CHAPTER 4

ECOLOGY

RESULTS

Population size, composition and biomass of Reptiles and Amphibians in the Ecosystem Study Area

As mentioned previously, there are 18 amphibian, 3 tortoise, 1 terrapin, 23 lizard, 1 amphisbeanian and 29 snake species recorded as occurring on the Nylsvley Nature Reserve. This spectrum is similar to that occurring in the savanna at Lamto on the Ivory Coast, where a total of 64 species, made up of 24 amphibians, 8 lizards, 3 tortoises and 29 snakes are found, Barbault (1975). The larger number of amphibian species in the latter, results from the high rainfall of that area. Noteworthy is the paucity of lizard species at Lamto, but this deficiency is compensated for by a larger number of lizards at Lamto than at Nylsvley. It is apparent that lizard species diversity increases the more arid an area becomes. This is especially pronounced in the deserts of Australia where as many as 40 species coexist, Pianka (1969).

In the study area a total of 11 amphibian and 41 reptile species were recorded as resident. Several species such as Rana fasciata and Pyxicephalus a. adspersus were only rarely encountered in the Burkea africana - Eragrostis pallens savanna and then only at the height of the rainy season. They were, therefore, only transient, as they are species typical of the low-lying areas along drainage lines and the Nyl river. Table 2 shows the taxonomic composition of the reptiles and amphibians in the study area. Some lizards such as the common flap-necked chameleon (Chamaeleo d.dilepis), the three-lined skink (Mabuya capensis), Mozambique rough-scaled sand lizard (Ichnotropis squamulosa), and the green water snake (Philothamnus hoplogaster), are also very rare in the study area and most are only visitors to the Burkea africana - Eragrostis pallens savanna. In fact, the three-lined skink was only captured in a trap after two years, indicating an extremely low density. In all animal communities there are high density and low density species. The former are most common as they can tolerate crowded conditions and in fact thrive, whereas low density species are usually solitary and dispersed, only coming into contact with another of its species during the mating season. This is converse to the view normally held of tropical ecosystems. The Nylsvley Nature Reserve is composed of a variety of vegetation types described previously, and by Coetzee et al (1976).

Table 2. Taxonomy of reptiles and amphibians in the Study Area, May 1975 to May 1977.
* Rare occurrences in the Study Area.

Class	Amphibia	
Order	Anura	
Family	Bufonidae	
	Bufo gutturalis	Gutteral toad
	B. garmani	Northern mottled toad
	B. carens	Red toad
Family	Microhylidae	
	Breviceps a. adspersus	Common short-headed frog
	Phrynomerus b. bifasciatus	Red-banded frog
Family	Ranidae	
	*Pyxicephalus a. adspersus	Bull frog
	Tomopterna cryptotis	Striped sand frog
	T. natalensis	Natal sand frog
	*Rana f. fasciata	Striped stream frog
	*Ptychadena anchietae	Red-backed grass frog
	Phrynobatrachus natalensis	Common puddle-frog
	Cacosternum boettgeri	Boettger's caco
	Kassina senegalensis	Bubbling Kassina
Class	Reptilia	
Order	Chelonia	
Family	Testudinidae	
	Kinixys belliana spekei	Hinged tortoise
	Psammobates oculifer	Kalahari geometric tortoise
	Testudo (Geochelone) pardalis babcocki	Leopard tortoise
Order	Squamata	
Suborder	Sauria	
Family	Gekkonidae	
	Lygodactylus c. capensis	Cape dwarf gecko
	Pachydactylus c. capensis	Cape thick-toed gecko
	P. bibronii	Bibron's thick-toed gecko

Table (continued)

Family	Agamidae	
	Agama atricollis	Tree agama
	A. aculeata	Spiny agama
Family	Chamaeleontidae	
	Chamaeleo d. dilepis	Common flap-necked chameleon
Family	Scincidae	
	Mabuya capensis	Three-lined skink
	M. varia	Variable skink
	M. striata punctatissimus	Striped skink
	Lygosoma s. sundevallii	Sundevall's skink
	Panaspis wahlbergi	Snake-eyed skink
Family	Lacertidae	
	Nucras intertexta	Spotted sandveld lizard
	Ichnotropis squamulosa	Mozambique rough-scaled lizard
	I. capensis	Cape rough-scaled lizard
Family	Varanidae	
	Varanus exanthematicus albigularis	Veld monitor
Family	Cordylidae	
	Gerrhosaurus f. flavigularis	Yellow-throated plated lizard.
Suborder	Amphisbaenia	
Family	Amphisbaenidae	
	Monopeltis c. capensis	Cape worm-lizard
Suborder	Serpentes	
Family	Typhlopidae	
	Typhlops bibronii	Bibron's blind snake
Family	Leptotyphlopidae	
	Leptotyphlops distanti	Transvaal worm-snake
Family	Pythonidae	
	Python sebae	African python

Table (continued)

Family	Colubridae	
Subfamily	Colubrinae	
	Boaedon f. fuliginosus	Brown house snake
	Lycophidion capense	Cape wolf snake
	Mehelya capensis	Cape file snake
	M. nyassae	Black file snake
	Philothamnus s. semivariegatus	Spotted bush snake
	*P. hoplogaster	Green water snake
	Prosymna sundevallii	Sundevall's shovel-snout
	*Pseudaspis cana	Mole snake
Subfamily	Dasypeltinae	
	Dasypeltis s. scabra	Common egg-eater
Subfamily	Boiginae	
	Telescopus s. semiannulatus	Tiger snake
	Crotaphopeltis h. hotamboeia	Herald snake
	Dispholidus t. typus	Boomslang
	Thelotornis capensis	Vine snake
	Psammophis sibilans brevirostris	Short-snouted sand snake
	*P. angolensis	Pygmy sand snake
	P. jallae	Jalla's sand snake
	*Amblyodipsas polylepis	Purple-glossed snake
	Xenocalamus bicolor australis	Bicoloured quill-snouted snake
	Aparallactus capensis	Cape centipede-eater
Family	Elapidae	
	Naja haje annulifera	Egyptian cobra
	N.m. mossambica	Mozambique spitting cobra
	Dendroaspis p. polylepis	Black mamba
Family	Viperidae	
	Bitis a. arietans	Puff adder

These types, which are edaphically controlled, present a variety of habitats for vertebrates, some of which show a decided preference for a particular habitat. Mention thereof has already been made, but as only some vegetation types are discussed, the following table illustrates this trend, (Table 3).

Table 3. Numbers of species of amphibians, reptiles and mammals according to vegetation type at Nylsvley (after Jacobsen, 1977).

Vegetation type	Amphibians	Reptiles	Mammals	Total
Burkea africana savanna	11	41	43	95
Diplorhynchus savanna (rocky outcrop)	5	32	25	62
Combretum apiculatum savanna	7	35	39	81
Acacia tortilis savanna	12	33	37	82
Bushclump savanna	10	35	37	82
Grassland	14	18	31	73
Nyl river floodplain	15	11	17	43

The greater diversity of species in the Burkea africana savanna is due to the sandy nature of the soil which gives another dimension to the structure of this habitat. There are at least four species of vertebrates restricted to the study area while several others occur more abundantly in this habitat than elsewhere in the Reserve. Each major vegetation type has 'endemic' species which could be used to diagnose the habitat.

Within these vegetation types, which together form Acock's Mixed Bushveld type, each reptile and amphibian species has its preferred area or microhabitat. Figure 12 attempts to show diagramatically how the lizards show their preference. Taking one vegetation type alone, such as that of the study area, it can be seen that the lizards have occupied every available ecological niche by means of morphological and behavioural adaptations. A zonal or stratified distribution pattern is evident as is outlined below:

Soil	deep (up to 30 c,)	Monopeltis capensis
	shallow (up to 5 cm)	Lygosoma sundevallii
		Monopeltis capensis

