

Figure 32. Monthly incidence of main prey orders in the stomachs of *Ichnotropis capensis* in the Study Area.

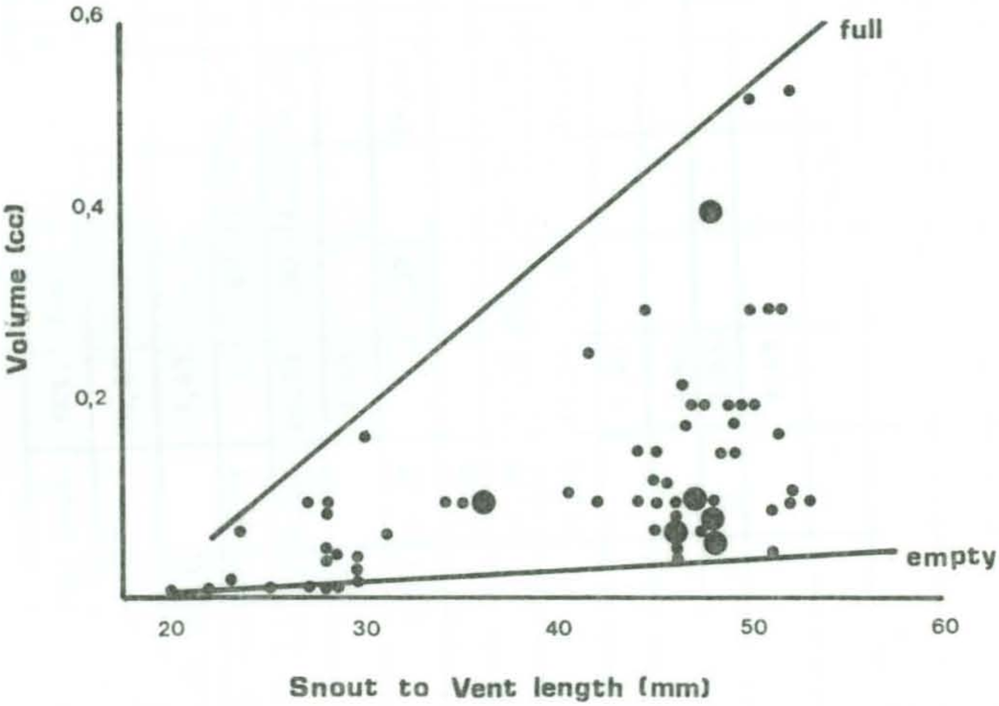

Figure 33. Stomach capacity in relation to size of Ichnotropis capensis in the Study Area.

Table 15. Monthly percentage occurrence of prey in the stomachs of _Ichnotropis capensis_ in the _Burkea africana_ - _Egrostis pallens_ Study Area : May 1975 - May 1977.

Order	M	J	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	F	Mar.	Apr.	M	June	J	Aug.	S	Oct.	N	Dec.	J	F	Mar.	A	M	Total	%
Isoptera			25,0	16,67		20,69	41,17	9,69				40,0		33,3		7,50							58,33			33	23,74
Diplopoda			2,50	8,33		3,45																				3	2,16
Orthoptera			50,0	16,67	23,57		5,88	27,27	16,67					33,33				33,33		20,0			16,67			20	14,39
Araneae				41,67	14,28	20,69	5,88	22,72	16,67		50,0	30,0				25,0		16,67		40,0			25,0			30	21,58
Chilopoda				8,33		3,45																				2	1,44
Hemiptera				8,33	14,28		5,88		16,67																	4	2,88
Neuroptera					14,28																					1	0,72
Coleoptera					14,28	27,58	35,29	26,36	16,67			10,0						16,67		40,0						28	20,14
Lepidoptera (larvae)					14,28	10,34	5,88		16,67			10,0														7	5,04
Diptera						3,45																				1	0,72
Homoptera						3,45																				1	0,72
Dictyoptera						3,45																				1	0,72
Lepidoptera (ad.)						3,45								33,33												1	0,72
Hymenoptera								4,54				10,0						33,33								4	2,88
Odonata									16,67																	1	0,72
Isoptera											50,0															1	0,72
Total			4	12	7	29	17	22	6		2	10		3		4		6		5			12			139	

From records, it was possible to group the stomachs into four categories, depending on the degree to which they contained food. Figure 34 records the percentage frequency of each of these groups according to the time of day. It can be seen that Ichnotropis capensis is a morning-and-afternoon feeder with only relatively little feeding taking place during the middle of the day. This is, no doubt, due to the high temperature at this time of day, which may have less tolerant lizards, such as the dwarf gecko, suffering severely from overheating if they come into contact with the soil at this time.

The two skinks are largely separated by size. Mabuya varia, the variable skink is, however, comparable to Ichnotropis but may become even heavier. It spends its time foraging over short distances and is often seen on and around rotting logs, rocks or the boles of trees. It uses these sites as vantage points but also forages at their bases where the leaf litter collects. It is not strictly speaking arboreal, but if chased may ascend into the branches of a tree. It surveys the area from these vantage points on the lookout for moving prey. Therefore, Isoptera only play a small part in its diet (Figure 31). Instead, it feeds more on Orthoptera and Coleoptera, which it captures following short swift dashes from its vantage point.

Although on occasions seen to cross open spaces, it normally does so by scuttling swiftly across only to rest up under the first cover it reaches. It is not a hunter but a 'percher'. Spiders and sucking bugs are also important food items but the former is less so than for Ichnotropis capensis. It is interesting to note again that only four of the 17 invertebrate groups make up approximately 69% of the food items. The species is also euryphagous, feeding on a wide variety of prey, (Table 16).

Among the stomach contents (see appendix for total list), were the tails of two Panaspis wahlbergi or snake-eyed skinks, while another captured adult with a mass of 3,1 g regurgitated the head and body of an adult male Panaspis which had very recently been ingested and weighed 0,5 g or 16% of the body mass of the predator. This indicates predation by Mabuya varia, or one lizard species on another. However, this is apparently a rare occurrence. Barbault (1975), also did not record any such instances of predation by lizards on lizards at Lamto.

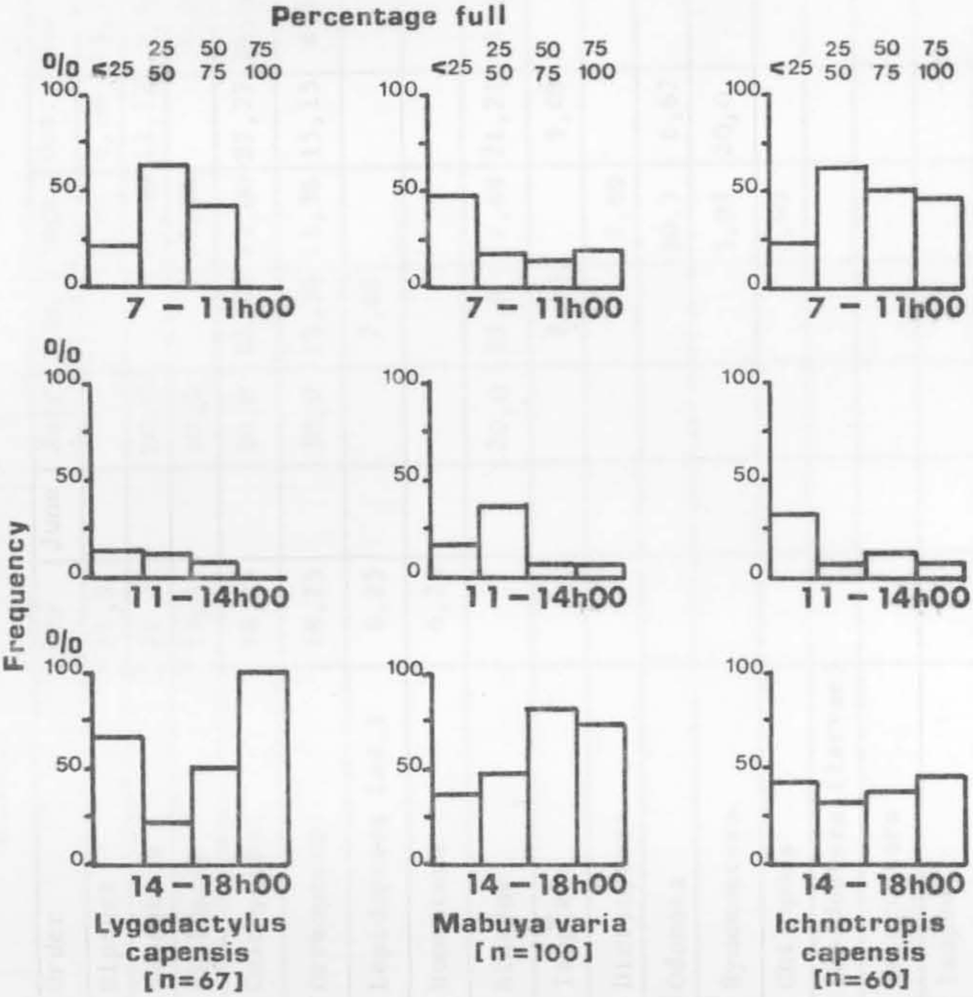

Figure 34. Feeding activity of three savanna lizards in the *Burkea africana* Study Area.

Table 16. Monthly percentage occurrence of prey in the stomachs of Mabuya varia in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977.

Order	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Diptera	12,5				7,69	6,06	13,33						
Hemiptera	25		20,0		23,00	13,12	6,67			12,5		13,3	
Diplopoda	12,5		10,0		15,38		6,67						
Coleoptera	18,75		20,0	46,15	23,00	27,27	26,67	16,67	25,0	18,75	33,33	33,33	
Orthoptera	18,75		30,0	15,38	15,38	15,15	6,67	50,0	10,0	25,0	55,55	26,67	
Lepidoptera (ad.)	6,25			7,69					5,0				
Homoptera	6,25												
Araneae			20,0	23,0	7,69	21,21	13,33	33,33	15,0	25,0		13,33	
Isoptera				7,69		9,09			5,0			6,67	
Dictyoptera					7,69				5,0				
Odonata					30,3	6,67						6,67	
Hymenoptera					3,03	20,0				6,25	11,11		
Chilopoda					3,03								
Lepidoptera (larvae)									20,0	6,25		20,00	
Heteroptera									5,0				
Isopoda									10,0	6,25			
Neuroptera													
Total	16		10	13	13	33	15	6	20	16	9	15	

Table 16 continued.

Order	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Total	%
Diptera					6,25								8	2,76
Hemiptera	18,18		6,25		6,25							14,28	25	8,6
Diplopoda													6	
Coleoptera	22,73	33,33	12,5		31,25	100,0	33,33	27,27		33,3	16,67		68	23,4
Orthoptera	13,63	16,67	37,5		25,0		16,67	45,45	40,0	46,67		28,57	69	23,79
Lepidoptera (ad.)	4,54				6,25				6,67				6	2,07
Homoptera	4,54	16,67							6,67	13,33			6	2,07
Araneae		16,67	31,25		12,5			9,09	26,67		50,0	28,57	45	15,52
Isoptera	9,08		6,25				16,67	9,09			16,67	14,28	13	4,48
Dictyoptera	4,54	16,67	6,25		12,5			9,09	13,33			14,28	11	3,79
Odonata									6,67				4	1,38
Hymenoptera	4,54						16,67				16,67		9	3,10
Chilopoda													1	0,34
Lepidoptera (lar.)	13,63				6,25		16,67			6,62			14	4,83
Heteroptera													1	0,34
Isopoda													3	1,03
Neuroptera	4,54												1	0,34
Total	22	6	16		16	1	6	11	15	15	6	7	290	

A total of 184 stomachs was volumetrically assessed, of which 30 (16,3%) were empty or virtually so. Again, when volume is plotted against S/V length, a similar graph (Figure 35) to that of Ichnotropis capensis is obtained. There is only a gradual increase in size and volume of the stomach of Mabuya varia with a 30,0 mm S/v length animal having a total empty volume of 0,01 ml as opposed to a 53,0 mm animal having a volume and size of 0,05 ml. However, when fully distended, a volume of 0,1 ml for the former is possible while the latter may reach 0,4 ml or even greater, an increase of 8 to 10 fold As in Ichnotropis capensis, the stomachs were subjectively assessed in the four categories depending on their contents (Figure 34). It is apparent that Mabuya varia feeds mostly during the afternoon. Mabuya varia appears to be comparable to Mabuya perotetti of the Ivory Coast, in its feeding and prey selection although M. perotteti is a larger species.

It is also apparent (Figure 36) that the monthly incidence of the main prey of Mabuya varia varies considerably. Prey most consistently eaten appear to be the beetles (Coleoptera), while the incidence of grasshoppers (Orthoptera) fluctuates considerably from month to month, with peaks of feeding coinciding with the rainy season when this group is most abundant. The Hemiptera (Sucking bugs) curiously, are eaten mostly during autumn and winter and, rarely during summer. The spiders (Araneae), are irregularly consumed probably only when found, and are not actively sought after to the same extent that beetles appear to be.

Panaspis wahlbergi is the other main skink species in the Study Area, a small lizard which rarely exceeds 70 mm in total length and a mass of 1,0 g. On account of its elongated body and tail and its reduced legs, it is a lizard that skulks, moving from leaf pile to leaf pile and as rapidly as possible across open ground. They therefore live in and under the leaf litter, foraging under leaves and among other vegetation debris. Although only a total of 15 stomach samples were investigated, again the prey is dominated by four orders (Table 17). Araneae (spiders) appear to be most frequently eaten, followed by Isoptera or (termites), Homoptera (plant bugs) and Hymenoptera (ants) which together account for 84,21% of the snake-eyed skink's diet. This is very similar to the diet of Panaspis nimbaensis, a larger snake-eyed skink from Lamto, which fed primarily on Isoptera and spiders, although the third most abundant food was Orthoptera, as opposed to Homoptera which in turn only formed less than 1% of the diet of P. nimbaensis. Ants (Hymenoptera) also only formed 1% of the latter species' diet, Barbault (1974a, 1976a).

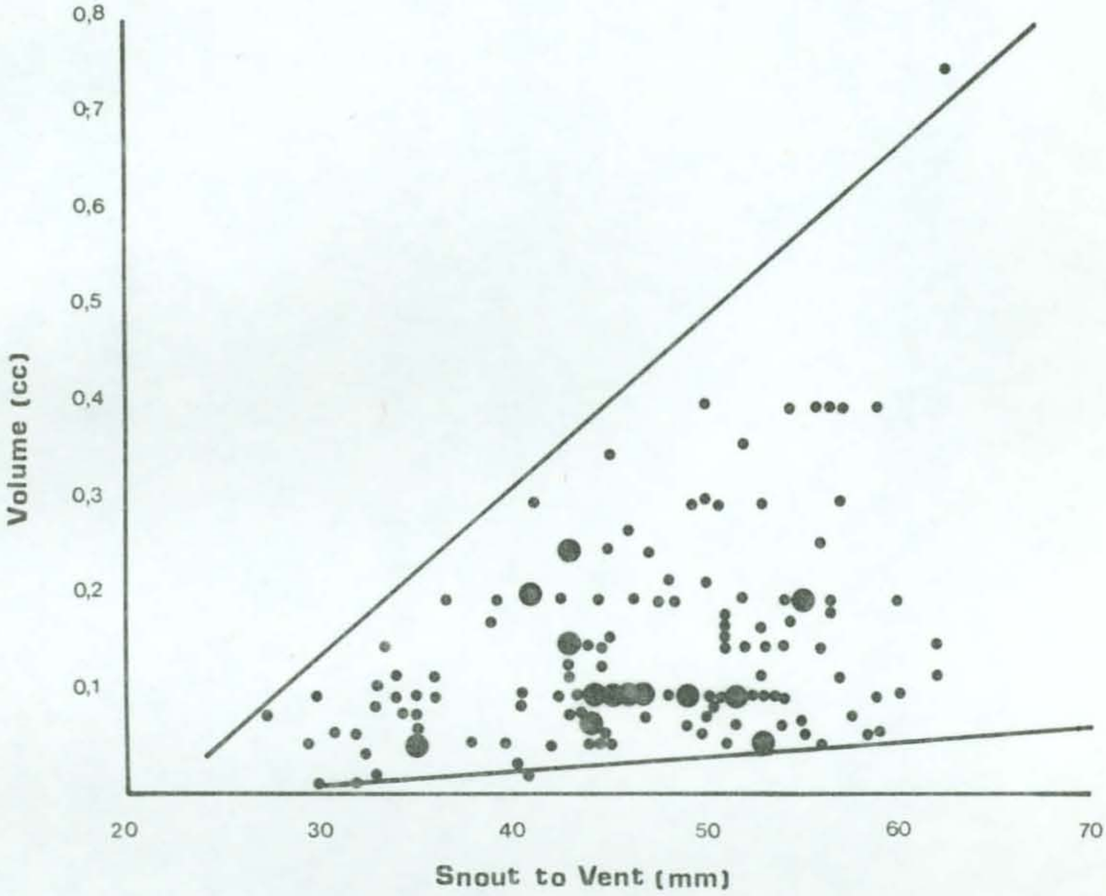

Figure 35. Stomach capacity in relation to size of Mabuya varia in the Study Area.