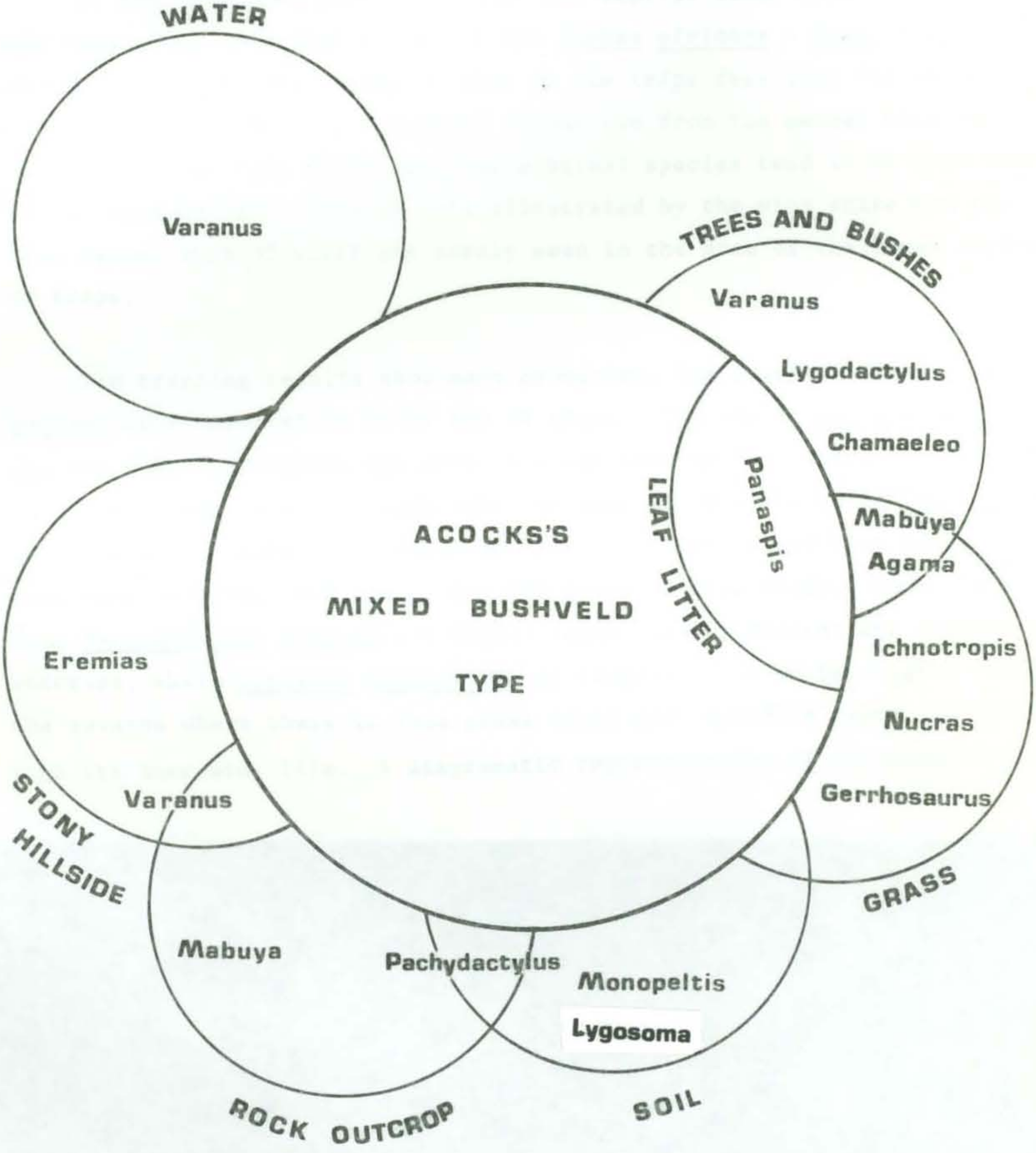

Figure 12. Habitats and microhabitats occupied by various Saurian genera on the Nylsvley Nature reserve.

Soil surface	grassy and open areas	*Ichnotropis capensis*
		Agama aculeata
		Gerrhosaurus flavigularis
		Varanus exanthematicus albigularis
	leaf litter	*Panaspis wahlbergi*
	around the bases of trees and shrub	*Mabuya varia*
		Ichnotropis capensis
		Panaspis wahlbergi
Shrub	bole and branches	*Lygodactylus capensis*
		mainly subadults and juveniles.
Trees	bole and branches	*Lygodactylus capensis*
		adults
		Agama atricollis
		Mabuya varia
Dead logs		*Lygodactylus capensis*
		Pachydactylus capensis
		Mabuya varia
		Varanus exanthematicus albigularis

It was mentioned previously that the reptile study area incorporated two variations (see vegetation) of the *Burkea africana* - *Eragrostis pallens* savanna. However, only eight or nine of the traps fell into the second category (b), but as there is a gradual transition from the denser tree variation (a) towards the less dense (b), the arboreal species tend to be more common in (a) than in (b). This is well illustrated by the vine snake and the tree agama, both of which are rarely seen in the area of the lower series of traps.

The trapping results show many anomalies, for example, almost all *Bufo garmani* were captured in 18 of the 49 traps. Similarly, *Kassina senegalensis* was found throughout the area, but the vast majority were captured in 22 of the traps, most of which were the same as those in which *Bufo garmani* were captured. Apparently these anomalies are associated with microclimatic requirements which were not within the scope of this study. Some, of course, like *Pachydactylus bibronii* are highly restricted in habitat and inhabit rocky outcrops, while *Lygosoma sundevallii* is largely found on the higher ridge of the savanna where there is less grass cover and therefore roots, to interfere with its burrowing life. A diagramatic representation of the anomalies can be seen in the appendix an[illegible] further studies are considered. The diversity of species in the reptile and amphibian study area has already been mentioned, but most of these species have a very low density, so that only a few species were responsible for the majority of captures. This appears to be found within all the vertebrate groups in the Savanna Ecosystem Study area and is possibly a direct result of the seasonality of the area which imposes restrictions in climate. The *Burkea africana* savanna appears to offer many more niches during the summer months but little of each, whereas the *Acacia* woodland with its basic uniformity offers fewer niches, but owing to its continuity has more of each niche and, therefore, permits a greater number of individuals. Although this study did not involve much work in the *Acacia* woodland, it was possible to determine that there were fewer species of reptiles and amphibians present in the *Acacia* patches as opposed to the adjacent *Burkea* savanna. However, this fact could be due to the younger nature of these *Acacia* patches, as they are obviously man-induced.

Snakes

The snakes are represented mainly by two species, one of which, the short-snouted sandsnake (*Psammophis sibilans brevirostris*), was captured by trapping, while the other, *Thelotornis capensis* or vine snake, was captured by methodically surveying the area, (see Methods). Figure 13 shows the diversity and biomass of the snakes as recorded by trapping and excludes the vine snake as it was not easily trapped, being largely arboreal. The snakes are represented by a total of 23 species which are actually 'resident' within the *Burkea africana* - *Eragrostis pallens* study area. Three species make up 53% of the total numbers captured over the period May 1975 to May 1977, while only seven make up 77%. Similarly, 53% of biomass is represented by two species, while only five make up 84%. This is due to the occurrence of the puff adder (*Bitis arietans*) and mamba (*Dendroaspis polylepis*), which account for 20% of the biomass while not being significant in numbers. The greatest biomass of the snakes is represented by *Naja haje annulifera* or Egyptian cobra, which accounts for 42% by mass but only 8,6% in number. *Psammophis sibilans* is most abundant but as it is a relatively small snake, ranks second to the Egyptian cobra in contributing biomass.

The majority of snakes are small species, usually under 90 cm in total length (Table 4). This is no doubt attributable to the size of prey

Figure 13. Spectrum of (A) snake species composition and (B) proportionate biomass in the Burkea africana - Eragrostis pallens Study Area: May 1975 - May 1977. (excluding Thelotornis capensis)

Ch	=	Crotaphopeltis hotamboeia
Lc	=	Lycophidion capense
Ac	=	Aparallactus capensis
Psun	=	Prosymna sundevallii
Dp	=	Dendroaspis polylepis
Pj	=	Psammophis jallae
Mc	=	Mehelya capensis
Nm	=	Naja mossambica
Ts	=	Telescopus semiannulatus
Ba	=	Bitis arietans
O	=	Others
Ps	=	Psammophis sibilans brevirostris
Nh	=	Naja haje annulifera
Psem	=	Philothamnus semivariegatus
Ds	=	Dasypeltis scabra
Mn	=	Mehelya nyassae
Dt	=	Dispholidus typus

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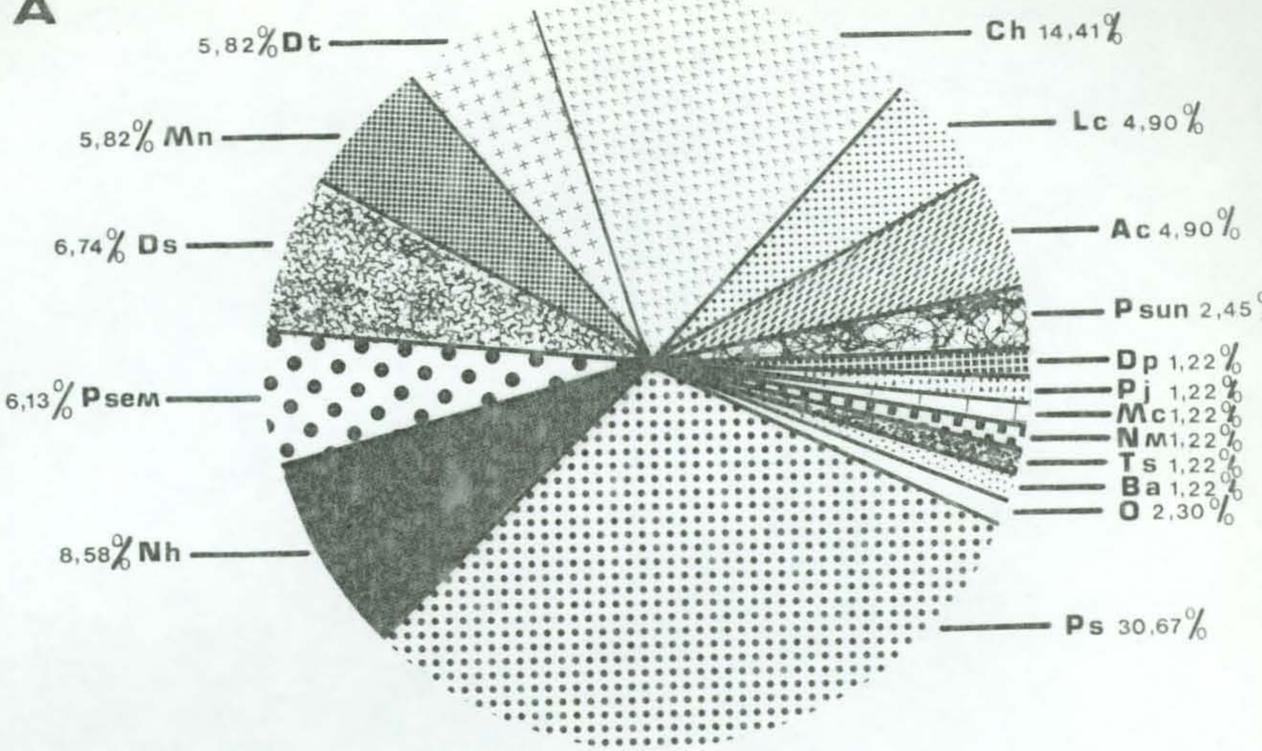

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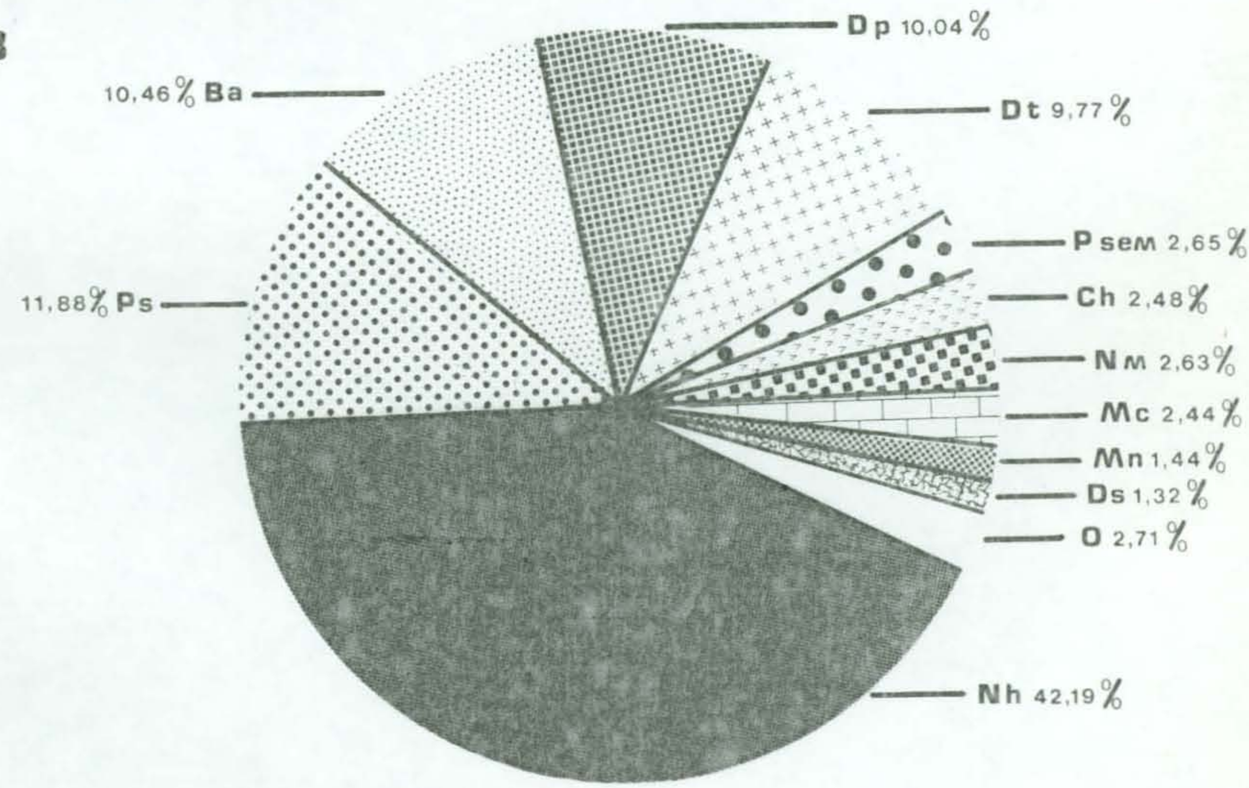

BIOMASS

most commonly found in the reptile and amphibian study area. The lizards, for instance, are made up of species mostly under 10 g in mass, and a snout to vent length of less than 20 cm. Similarly, the amphibians are mainly composed of small species or the juveniles of the larger types.

Table 4. Mean snout to vent length and mass of snakes in the Burkea africana - Eragrostis pallens Study Area.

Species	Sample No.	S/V (mm) Mean	Range	Mass (g) Mean	Range
Thelotornis capensis	229	591,56	(243,00-785,00)	42,80	(3,97-116,90)
Crotaphopeltis h. hotamboeia	52	345,54	(140,00-490,00)	18,45	(1,40-42,65)
Dispholidus t. typus	23	655,47	(297,00-1115,00)	133,60	(7,10-345,00)
Psammophis jallae	5	400,40	(203,0-532,00)	24,98	(2,70-48,60)
Boaedon f. fuliginosus	2	296,00	(238,00-354,00)	10,72	(6,45-15,00)
Naja haje annulifera	29	858,13	(347,00-1585,00)	391,23	(19,90-1705,00)
Naja mossambica	8	586,24	(278,00-1060,00	171,27	(11,10-600,00)
Xenocalamus bicolor	2	358,33	(205,00-475,00)	13,60	(2,00-18,00)
Mehelya nyassae	20	382,94	(229,00-485,00)	19,80	(4,80-41,40)
Mehelya capensis	4	627,00	(432,00-980,00)	158,89	(19,00-290,60)
Prosymna sundevallii	12	219,67	(114,00-282,00)	7,20	(5,70-12,70)
Leptotyphlops distanti	2	143,50	(134,00-153,00)	0,57	(0,50-0,65)
Dendroaspis p. polylepis	4	1410,00	(460,00-2080,00)	651,75	(17,10-1160,00)
Telescopus s. semiannulatus	4	505,00	(487,00-550,00)	25,96	(24,90-26,75)
Psammophylax t. tritaeniatus	6	400,67	(247,00-595,00)	32,75	(7,90-95,00)
Amblyodipsas p. polylepis	2	418,50	(407,00-430,00)	29,07	(25,46-32,55)
Bitis a. arietans	9	697,55	(584,00-805,00)	679,07	(315,70-752,90)
Aparallactus capensis	26	256,26	(210,00-316,00)	4,95	(2,70-6,80)
Lycophidion capense	18	283,54	(220,00-360,00)	10,84	(5,30-13,20)
Psammophis sibilans brevirostris	146	428,12	(192,00-750,00)	30,85	(3,3-112,30)
Dasypeltis s. scabra	24	356,70	(206,00-605,00)	15,66	(2,75-38,1)
Philothamnus s. semivariegatus	23	440,21	(230,00-579,00)	34,43	(4,35-36,10)

Lizards

The picture is essentially similar for the lizards (Figure 14). Two species, that is Mabuya varia and Ichnotropis capensis, make up 84,93% of the total number of lizard captures in traps 1-49 over a period of two years. If Panaspis wahlbergi is included, then the three species make up 95,92% of all the species by number. The picture is very similar if one considers the biomass of the animals captured. Again, the first two species mentioned make up 76,83% of the mass of all the lizards captured with the exception of the veld monitor (Varanus exanthematicus albigularis) and the Cape dwarf gecko (Lygodactylus capensis). The former was excluded from these calculations as they may exceed a kilogram in weight and were only very sporadically found. The latter is excluded as it was surveyed using a different method and therefore could not be compared. If the third lizard species is included, then the three together make up 90,30% of the mass of all the species. The third lizard in this instance is Agama atricollis, and as can be seen in the diagram, does not contribute very much by number, but as it is a robust and fairly large lizard, it displaces the small Panaspis wahlbergi. Table 5 shows the mean mass and snout/vent lengths of the lizard species.

Table 5. Mean Snout-to-Vent length and Mass of lizards in the Burkea africana - Eragrostis pallens Study Area

Species	Sample No.	S/V (mm) Mean	S/V (mm) Range	Mass (g) Mean	Mass (g) Range
Lygodactylus capensis	100	29,84	21-37	0,76	0,20-1,30
Pachydactylus c. capensis	34	54,00	46-60	4,24	2,40-5,25
P. bibronii	8	65,00	54-83	7,73	3,40-11,20
Agama atricollis	15	115,80	46-147	64,11	3,50-119,70
A. aculeata	5	56,60	49-78	6,58	4,90-11,70
Chamaeleo d. dilepis	2	135,50	130-141	31,00	30,90-31,90
Mabuya capensis	1		62,00		5,35
M. varia	100	51,81	27-70	3,28	0,25-9,00
M. striata punctatissimus	1		61,00		4,55
Lygosoma sundevallii	35	62,94	25-91	3,65	0,35-9,70
Panaspis wahlbergi	100	36,93	16-44	0,66	0,05-1,10
Nucras intertexta	7	59,85	38-75	4,39	0,85-8,05
Ichnotropis squamulosa	1		63,00		6,00
I. capensis	100	48,79	38-60	2,49	1,10-4,10
Varanus exanthematicus albigularis	20	318,85	118-560	1053,13	20,85-4550,00
Gerrhosaurus f. flavigularis	11	61,90	45-91	6,31	1,45-16,70

Figure 14. Spectrum of (A) lizard species composition and (B) proportionate biomass in the Burkea africana - Eragrostis pallens Study Area; May 1975 - May 1977. (excluding Lygodactylus capensis).