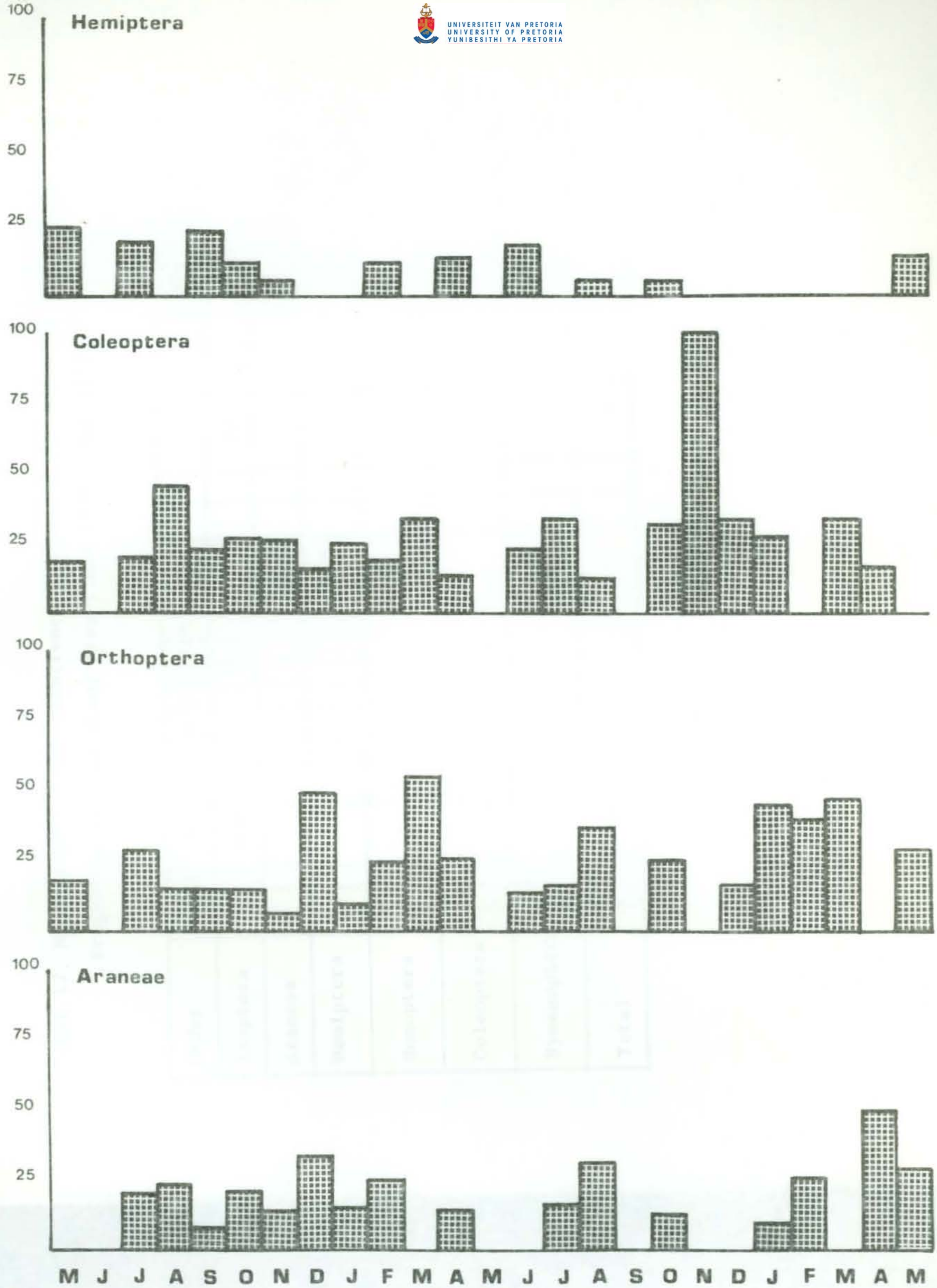

Figure 36. Monthly incidence of main prey orders in the stomachs of Mabuya varia in the Study Area.

Table 17. Monthly percentage occurrence of prey in the stomachs of Panaspis wahlbergi in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977.

Order	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	Total	%
Isoptera				100											100								60,00			5	26,32
Araneae												66,67								100		20,00	20,00		33,33	6	31,58
Hemiptera												33,33														1	5,26
Homoptera																						40,00			33,33	3	15,79
Coleoptera																						20,00				1	5,26
Hymenoptera																						20,00			33,33	2	10,52
Total				1								3			1					1		5	5		3	19	

In accordance with their mode of life, they forage mostly in leaf litter, moving over and under leaves in search of food. Such leaf piles, as mentioned previously, are mostly found around the bases of shrubs, particularly *Ochna pulchra* and *Grewia flavescens*. Food is located in these places. Open spaces are crossed rapidly, the animal frequently stopping once cover is reached. This species, therefore, does appear to compete with *Ichnotropis capensis* to a certain extent, but on account of its small size, cannot consume as much, while it is also able to go further under the leaves and therefore forages deeper to find food, as opposed to the larger rough-scaled lizard, which must actively force and dig its way to get to the soil layer where the Isoptera are to be found.

The Cape dwarf gecko (*Lygodactylus capensis*) is an arboreal species. Adults and hatchlings alike have ventrally a double row of lamellae under the tip of the tail which is very similar to that found on the extremities of the digits and which assist it in climbing. Greer (1967) indicates that it may be a tactile sensory organ which would be an added advantage in an arboreal life. These geckos are most frequently found in the Study area on *Burkea africana* trees, but also on rotting logs and stumps, as well as trees with available cover in the form of loose bark and crevices. It is a small lizard rarely exceeding 70,0 mm in total length. It is diurnal, foraging for prey, both during the morning and in the afternoon (Figure 34). It would appear that foraging is more pronounced during the afternoon as 100% of the fully distended stomachs were recorded at this time. This is in agreement with Greer (*loc. cit.*), who mentions that the period of greatest activity is in the late afternoon. Again very little feeding activity took place during the noon hours. A total of 174 stomachs were examined of which 47 (27,0%) were empty. In contrast to the other two main species, i.e. *Mabuya varia* and *Ichnotropis capensis*, the Cape dwarf gecko does not even show a slight increase in empty stomach volume with increase in size (Figure 37). However, the fully distended volume increases from three times its empty volume at 21,0 mm S/V length to 15 times and possibly even more at S/V length of 33,0 mm.

These animals forage and bask up and down the tree trunk, depending on the time of day. Most foraging is done within a metre of the ground, and the lizard is seen clinging head down, to the bole. From this position, they keep an alert watch over the ground in their vicinity. Any movement is investigated, with the animal scurrying down to snap up the prey. They have been seen to rob ant columns of their larvae and even prey.

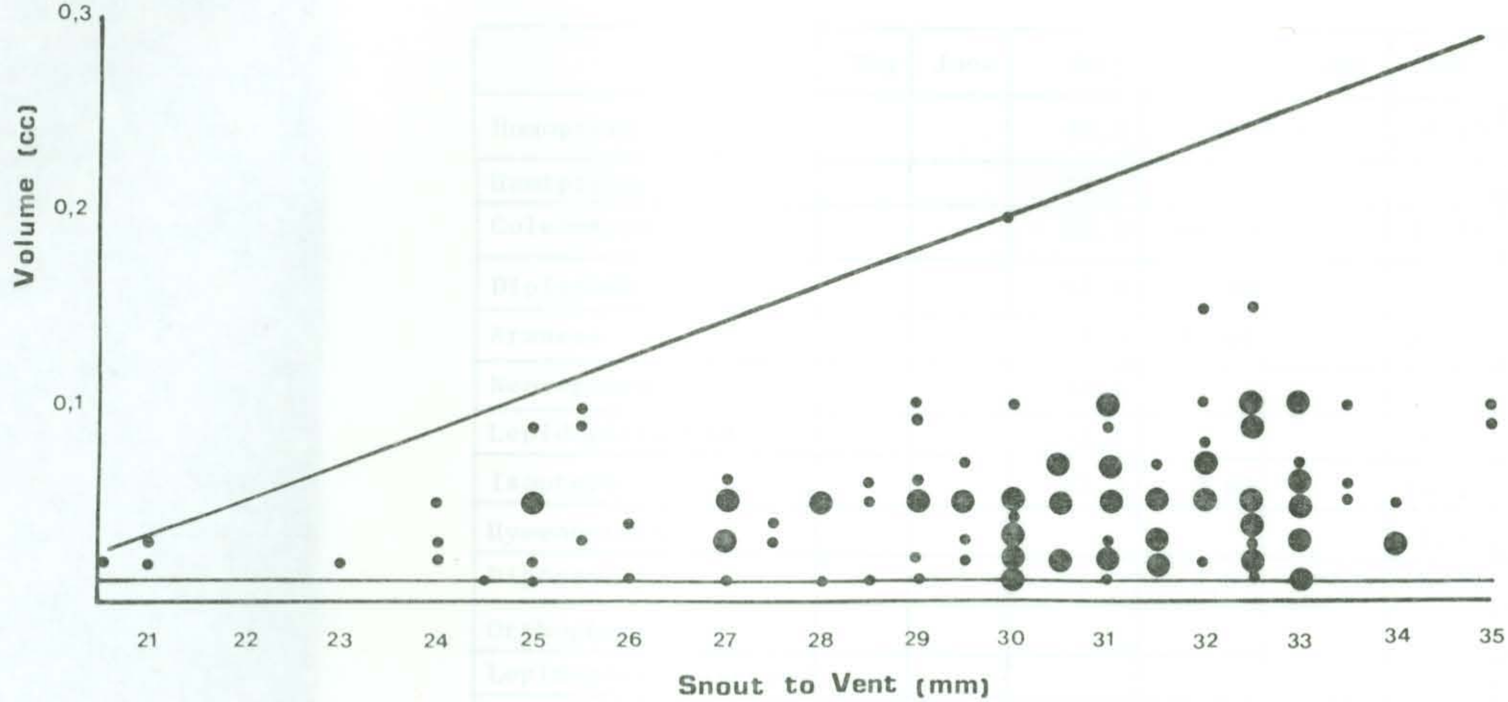

Figure 37. Stomach capacity in relation to size of _Lygodactylus capensis_ in the Study Area.

Table 18. Monthly percentage occurrence of prey in the stomachs of Lygodactylus capensis in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977.

	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Homoptera			12,5	7,69		8,33	10,34		13,33			8,33	
Hemiptera			12,5				3,45			4,09	5,26	25,0	
Coleoptera			12,5	46,15		33,33	24,14	100,0	20,0	27,27	21,05	16,67	
Diplopoda			12,5	7,69									
Araneae			12,5	23,07		25,0	13,37		13,33	27,27	26,31	8,33	
Neuroptera			12,5										
Lepidoptera (ad.)			12,5				3,45		6,67				
Isoptera			12,5	7,69		16,67	3,45		5,26				
Hymenoptera						8,33	6,9		13,33	9,09	5,26	25,0	
Diptera				7,69	100,0	8,33	10,34		6,67		5,26	8,33	
Orthoptera							6,9		6,67		5,26		
Lepidoptera (larvae)							13,79		20,0	18,18	26,31	8,33	
Mollusca							3,45						
Psocoptera										9,09			
Pseudoscorpiones													
Acarina													
Odonata													
Dictyoptera													
Total			8	13	1	12	29	1	15	11	19	12	

Table 18 continued.

Order	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Total	%
Homoptera	2,94	6,25			8,33		6,25						13	5,00
Hemiptera	11,76		7,69				12,5						15	5,77
Coleoptera	8,82	18,75	26,92		33,33		6,25	40,0	16,67			10,0	54	20,77
Diplopoda	5,83												4	1,54
Araneae	17,65	12,5	23,07		16,67		43,75		25,0			40,0	52	20,00
Neuroptera													1	0,38
Lepidoptera (ad.)	8,82												6	2,31
Isoptera	8,82	6,25			8,33		12,5	20,0	8,33	25,0			17	6,54
Hymenoptera	17,64	25,0	11,54				6,25	40,0	16,67	6,26		10,0	34	13,08
Diptera	2,94	6,25	3,34										12	4,62
Orthoptera		6,25	15,28		16,67		6,25		25,0	12,5		10,0	17	6,54
Lepidoptera (larvae)	8,62	12,5			8,33				8,33			10,0	24	9,23
Mollusca													1	0,38
Psocoptera													1	0,38
Pseudoscorpiones			11,54				6,25						4	1,54
Acarina	2,94				8,33								2	0,74
Odonata		6,25											1	0,38
Dictyoptera	2,94											10,0	2	0,76
Total	34	16	26		12		16	5	12	8		10	260	

The dwarf gecko is very versatile and therefore feeds on a wide range of food. Of the 18 groups of food items recorded in Table 18, half have an incidence of 5% or greater, which makes them considerably less specialised than the previously discussed species. Four orders combine to form in excess of 60% of their food, which corresponds well with that of the previously discussed species. These four include Coleoptera, Araneae, Hymenoptera - espesially of the family Formicidae (Crematogaster sp.) and Lepidopteran larvae. Both the latter are arboreal and the cocktail ants are commonly found in hollow branches or under the bark of dead branches. Arachnids are widespread in all habitats, particularly the Salticidae or jumping spiders, crab spiders (Argosidae) and wolf spiders (Lycosidae) (pers. obs.). It can be seen from Figure 38 how the incidence of the major prey species fluctuate, depending on availability and preference of these lizards. Abnormally high values can be due to lack of adequate samples. The Coleoptera exhibit a wave-like pattern with low values during the winter months when these insects are probably dormant. It also appears that beetles were less plentiful during the 1976/77 rainy season, as ants and spiders constituted the greater part of the diet. Similarly, Lepidopteran larvae were more plentiful during the 1975/76 rainy season.

The other terrestrial lizards were only sporadically found and few stomach samples examined. Agama atricollis was observed to feed on Hymenoptera. An adult captured in the Study Area opened its mouth in threat and six bee stings were seen inside. Obviously a variation on the normal diet of formicid ants. Nucras intertexta feeds on Coleoptera, Araneae and Orthoptera, while Nucras taeniolata ornata, although not occurring in the Study Area, had fed on Isoptera and Dictyoptera. Another Burkea africana savanna lizard, Gerrhosaurus flavigularis, feeds on Orthoptera and Arachnida. The veld monitor (Varanus exanthematicus albigularis), feeds on a variety of prey, but being relatively sluggish, consumes large numbers of Tenebrionidae (weevils), millipedes (Diplopoda), as well as the young of birds (Table 19). A juvenile had eaten a scorpion (Opisthopthalmus glabrifrons).

Table 19. Feeding records of the less numerous lizard species on the Nylsvley Nature Reserve.

Species	No. in sample	Orders
Agama atricollis	2	Hymenoptera, Coleoptera
Nucras intertexta	4	Orthoptera, Araneae , Coleoptera.
N. taemiolata ornata	1	Isoptera, Dictyoptera
Gerrhosaurus flavigularis	2	Orthoptera, Araneae
Varanus exanthematicus albigularis	5	Coleoptera, Tenebrionidae Aves, Scorpiones Diplopoda
Lygosoma sundevallii	1	Isoptera, Hymenoptera (Formicidicae)

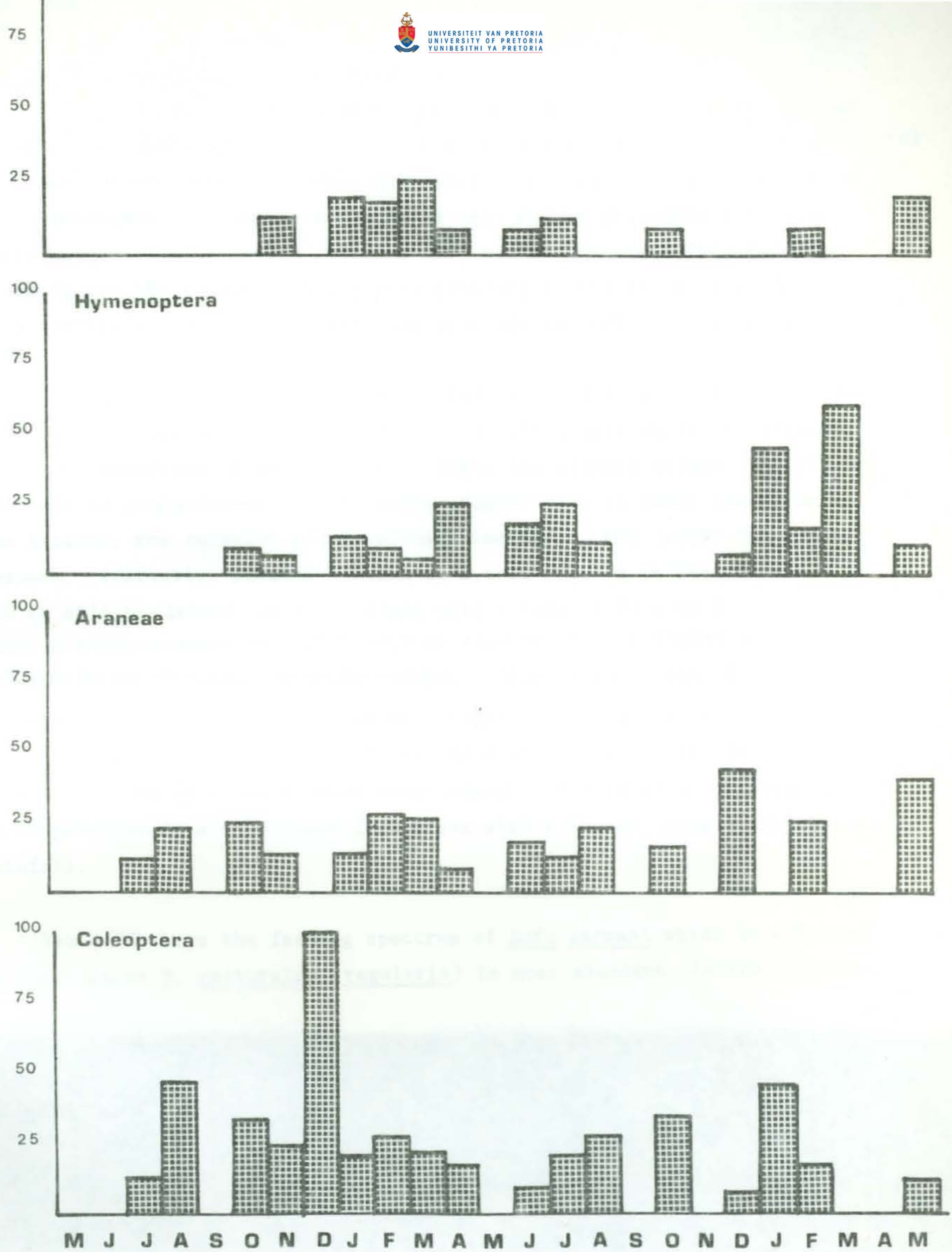

Figure 38. Monthly incidence of main prey orders in the stomachs of Lygodactylus capensis in the Study Area.

Amphibians

The eleven species of amphibian, in the Study Area are characterized by their reliance on rainfall before activity takes place. Only three species occur in large numbers in the area. Among these is the northern mottled toad, among the first to emerge from hibernation and may appear on warm nights in September (Figure 27). These and the other toads are voracious feeders, ingesting large numbers of prey animals. They forage at night, possibly finding food which they disturb, during these perambulations. If they find a particularly constant source of food, they will feed there until the supply is exhausted or until their appetites are sated. The amphibians are capable of ingesting an enormous volume. To illustrate this, a Breviceps adsperus was found to have a total volume displacement of 6,0 ml. Of this, the stomach plus contents displaced 2,5 ml and the contents alone were 2,3 cc or 38,3% of the animals mass. A 73,0 mm toad (B. garmani) with a half-full stomach, had a stomach volume of 4,0 ml.