Ic = Ichnotropis capensis

Aa = Agama atricollis

Pw = Panaspis wahlbergi

Pb = Pachydactylus bibroni

Cd = Chamaeleo dilepis

Ls = Lygosoma sundevallii

Gf = Gerrhosaurus flavigularis

O = Others

Mv = Mabuya varia

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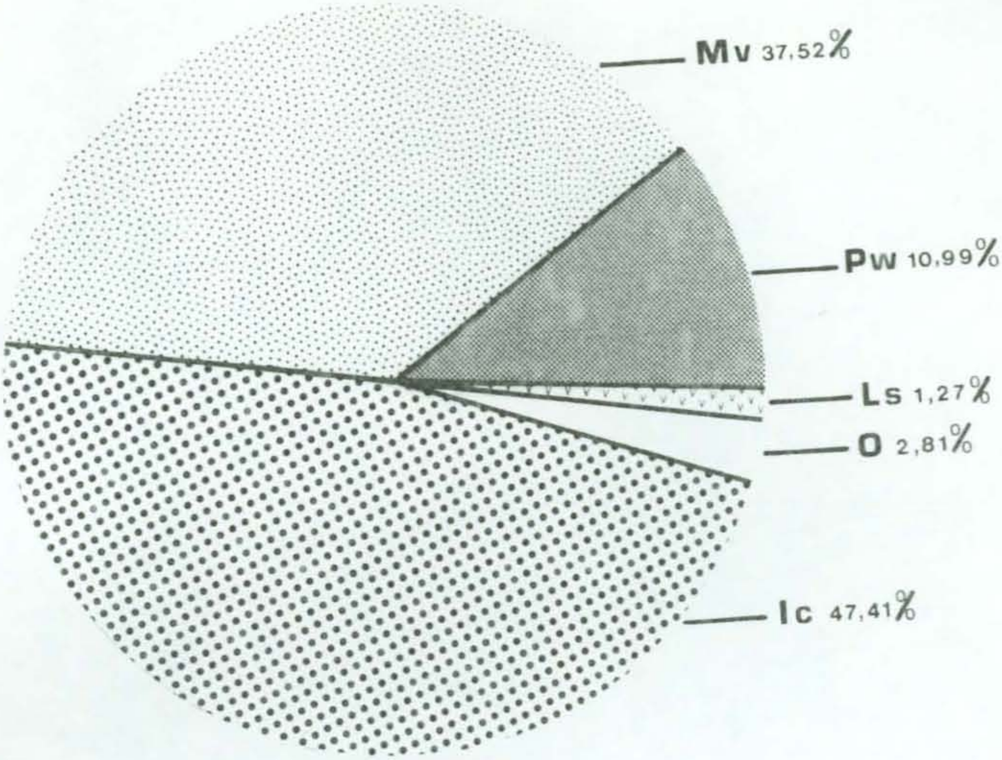

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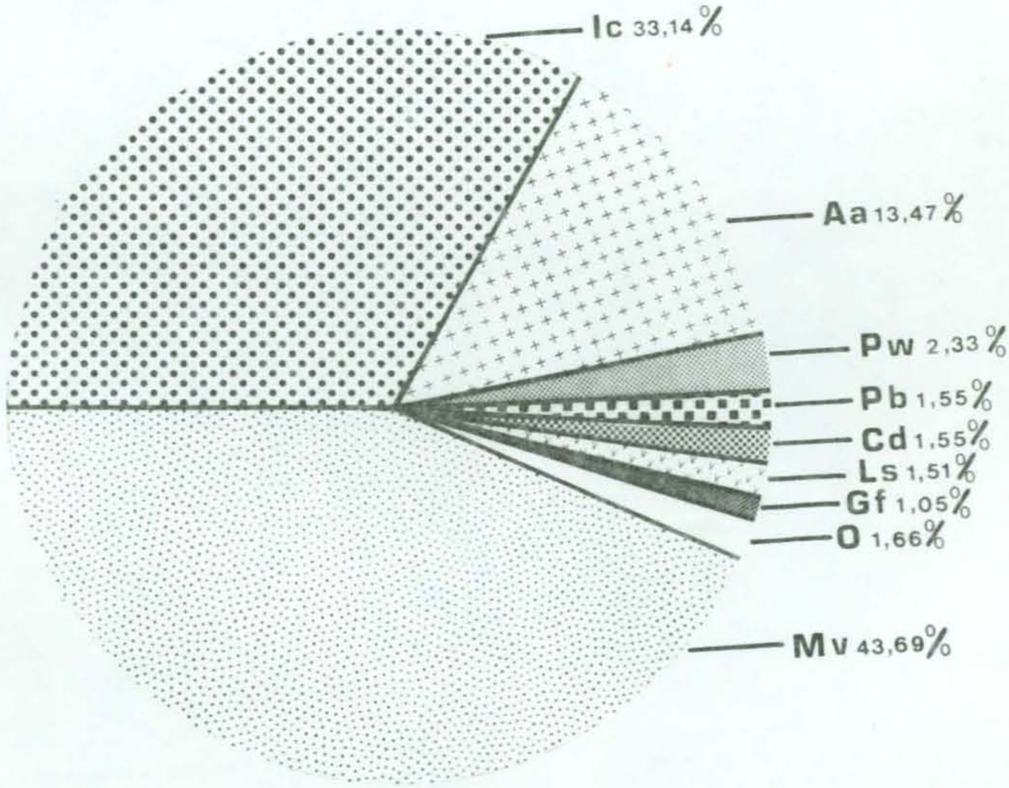

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Amphibians

The amphibians show a similar pattern in that two species, Bufo garmani and Kassina senegalensis, make up 86,4% of the numbers captured. If one includes a third, namely Breviceps adspersus, then the three species make up 95,23% of all the amphibians captured, (Figure 15). If one considers mass, then one species B. garmani alone makes up 76,0%. Table 6 refers to the mean size and mass of amphibians in the Study Area. It is apparent that in all three groups, that is, snakes, lizards and amphibians, a small proportion of species contribute the most. These species will be discussed in more detail in other chapters.

Table 6 Mean Snout-to-Vent length and mass of amphibians in the Burkea africana - Eragrostis pallens Study Area

Species	Sample No	S/V (mm) Mean	Range	Mass (g) Mean	Range
Bufo garmani	100	85,41	46,00-99,00	47,00	8,50-89,55
Bufo gutturalis	30	72,47	38,00-96,00	39,76	8,50-73,00
Bufo carens	11	65,36	53,00-78,00	19,45	8,20-29,55
Breviceps adspersus	100	31,06	21,00-57,00	4,26	0,90-11,90
Phrynomerus bifasciatus	30	45,28	32,00-59,00	6,45	2,20-14,25
Pyxicephalus a. adspersus	1		86,00		42,90
Ptychadena anchietae	1		42,00		7,65
Tomopterna cryptotis	36	40,94	34,00-49,00	6,92	3,05-14,40
Tomopterna krugerensis	1		46,00		11,60
Phrynobatrachus natalensis	14	23,31	21,00-28,00	1,33	0,90-2,05
Cacosternum boettgeri	15	19,06	17,00-22,00	0,48	0,30-0,70
Tomopterna natalensis	2	41,00	37,00-45,00	5,92	4,05-7,80
Kassina senegalensis	100	38,54	29,00-47,00	3,49	1,50-5,55

Seasonal fluctuation of the populations

The seasonal fluctuation of abundance and biomass of snakes, lizards and amphibians was studied over a period of two years from May 1975 to May 1977. On account of the climate, particularly the pronounced dry cold winters, numbers of active animals fluctuated in similar fashion (Figure 16). There was, therefore, a peak of activity during the warm and moist months of the year and, correspondingly very little activity during winter. The various peaks and troughs displayed in the graph reflect on various climatic vagaries to which the reptile and amphibian populations respond. For instance, a period of low rainfall experienced during November and December

Figure 15. Spectrum of (A) Amphibian species composition and (B) proportionate biomass in the Burkea africana - Eragrostis pallens Study Area: May 1975 - May 1977

Bg = Bufo garmani

Ks = Kassina senegalensis

Bgut = Bufo gutturalis

Ba = Breviceps adspersus

Pb = Phrynomerus bifasciatus

Tc = Tomopterna cryptotis

O = Others

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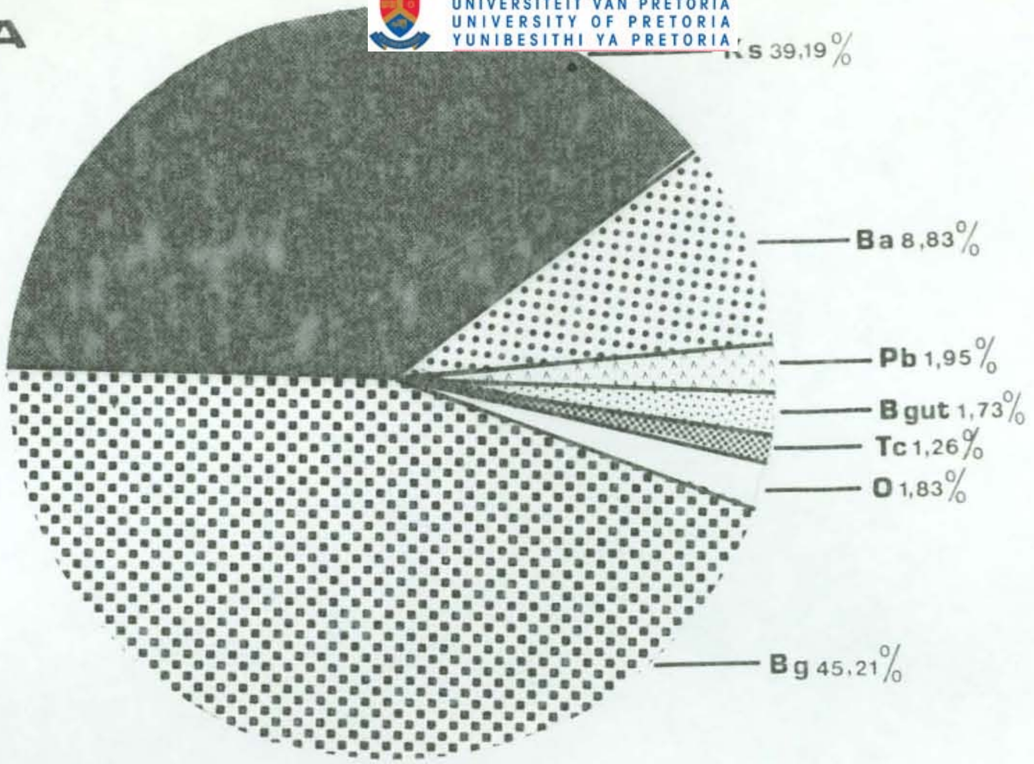