It is, therefore, apparent that the amphibians have a far greater capacity for 'making the most' of a good thing and this is no doubt correlated with the erratic nature of their emergence from their hiding places, which is so dependent on climatic vagaries as well as the prolonged nature of their hibernation, a period covering five months or more. They feed by flicking out the tongue with the prey adhering to the sticky tip. The tongue of a Breviceps, 30,0 m in length, may protrude as much as 10,0 mm.

Stomach samples were collected sporadically. A total of 64 stomachs of Bufo garmani was examined. Of these 20 (31,25%), were empty or virtually so. In a comparison of snout-to-vent length and stomach volume, the rate of increase is proportional to the length (Figure 39). In other words, as in the lizards, the capacity of the stomach increases, the larger the animal becomes. Initially, an empty volume of a toad 40,0 cm in length is 0,2 ml but is able to distend it to 10 times this volume. A 73,0 mm S/V length toad, with an empty stomach of 0,25 to 0,5 ml will be able to ingest approx. 8,0 ml or from 16 to 32 times the empty volume. This is in excess of that of lizards which are less susceptible to climatic vagaries and can replenish their energy supplies more frequently, if need be even during winter. This is an adaptation to the seasonal climate experienced in the savanna. Unfortunately, no comparative data were found from areas with a higher, more evenly spread rainfall.

Table 20 shows the feeding spectrum of Bufo garmani which in contrast to Lamto where B. gutturalis (regularis) is most abundant, is the commonest

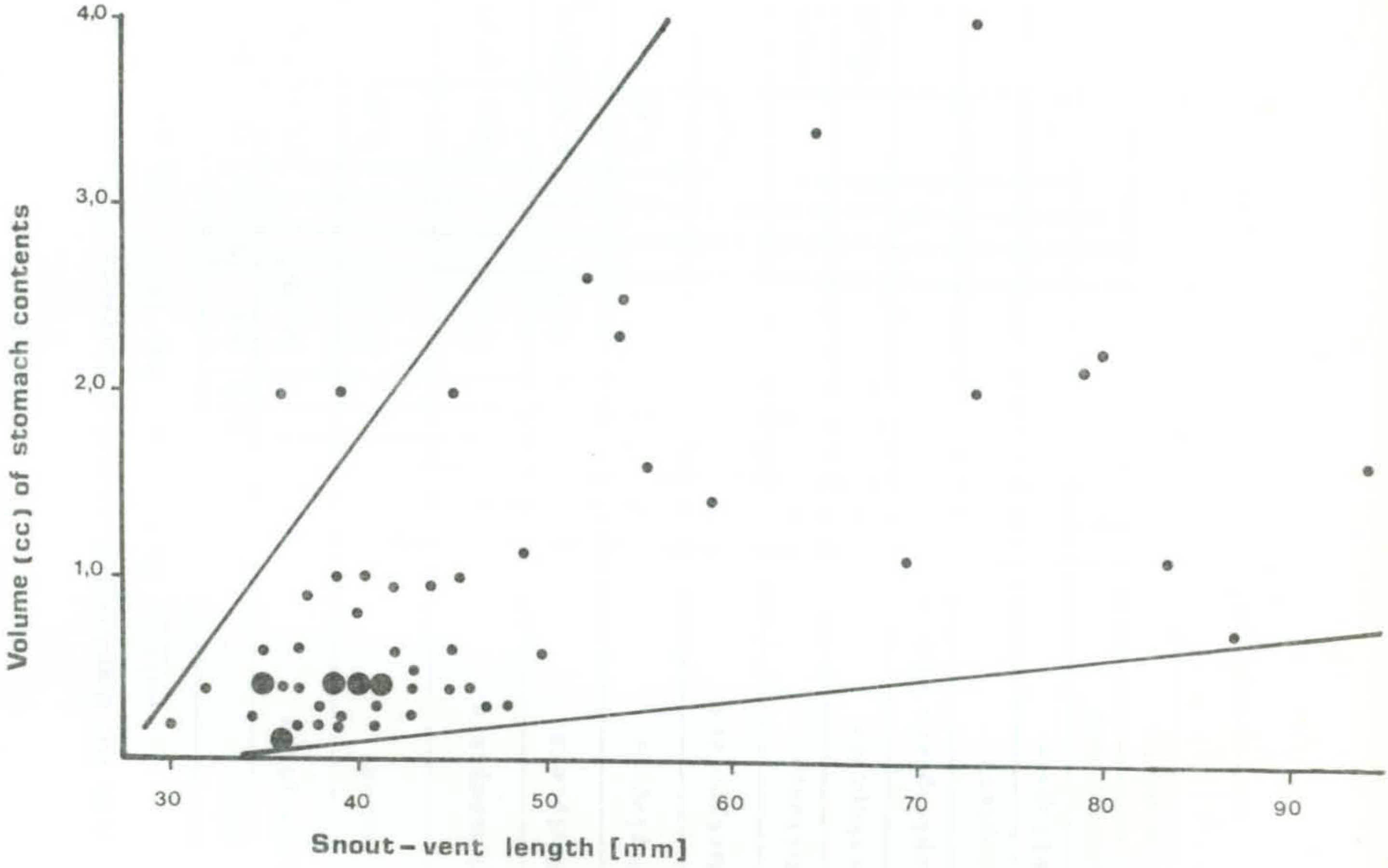

Figure 39. Stomach capacity in relation to size of *Bufo garmani* in the Study Area.

Table 20. Monthly percentage occurrence of prey in the stomachs of _Bufo garmani_ in the _Burkea africana_ - _Eragrostis pallens_ Study Area : May 1975 - May 1977.

Order	M	J	J	A	S	Oct.	N	D	J	Feb.	Mar.	A	M	J	J	A	S	Oct.	Nov.	Dec.	Jan.	Feb.	M	A	M	Total	%
Coleoptera						36,36				33,33	20,0							30,76	16,67	23,07		43,59				35	33,02
Araneae						27,27				6,67								23,07		7,69		2,56				9	8,49
Hymenoptera						27,27				40,0	20,0							7,69	16,67	23,07	25,0	41,02				32	30,19
Hemiptera						9,09				6,67	20,0							23,07	16,67	15,38		2,56				10	9,43
Diplopoda										6,67																1	0,94
Dictyoptera										6,67											25,0					2	1,88
Mollusca											20,0															1	0,94
Orthoptera											20,0							15,38	16,67	7,69	25,0	2,56				7	6,60
Lepidoptera (lar.)																			16,67	7,69						2	1,88
Isoptera																			16,67	7,69		5,12				4	3,77
Chilopoda																				7,69						1	0,94
Heteroptera																					25,0					1	0,94
Psocoptera																						2,56				1	0,93
Total						11				15	5							13	6	13	4	39				106	

toad at Nylsvley. It is also similarly euryphagous, feeding on 13 different categories of prey, but feeds more on beetles (Coleoptera) (86% of 30 stomachs) than on formicid ants (80% of 30 stomachs). The opposite occurs at Lamto. Figure 40 shows the monthly incidence of the four main groups of prey. It is apparent that although collections were somewhat intermittant they still show increases and decreases in the type of prey ingested. Although only five groups of prey are found in excess of 5% of the total prey spectrum and together form 87,73% of all prey consumed, two of these groups, mentioned previously, contribute 63,21%

In contrast to this, Kassina senegalensis shows a wider food spectrum involving also 13 groups, but of these, eight occur in 5% or more of the stomachs examined (Table 21). Together, these account for 90,18% of the prey diversity. Figure 41 compares the main prey groups eaten by the three most abundant amphibian species. It can be seen that the main prey, beetles (Coleoptera) ranks highest for both Bufo garmani and Kassina senegalensis, but the latter consumes more orthopterans, isopterans and lepidoptera larvae. Competition is likely between these two species, particularly when there is a large influx of juvenile B. garmani during January at the same time as when the kassinas are also at their most abundant (Figures 27 & 29). The juvenile toads then are equal in size to those of the adult Kassinas. It would appear, however, that the toads have a greater stomach capacity than do the Kassinas, and as mentioned previously, are able to move about when the climate may be adverse to the Kassinas. The graph of snout-to-vent length plotted against stomach volume for Kassina senegalensis indicates a shallow J-shaped curve with stomach capacity increasing rapidly with increase in S/V length (Figure 42). For a frog with 38,0 mm S/V length, an empty stomach volume of approximately 0,04 ml is apparent. The fully distended stomach has a capacity 20 times or more of that of the empty volume which indicates how important feeding is to these animals and that they make the most of these feeding opportunities.

Figure 43 records the monthly incidence of the main prey species. Again, increases in some groups, respond by a decrease in the other groups. These amphibians are opportunistic, taking what is most abundant at the time. A total of 96 stomachs was investigated, of which 43 (44,79%) were empty, as the frogs had not fed prior to capture.

The third most abundant amphibian was Breviceps a. adspersus or the common short-headed frog. A total of 39 stomachs was analysed.