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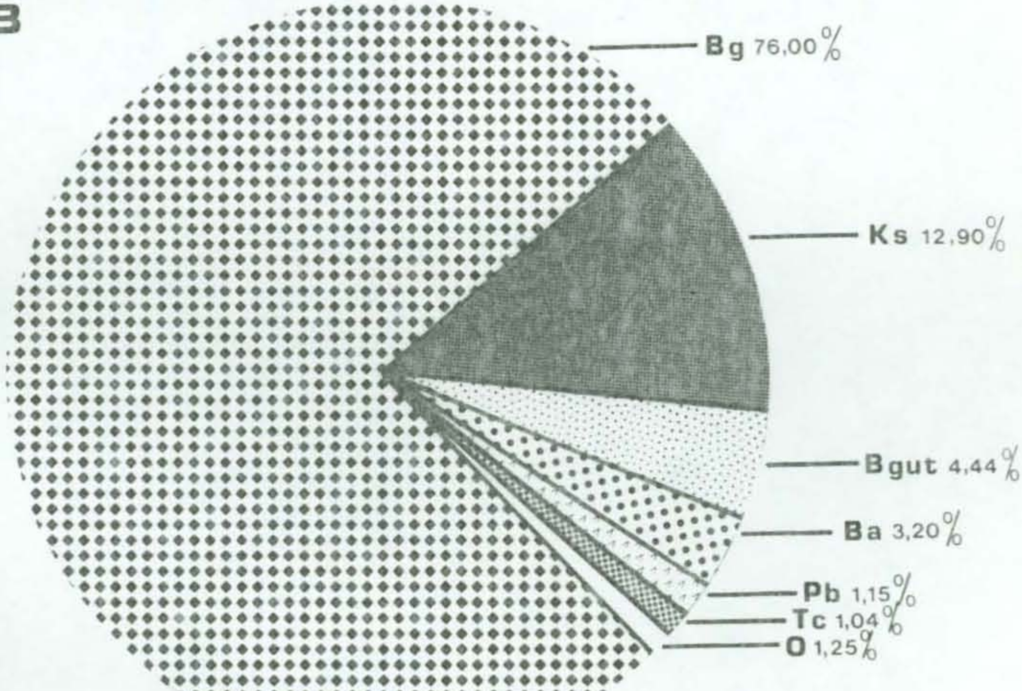

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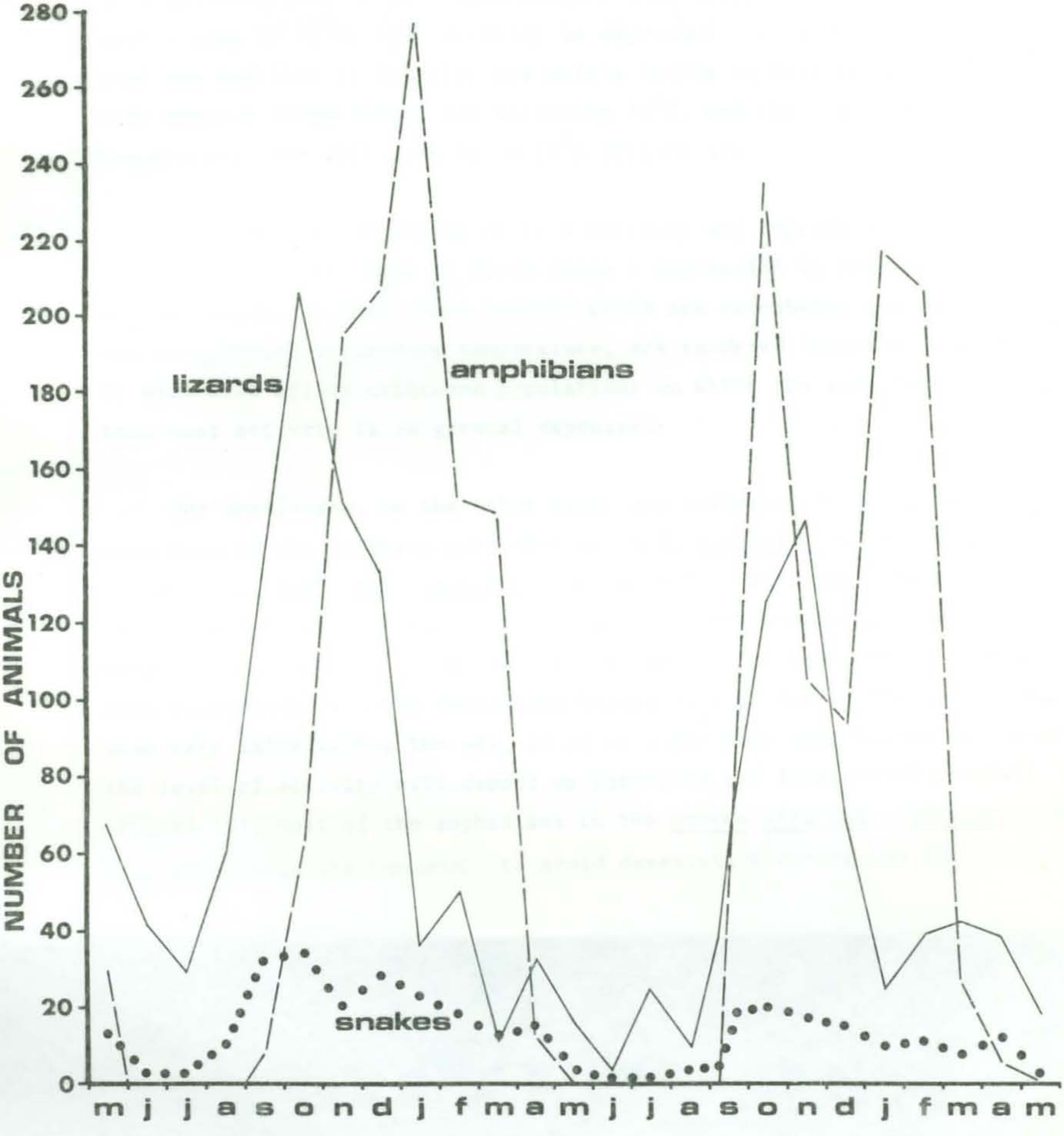


Figure 16. Number of animals captured in the trapping grid from May 1975 to May 1977 in the Burkea africana- Eragrostis pallens Study Area.

1976, resulted in a paucity of amphibians.

The reptiles are largely independent of rainfall, but are dependent on it to create a favourable climate for the hatching of eggs. The reptiles are, however, totally dependent on temperature and, although some animals were active even during the winter months (27,28% of the lizards, 2,84% of amphibians and 30,63% of snakes), the great majority were only active from the middle of September until the middle of May. In particular, there is a pronounced peak in activity during the first two months following hibernation, namely in September/October, which is also the period preceding the main rains which fall from November to April. It also coincides with the period when the mean temperature fluctuates around 25°C, although a wide range may occur. The reptiles therefore emerge from hibernation during the latter half of September when mean ambient temperatures hover above a threshold of 17°C. From cursory observations, most activity takes place when mean minimum temperatures are between 10-13°C and mean maximum temperatures reach above 29°C, which together give a mean daily temperature of between 19,5-21°C. When temperatures fall below a mean of 17°C or exceed a mean of 25°C, then activity is depressed. It would, therefore, appear that the reptiles at Nylsvley are mainly active on days which are moderate, with maximum temperatures not exceeding 30°C, and the nights are mild with temperatures not declining below 10°C (Figure 17).

Other factors affecting reptile activity and reproduction are rainfall and cloudy weather, both of which cause a depression in temperature as well as insolation, so that these animals which are ectotherms and rely on the sun to increase their body temperature, are rendered inactive (Figure 18). It will also affect arthropod populations on which the reptiles feed, so that most activity is in general depressed.

The amphibians, on the other hand, are activated by moisture and in fact, some such as the northern mottled toad (Bufo garmani) and the common short-headed frog (Breviceps adspersus), become active even when there is no surface moisture, but the humidity is high. Temperature is also important for many species, but not to the same extent as for the reptiles. For example, when rain falls, all the amphibians become active, but as they are nocturnal, when rain falls during the day, it is at night that they become active and the level of activity will depend on intensity and duration of rainfall (Figure 19). Most of the amphibians in the Burkea africana - Eragrostis pallens Study Area are fossorial to avoid dessication during the dry winter months.