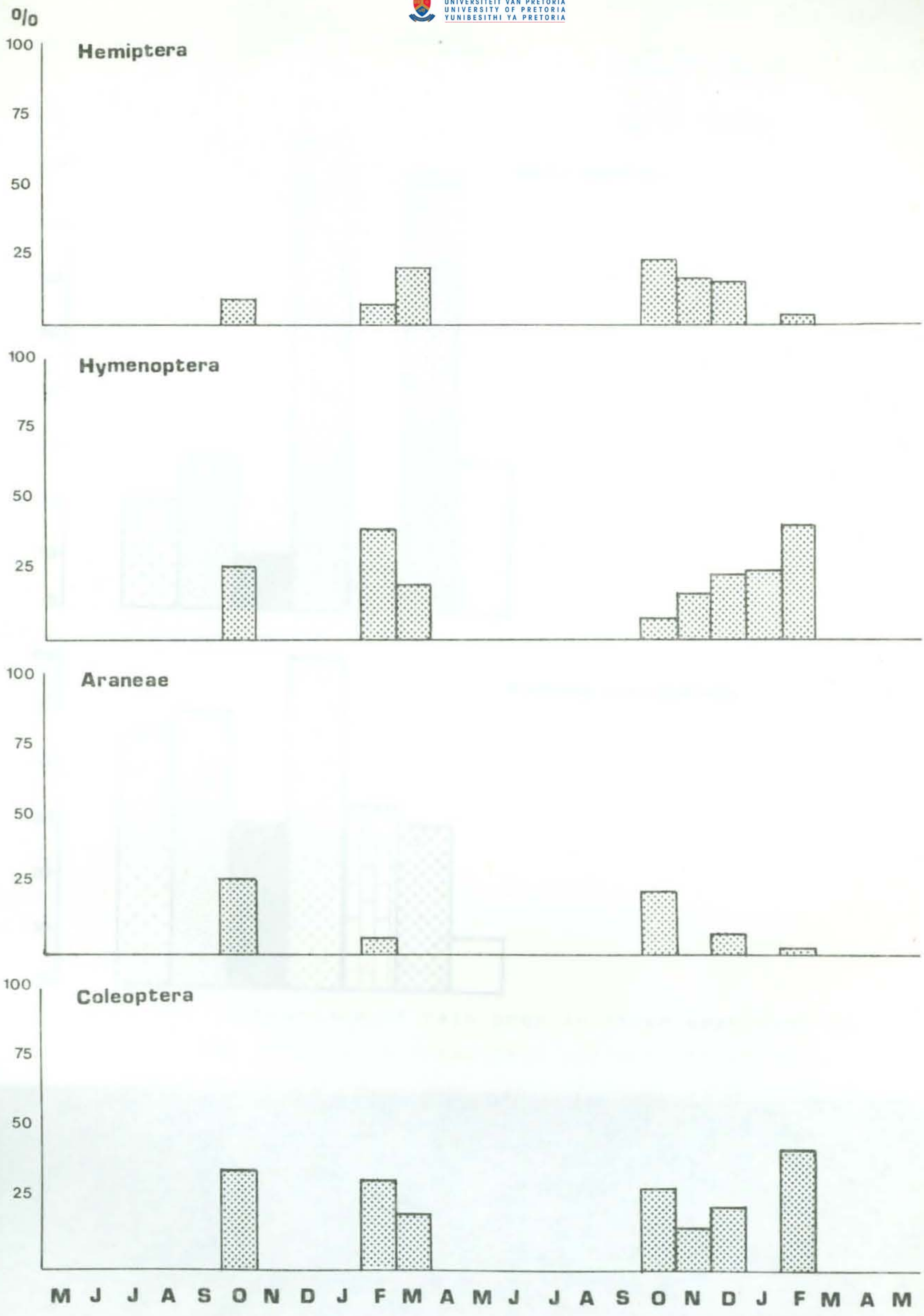

Figure 40. Monthly incidence of main prey orders in the stomachs of Bufo garmani in the Study Area.

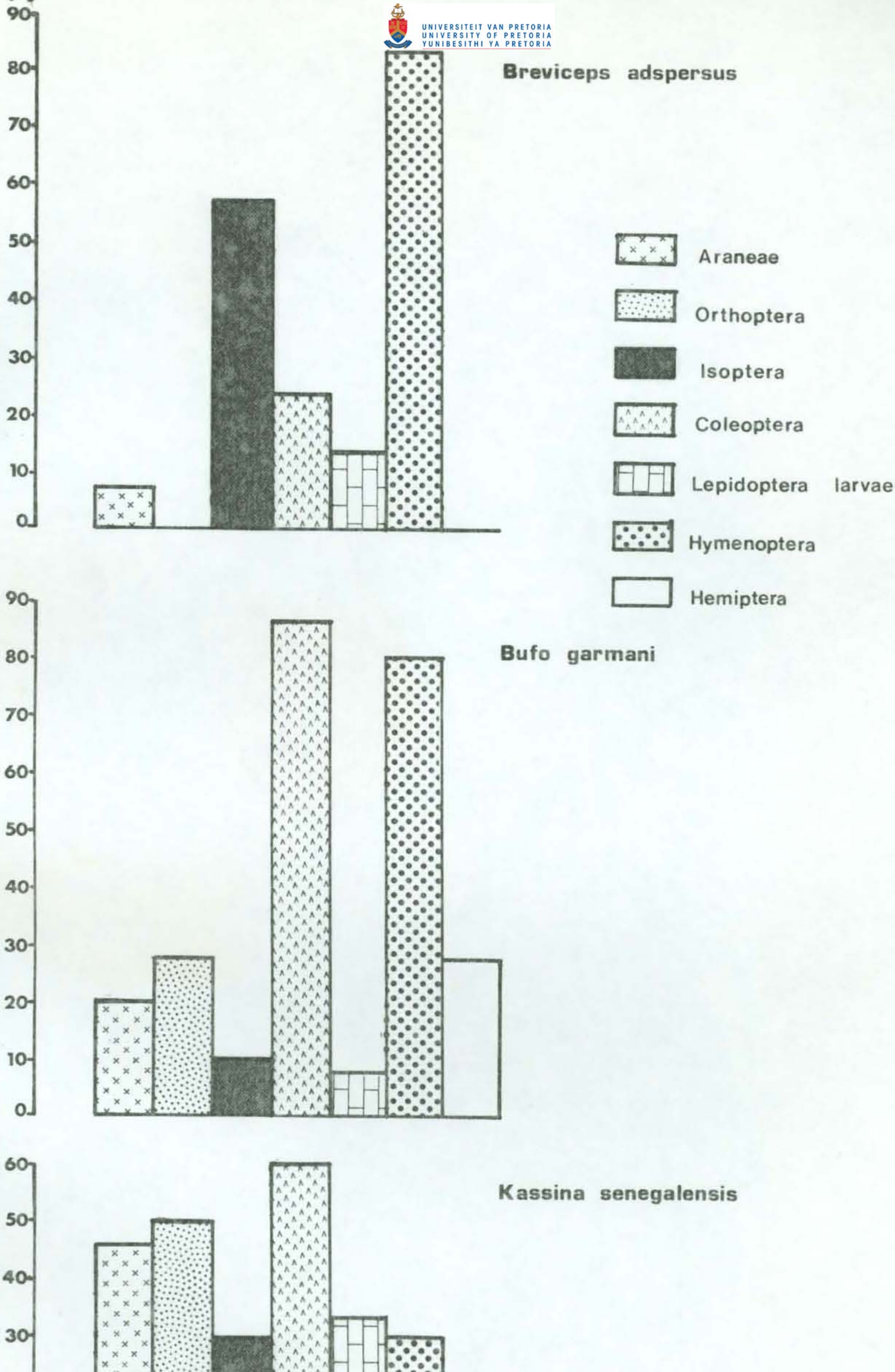

Figure 41. Comparison of main prey in three amphibian species in the Burkea africana - Eragrostis pallens Study Area.

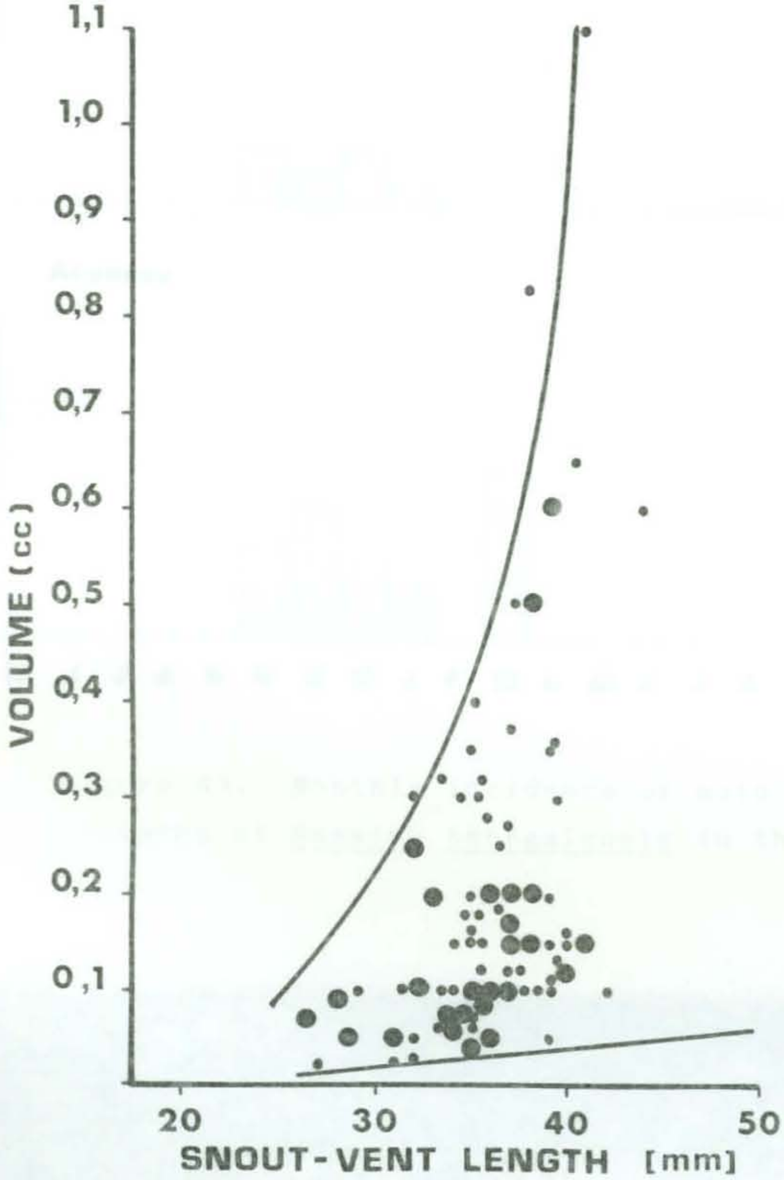

Figure 42. Stomach capacity in relation to size of Kassina senegalensis in the Study Area.

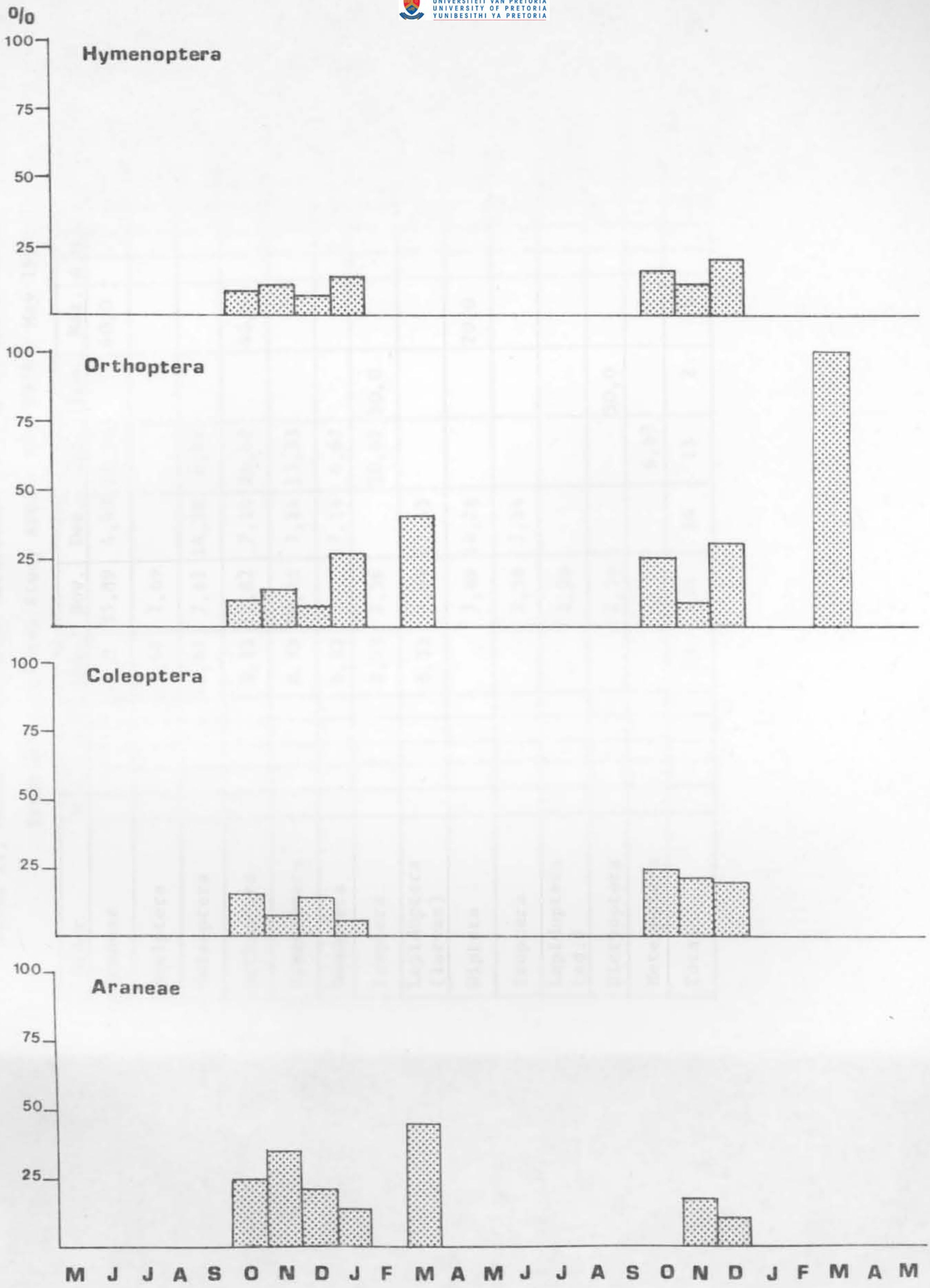

Figure 43. Monthly incidence of main prey orders in the stomachs of Kassina senegalensis in the Study Area.

Table 21. Monthly percentage occurrence of prey in the stomachs of Kassina senegalensis in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977.

Order	M	J	J	A	S	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	A	M	J	J	A	S	Oct.	Nov.	Dec.	Jan.	F	Mar.	A	M	Total	%
Araneae						25,0	35,89	4,43	13,33		40,0								17,3	10,0						34	20,86
Hemiptera						16,67	7,69											8,33	5,77							9	5,52
Coleoptera						16,67	7,69	14,28	6,67									25,0	21,15	20,0						24	14,72
Orthoptera						8,33	12,82	7,14	26,67		40,0							25,0	9,61	30,0			100,0			25	15,34
Hymenoptera						8,33	10,25	7,14	13,33									16,67	11,54	20,0						18	11,04
Homoptera						8,33		7,14	6,67										3,84							5	3,07
Isoptera						8,33	2,56		26,67	50,0								8,33	3,84	10,0						11	6,75
Lepidoptera (larvae)						8,33	7,69	21,43											15,38							15	9,20
Diptera							7,69	14,28			20,0							8,33	5,77	10,0						11	6,75
Isoptera							2,56	7,14										8,33	1,92		10,0					5	3,07
Lepidoptera (ad.)							2,56																			1	0,61
Dictyoptera							2,56			50,0									3,84							4	2,45
Heteroptera									6,67																	1	0,61
Total						12	39	14	15	2	5							12	52	10	1		1			163	

The main prey groups are compared in Figure 41. It is apparent that this frog is a specialised feeder, consuming mostly formicid ants as well as termites. It will be seen that a considerable degree of overlap occurs between Bufo garmani and Breviceps adspersus, but as the toads are larger, they consume larger ant species, whereas Breviceps tend to feed on medium to small species. There would be considerable competition between juvenile toads and the short-headed frog were it not for the fact that they peak in abundance at different times, thereby largely avoiding such a competitive situation. It is also not recorded that B. garmani juveniles feed on small ants, such as Crematogaster spp. and Pheidole spp. which are eaten in large quantities by Breviceps adspersus. Table 22 shows the range of prey groups which number eight. Even Pseudoscorpions are fed on.

Mention has been made of the feeding capacity of this frog. From the available data, a J-shaped graph is seen in Figure 44. The empty stomach volume of the 35,0 mm snout-to-vent length frog was 0,20 ml after the contents were removed. Together with the contents, a fully distended stomach volume of 2,5 ml was measured or 12,5 times the empty volume. Large numbers of termites and ants are therefore consumed.

Although these frogs are usually considered as ant and termite feeders, they also include a variety of other insects in their diet. Poynton & Pritchard (1976) examined 96 specimens in the Durban and Natal Museums and found that their stomach contents composition could be subdivided as follows:

48% alate termites (Isoptera)

27% worker ants (Hymenoptera)

19% worker and soldier termites (Isoptera)

Unfortunately, the authors do not mention the occurance of any other invertebrate orders. Van Dijk (1971) recorded Isoptera (Family : Termitidae) as being the most favoured in other Provinces, but at Nylsvley, Coleoptera are a favoured item. These animals forage by running in short bursts across the ground. If prey is located they will feed for as long as the food lasts or until replete. This and the remarkable capacity of the stomach to distend accounts for the fact that the stomach contents may account for one-third of the total mass of the animal.

The stomach contents of the other amphibians can be seen in Table 23. Relatively few gatherings for these species were possible.

Table 22. Monthly percentage occurrence of prey in the stomachs of _Breviceps adspersus_ in the _Burkea africana - Eragrostis pallens_ Study Area : May 1975 - May 1977.