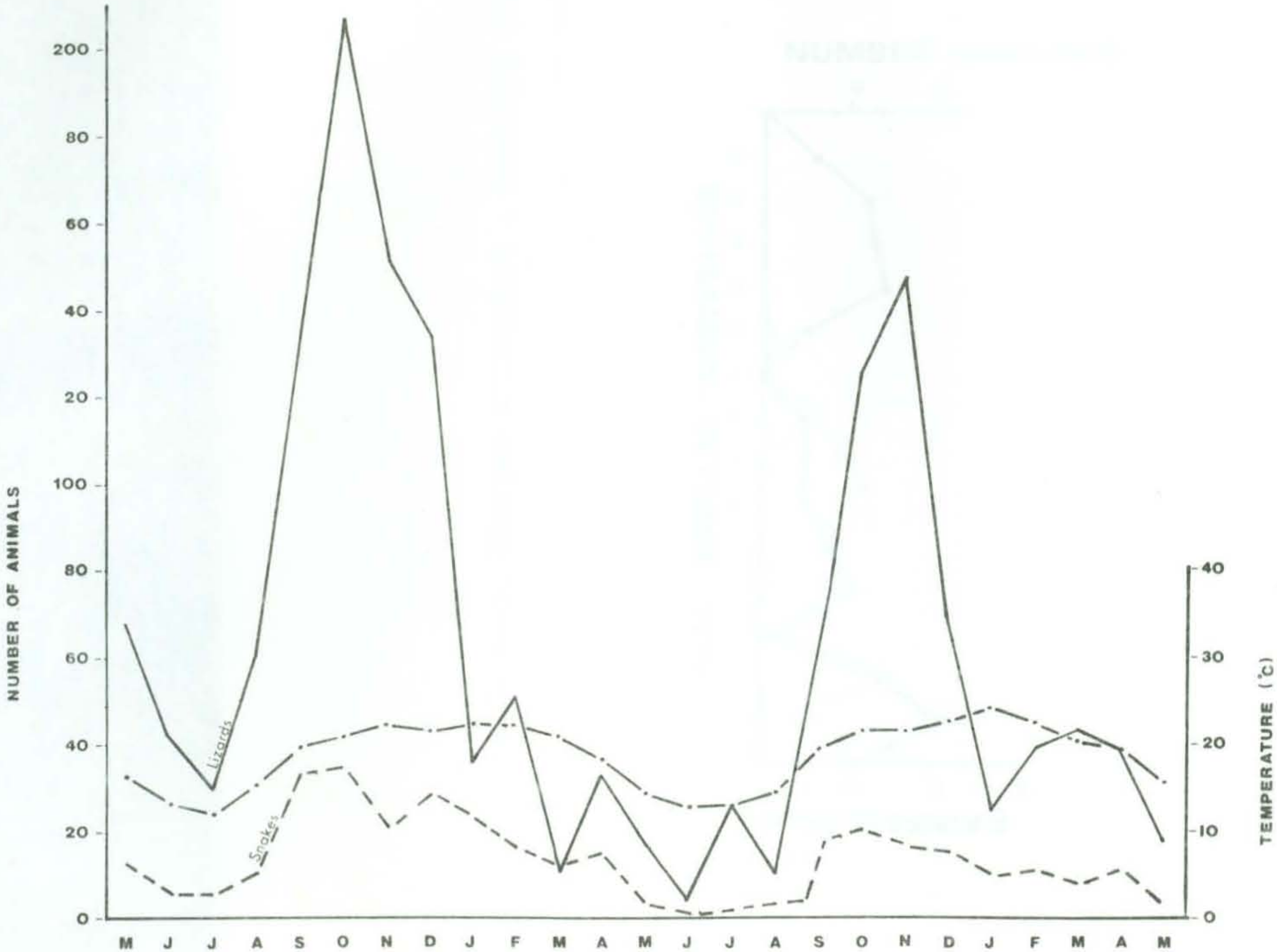


Figure 17. Effect of temperature on the activity of reptiles in the *Burkea africana* - *Eragrostis pallens* Study Area: May 1975 - May 1977.

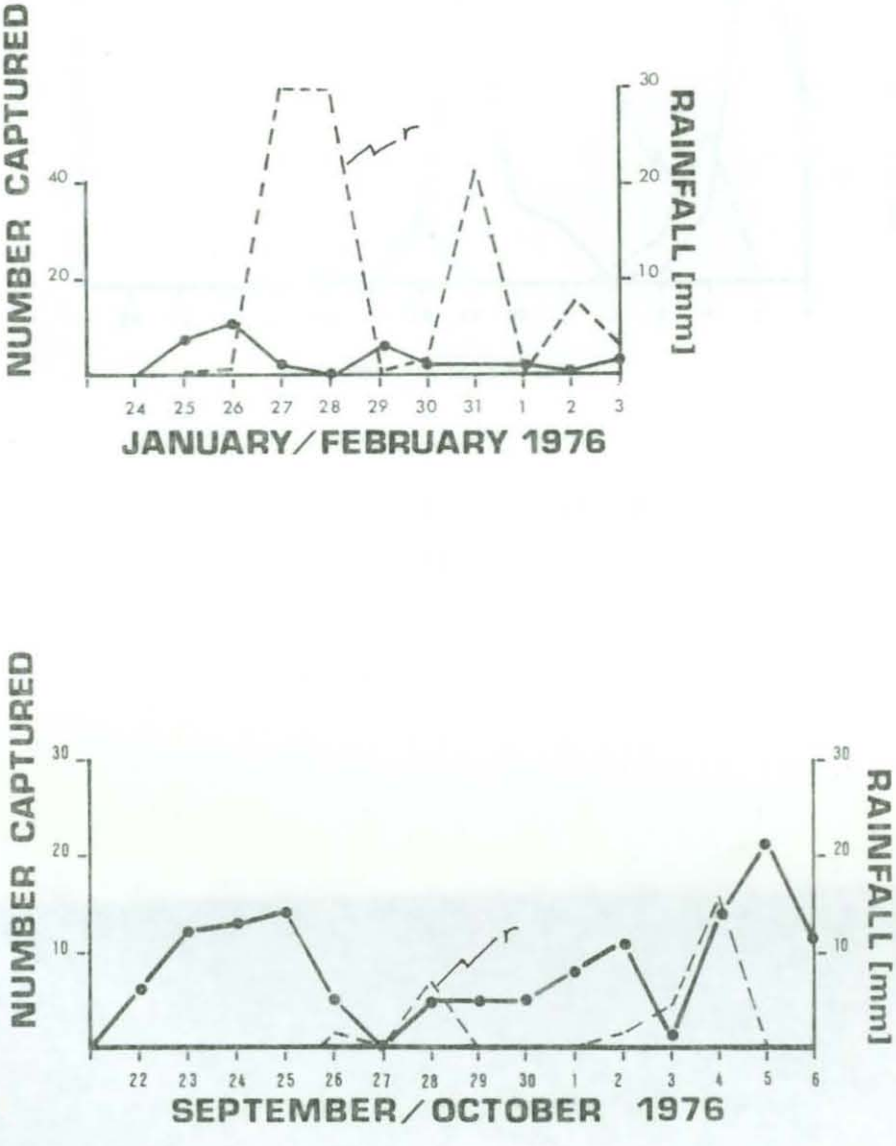


Figure 18. Effect of rainfall on the activity of lizards in the _Burkea africana_ - _Eragrostis pallens_ Study Area.

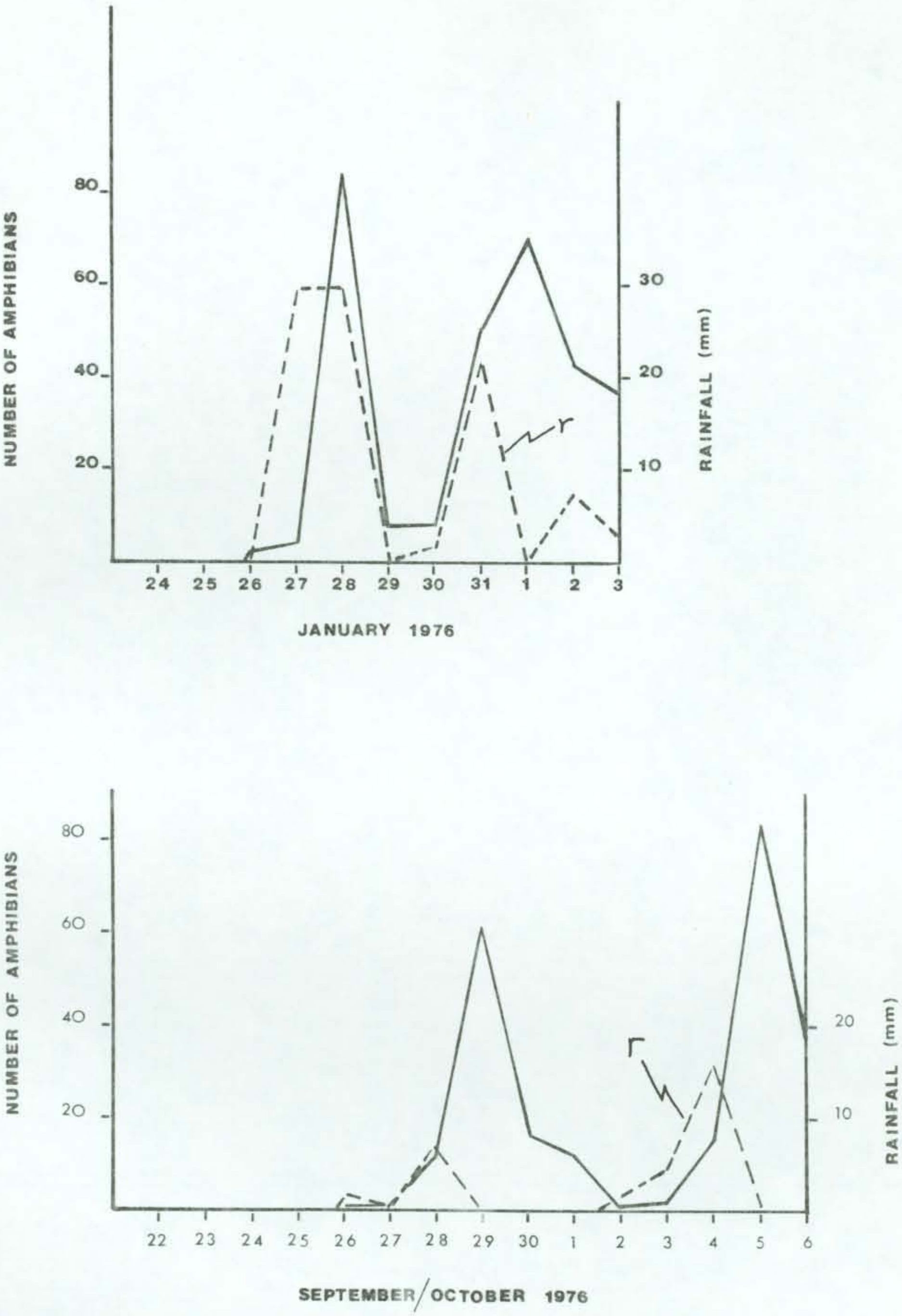


Figure 19. Effect of rainfall on the activity of amphibians in the Burkea africana - Eragrostis pallens Study Area.