Order	M	J	J	A	S	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	M	J	J	A	S	O	Nov.	Dec.	Jan.	F	Mar.	Apr.	M	Total	%
Hymenoptera						45,45	33,33	50,00	50,00		100,0	50,00							53,33	50,00	100,0		50,00			33	46,48
Isoptera						27,27	13,33	33,33	50,00	100,0		50,00							20,00	25,00			50,00	100,0		20	28,17
Acarina						9,09																				1	1,41
Coleoptera						9,09	20,00	8,33											13,33	25,00						8	11,27
Araneae						9,09	6,67												6,67							3	4,23
Lepidoptera (larvae)							13,33	8,33											6,67							4	5,63
Pseudoscorpiones							6,67																			1	1,41
Dermaptera							6,67																			1	1,41
Total						11	15	12	2	1	1	2							15	4	1		6	1			

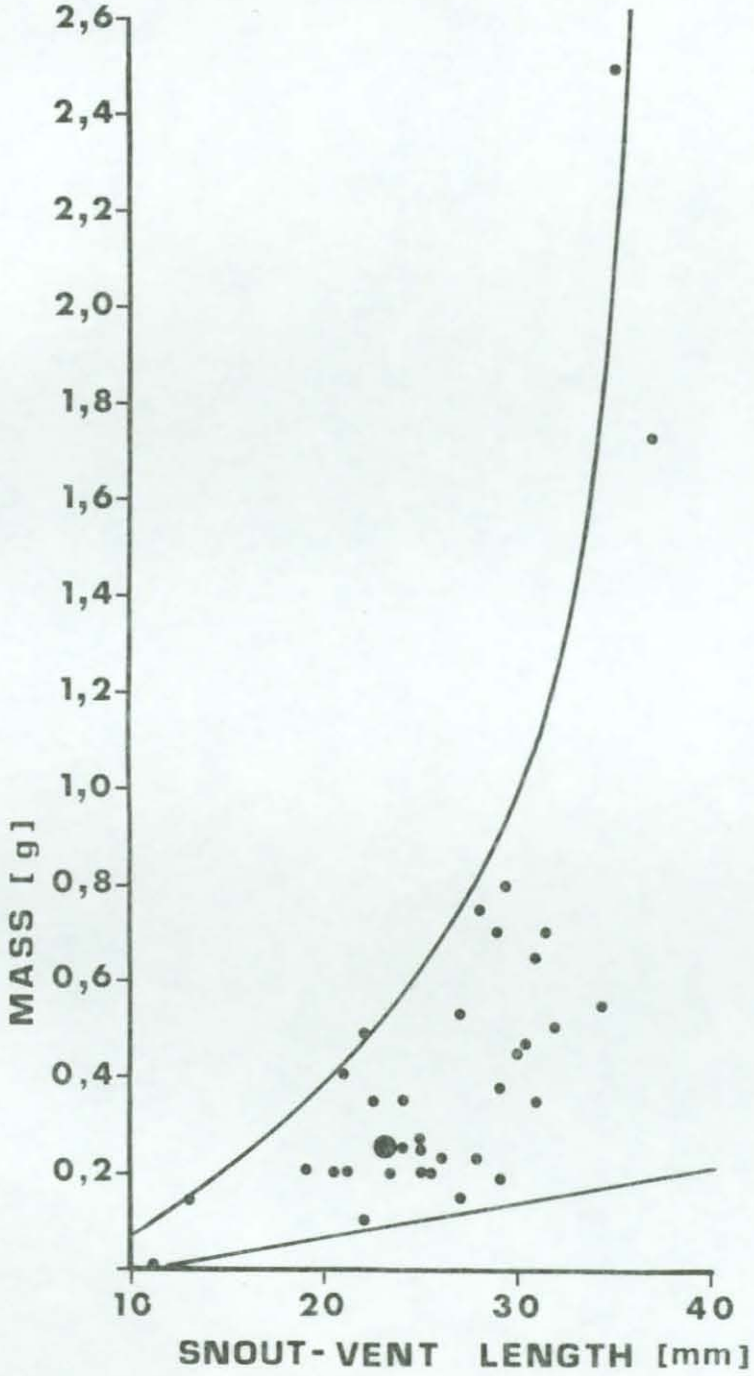

Figure 44. Stomach capacity in relation to size of *Breviceps adspersus* in the Study Area.

Table 23. Food of less numerous amphibians in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977.

Species	No. of stomachs	Orders
Phrynomerus bifasciatus	10	Hymenoptera (9), Isoptera (2) Araneae (1)
Tomopterna cryptotis	5	Coleoptera (4), Isoptera (2) Aranaea (2), Orthoptera (1)
Bufo carens	1	Hemiptera (1), Coleoptera (1) Hymenoptera (1)
Bufo gutturalis	2	Isoptera (1), Hymenoptera (1), Hemiptera (1), Coleoptera (1).
Phrynobatrachus natalensis	5	Hymenoptera (2), Isoptera (1), Araneae (1), Orthoptera (1).
Cacosternum boettgeri	6	Hymenoptera (5), Isoptera (2).

Barbault (1974) made specific mention of two amphibians at Lamto which he considered very specialised feeders. These were Phrynomerus microps, an arboreal strictly myrmecophagous frog and Hemisus marmoratus, which fed on ants and termites. At Nylsvley it was possible to examine 10 stomachs of Phrynomerus bifasciatus of which two were empty or virtually so. A full stomach capacity of 1,4 ml was recorded for one frog, 47,5 mm S/V length. The main prey of the above species was formicid ants but Isoptera (termites) were also included as well as an arachnid (spider). Hemisus marmoratum unfortunately does not occur at Nylsvley, although widespread in the Low-veld. What does appear to emerge as another specialist is the tiny Cacosternum boettgeri, of which six stomachs were examined, all of which contained mostly Hymenoptera and Isoptera. Barbault (1974b) came to the conclusion that at Lamto, apart from the specialised ant feeders, such as Phrynomerus microps and Hemisus marmoratus, the various amphibians of the savannas of Lamto were not very food-specific and the principal prey were made up of what is abundant in the ecosystem, such as ants, spiders, orthoptera and coleoptera. This is also the case in the savanna of the Nylsvley ecosystem. While the two first named, as well as the last, are to a large extent nocturnal and may be encountered by the amphibians while moving about, it is intriguing to speculate how they find orthopterans (Family Acrididae or grasshoppers) at night, as these are diurnal as opposed to crickets (Gryllidae), which are nocturnal, but featured rarely in the diet (see appendix).

Barbault (*loc.cit*) goes further and mentions that due to the fact of differences in their size, their habitat, their rhythm of activity and their methods of predation, the species of amphibians avoid feeding on the same prey species. This is in agreement with what has been discussed previously and which is borne out by a more detailed list of prey as far as it was possible to identify (see list of prey in the Appendix).

Table 24 lists the orders of invertebrates fed on by the nine amphibian species for which stomachs were analysed. It is apparent that the Hymenoptera (with one exception), and especially the Isoptera are fed on by all the amphibians.

Table 24. Invertebrate orders and their anuran predators in the *Burkea africana* - *Eragrostis pallens* Study Area : May 1975 - May 1977.

	Araneae	Hemiptera	Coleoptera	Orthoptera	Hymenoptera	Homoptera	Isoptera	Lepidoptera(lar.)	Lepidoptera (ad.)	Diptera	Isoptera	Dictyoptera	Heteroptera	Diplopoda	Mollusca	Chilopoda	Psocoptera	Acarina	Pseudoscorpiones	Dermaptera
Kassina senegalensis	X	X	X	X	X	X	X	X	X	X	X	X	X							
Bufo garmani	X	X	X	X	X		X	X				X	X	X	X	X	X			
Breviceps adspersus	X		X		X		X	X										X	X	X
Phrynomerus bifasciatus	X		X		X		X													
Tomopterna cryptotis	X		X	X			X													
Bufo carens		X	X		X															
Bufo gutturalis		X	X		X		X													
Phrynobatrachus natalensis	X			X	X		X													
Cacosternum boettgeri					X		X													

Differences in the size of formicid ant species have already been mentioned. *Bufo garmani* feeds on the larger *Camponotus* spp. while *Breviceps adspersus* feeds on the smaller species, although also on occasions feeding on *Camponotus* spp. as well (Appendix B). Unfortunately, many food items could not be identified to higher levels. There are, therefore, gaps in our knowledge, However, it is, for instance, unreasonable to assume that *Cacosternum boettgeri* would feed on *Camponotus* spp. as these are too large for this tiny frog. It therefore no doubt fed more on *Pheidole* and possibly other species which are difficult to distinguish. *Kassina senegalensis* also competes with *Breviceps*, *Bufo garmani*, *Phrynomerus bifasciatus* and probably *Bufo gutturalis* for the larger *Camponotus* spp. While most of these species feed on the smaller ants, only *Breviceps adspersus* includes a significant proportion in its diet. It is obvious that this amphibian is a specialised myrmecophagous feeder. *Kassina senegalensis* and *Bufo garmani* also compete for beetles (Coleoptera) but they are more frequently fed on by the latter. *Kassina senegalensis* feeds on a greater range of beetle families, but *Bufo garmani* consumed more curculionid beetles (weevils) which are rarely fed on by the other species.

Kassina senegalensis is the most euryphagous amphibian species in the Study Area, but shows a considerable predilection to spiders (Araneae) which do not feature very highly in the diet of any of the other species.

Apart from competition between the main species, other amphibians occur in such low densities that their contribution is negligible. Barbault (1974b) concludes that amphibian populations are governed by two factors. On the one hand, the availability of food is important to some species, particularly the specialists, but the most important factor is the variable rainfall regime which causes population fluctuations. This situation is also applicable to the Nylsvley savanna. Shortage of food certainly does not appear to be a problem, but the timing of rainfall has a very important bearing on the reproductive capabilities of most of the resident amphibians, especially as they must move out of the Study Area to find permanent water in which to breed.