Loveridge (1976), divides the fossorial anurans into those that dig their own burrows and those that utilize spaces under rocks or holes made by other animals. Hibernation or retraherence as Loveridge (loc.cit.) puts it, assures a microclimate of cool temperatures and high relative humidities which is why the amphibians of the Burkea africana - Eragrostis pallens Study Area have adopted the fossorial strategy. Kassina, Phrynomerus, Bufo and Cacosternum, generally make use of burrows formed by other animals, as well as natural crevices and rotting logs. Phrynomerus even use hollow branches in trees while holes in termitaria and the subsurface tunnels of the golden mole (Amblyosomus hottentotus) and the common mole-rat (Cryptomys hottentotus) are used by Kassina senegalensis. Those that dig their own burrows in the Study Area include the common short-headed frog (Breviceps adspersus), Tomopterna cryptotis, T. krugerensis, T. natalensis and Pyxicephalus adspersus. Most burrowing amphibians have large bladders, Loveridge (loc. cit.), and it would appear that they are very tolerant of dessication, being able to lose between 38-48% body weight before dying. Water absorption response if dehydrated is strong and has been demonstrated in the case of Bufo gutturalis (= B. regularis), Cloudsley-Thompson (1967). Unfortunately, similar data for many of the other species, such as Tomopterna and Phrynomerus are lacking. Senescent Phrynomerus bifasciatus, Bufo garmani and Kassina senegalensis, have been found with a milky mucus covering, indicating a response to continued dehydration. It is known that Pyxicephalus adspersus forms a cocoon around it under certain circumstances, which assists to prevent excessive dehydration, Parry & Cavill (1978). Loveridge (loc.cit.) allowed a 961 g animal to burrow into wet clay soil and the clay was allowed to dry out slowly at room temperature. After 229 days, the clay was broken open and the frog removed and weighed. It had only lost 45 g (4,6% of body mass) in this time. It is, therefore, obvious that the various strategies of the amphibians in the Nylsvley savanna are highly adapted to the seasonality of the climate and, in particular, rainfall.

Seasonal cycle of abundance and biomass

Density and biomass of the lizard, snake and amphibian populations fluctuate according to season. A total of 457 snakes, 2142 lizards and 2205 amphibians were marked and released from May 1975 to May 1977. I have included the month of May 1977 on account of the fact that May 1975 was incompletely sampled. Not included in these figures are those of the arboreal species, such as Lygodactylus capensis and Thelotornis capensis, which were sampled using different techniques and will, therefore, be considered separately.

The marked animals were subsequently recaptured and the following percentages were recorded for lizards (24,62%), snakes (11,45%) and amphibians (3,08%). It was not possible to assess population sizes of individual species as the recapture rate was too low, but combined together, a population estimate for each group as a whole was possible.

Snakes

From recaptures of a total of 457 snakes captured and marked, it was possible to compute the density of the snakes (Table 7). Density ranged from a low of 0,02/ha in winter, when temperatures may fall below freezing, to a peak of 10,3/ha in September/October 1975. Density of snakes was, however, much lower during the 1976/77 season. Nevertheless, the trend is similar from one season to the next (Figure 20). This trend is similar to that recorded by Barbault (1975), for both burnt and unburnt savanna (over a period of five years), although Lamto with its more tropical climate shows a less seasonal variation. For example, Barbault (loc.cit.) recorded a low of 0,75/ha during winter, rising to 7,5/ha during summer in burnt savanna, while in unburnt savanna he recorded a low of about 8,70/ha in winter, and a peak of 17,0/ha in summer.

Table 7. Density of Snakes showing upper and lower confidence limits (No/ha)

	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
Lower Limits	0,02	0,02	0,02	0,056	0,53	0,74	0,20	0,49	0,33	0,22	0,07	0,17	0,009	0,002	0,004	0,009	0,009	0,54	0,17	0,07	0,05	0,06	0,03	0,07	0,004
D	0,26	0,04	0,06	0,78	3,47	10,32	2,8	6,86	4,59	1,40	0,94	2,49	0,12	0,02	0,06	0,12	0,12	3,5	2,39	1,02	0,69	0,94	0,45	0,5	0,06
Upper Limits	5,17	5,16	5,16	15,11	19,63	201,25	54,49	133,64	89,49	8,0	18,29	48,52	2,38	0,39	1,19	2,38	2,38	19,86	46,53	19,89	13,52	18,29	8,75	2,82	1,19

The mean snout/vent lengths and mass of the snakes involved can be seen in Table 4. As density and mass (mean) enable one to calculate the biomass, it is logical to assume that they correspond (Figure 20). This ranges from approximately 1,0g/ha during winter when most animals are hibernating, to a peak of 459g/ha during the summer months. Hibernation lasts for three to four months, depending on the climate. During September 1976,

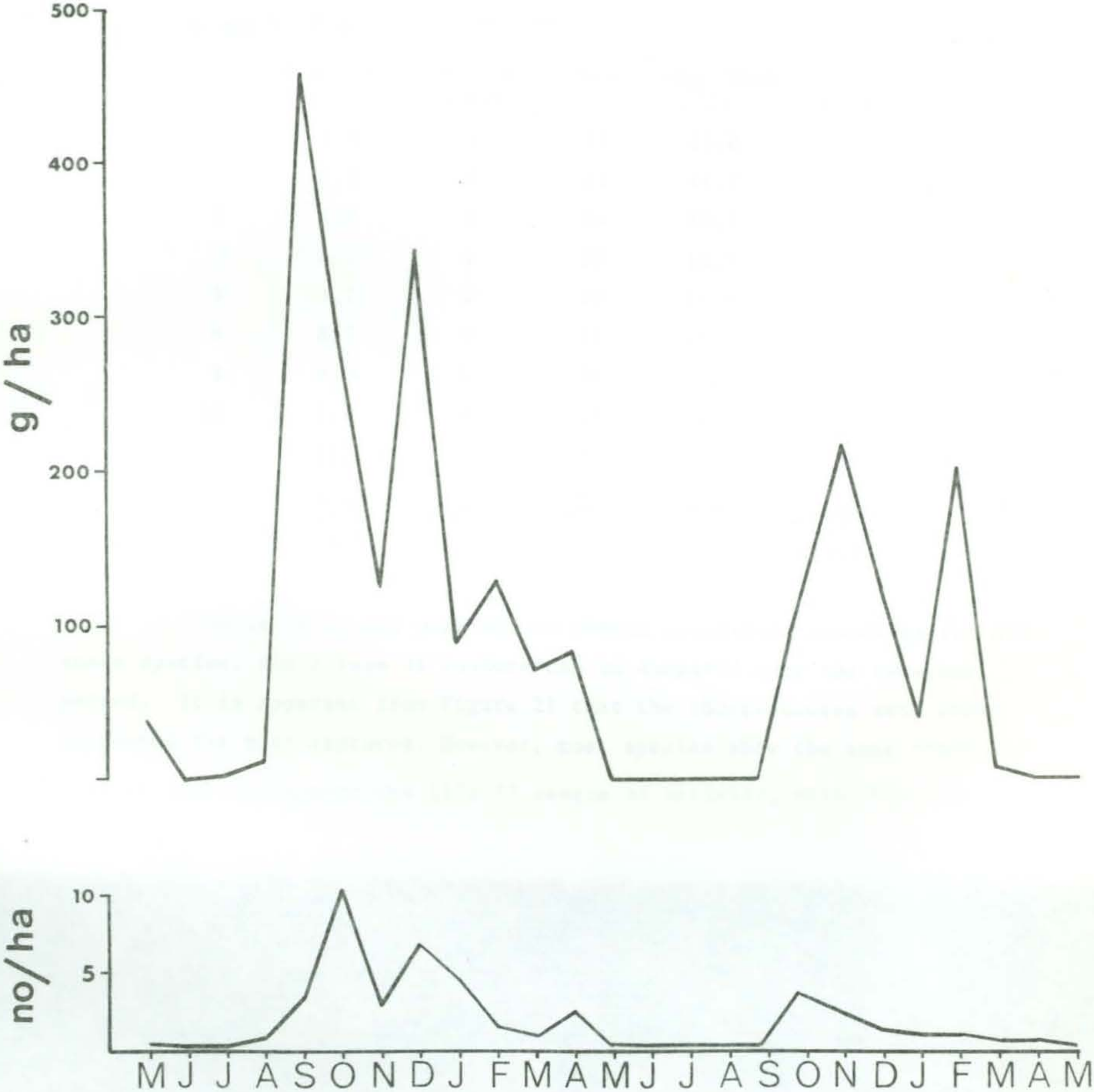


Figure 20. Density and biomass of snakes in the Burkea africana -Eragrostis pallens Study Area: May 1975 - May 1977 (excluding Thelotornis capensis)

two census periods were undertaken. One during the first half of the month and one during the latter half, extending into early October. This qualified what was already postulated from the capture data for 1975, which is that the reptiles are dependent on a mean minimum temperature of above 10°C before they come out of hibernation. The difference in temperature between the first census and the second during September, is highly significant (P = 0,001, t_{18} = 4,5324). A comparison of the mean number of reptiles captured over the same periods also show a significant difference (P = 0,05, t_{18} = 2,236). Were it not that rain fell during the second census period, thereby depressing reptile activity, this difference may have been even more significant. As can be seen from Table 8, the ten days of the second census indicated to what extent the animals became active under a higher mean minimum temperature of 12,6°C compared to 8,5°C for the previous census. Mean maximum temperatures were virtually the same during both periods, namely 26,12°C and 26,48°C respectively. (See also Figure 17).

Table 8. The influence of temperature on the activity of snakes during two census periods during September 1976, in the Burkea africana - Eragrostis pallens Study Area.

	Date	Min. Temp. (°C)	No. of snakes	Date	Min. Temp. (°C)	No. of snakes
	3	8,9	1	22	13,2	5
	4	7,2	0	23	11,7	0
	5	9,9	0	24	10,2	0
	6	4,0	1	25	10,9	3
	7	5,7	1	26	14,6	2
	8	8,9	0	27	13,7	3
	9	9,0	1	28	12,4	2
	10	7,5	0	29	12,1	0
	11	11,3	0	30	12,0	0
	12	12,6	1	1	15,8	3
Total	10	85,0	5	10	126,6	18
$\bar{x}$		8,5	0,5		12,6	1,8

While it is not possible to obtain population estimates for all snake species, their rate of capture can be compared over the two-year period. It is apparent from Figure 21 that the short-snouted sand snake accounted for most captures. However, most species show the same trend and numbers declined during the 1976/77 season of activity, with only the

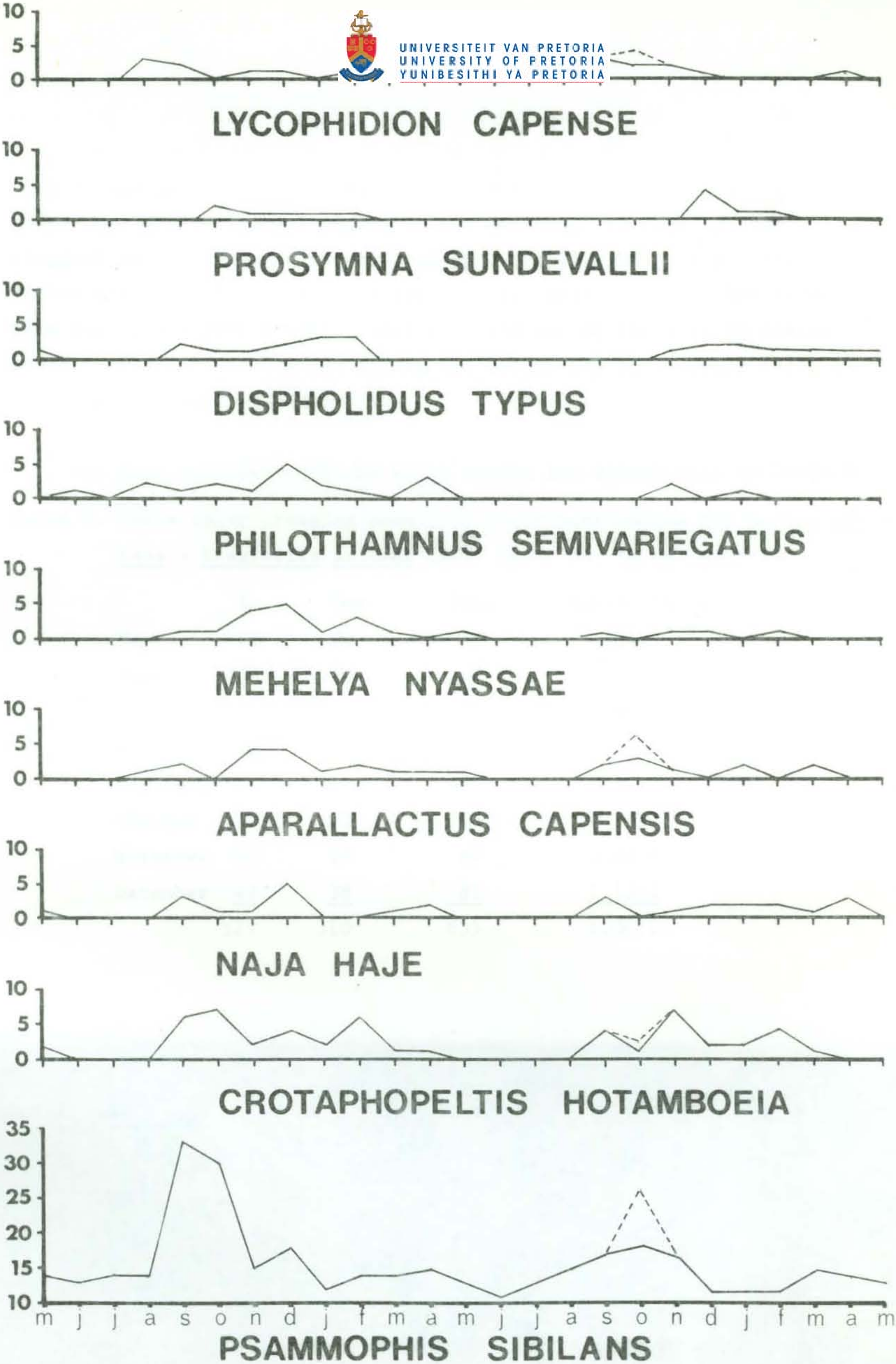


Figure 21. Monthly rate of capture of snake species in the Study Area, May 1975 to May 1977 (excluding Thelotornis capensis). (-------- = extrapolation as census period shortened).

sand snakes showing continuous activity throughout the two years of the survey. The wolf snakes also showed a similar spread, but do not appear to be active during late summer, preferring instead to advance their activity to include August and September. All other species tend to hibernate from May until September. In most species, activity declined during January 1976, coinciding with a concomitant decline in rainfall. In addition, it is postulated that there are indications that many of the snakes die after a year's activity, which may also account for the continual capture of unmarked specimens. This is especially so of the short-snouted sand snake. The hypothesis is supported from observations by Barbault (1971) at Lamto. (See also Chapter 6, Figure 46).

The paucity of recaptures is difficult to explain, as snakes which were captured and marked have been recaptured as much as six months later, and then in a trap 100 m distant from where they were originally caught. It is possible that the trauma of capture drove them out of the area and that they are constantly being replaced by new individuals, but this would then be applicable to all species which does not appear to be logical, as many, such as wolf snakes, shovel snouts and other terrestrial species are sluggish and probably do not move as far. It is also possible that snakes become trap shy, but this would apply to all species. In order to determine how much movement takes place into and out of the area by snakes, spoor crossings were counted during the period May to December 1975, along the roads surrounding Paddock 1.

The data recorded over the eight months are illustrated in Table 9.

Table 9. Snake spoor crossing counts on roads surrounding the Burkea africana - Eragrostis pallens Study Area, May to December 1975.

	In	Out	Total	Ratio (In:Out)
May	25	22	47	1,14:1
June	23	25	48	0,92:1
July	17	6	23	2,83:1
August	30	31	61	0,97:1
September	97	100	197	0,97:1
October	48	61	109	0,79:1
November	40	27	67	1,48:1
December	43	38	81	1,13:1
	323	310	633	1,04:1

Unfortunately during September rain fell and, therefore, recordings took place irregularly, as the soil packed too hard after rain to see spoor, particularly of small snakes, which were the most abundant. It is evident from the data collected over eight months that numbers of immigrating and emigrating snakes, with the exception of July, were very much the same. In July there was an influx almost thrice that of the efflux. However, the data show that snakes move freely in and out of the study area. It is also apparent that during the warmer months of the year, activity and, therefore, movement, is much higher, which may account for the continual capture of unmarked animals. Apparently most snake species move about considerably without a fixed home range or, alternatively, they had home ranges exceeding the current study area. Dargan & Stickel (1949), also came to the conclusion that their study area (8,96 ha) was too small and advocated that the study area for most species should encompass an area at least three times the home ranges of the snakes under study. In some common snakes, such as the black racer (*Coluber constrictor*), which has a home range diameter of 397,5 m, the present trapping area would be equivalent to approximately two home ranges. Owing to inadequate time and insufficient funds, a larger study area (81 ha), such as these two authors advocated, could not be considered. However, to compromise, an area of 49 ha was used and correspondingly, a considerably greater number of snakes were captured, although recapture frequencies were far too low to be able to calculate the home range of any of the terrestrial species.

On the other hand, Fitch & Shirer (1971), forcefed radio transmitters to 68 snakes of eight American species. These snakes were tracked for periods of 1 to 102 days. Most of the medium-sized species moved within home ranges varying from under 100 m to more than 400 m in diameter. This indicates that the study area at Nylsvley is of adequate size for most species except the very large snakes and also indicates that trapping is perhaps not a feasible method of mark-recapture population size estimates for snakes.

The vine snake (*Thelotornis capensis*) was recaptured sufficiently frequently to be able to calculate the density of this species in the study area. A total of 147 snakes were captured. Of these, 78 (53,06%) were recaptured on at least one, and some on as many as eight occasions. It is apparent that these animals exhibit two peaks of activity, during September and again in April, at which time most animals appear to be found.

An explanation for this phenomenon may be that during the latter half of September, these snakes become active following a winter hibernation. They are reproductively active at this stage and may be seen copulating. April precedes the month when snakes commence hibernation. However, many of these snakes do not hibernate per se as will be discussed later. During both these periods, these snakes exhibit a pronounced predilection for Grewia flavescens shrubs where they spend the day lying outstretched inside the shrub. The reason for this is not clear. It may be associated with food availability, as many of the lizards and probably also amphibians, forage at the base of such clumps. They are then more easily seen than when they may move to higher levels inside the canopy of trees, where they blend well with their surroundings. The mean density and biomass of vine snakes in the study area is 1,32 /ha and 56,49g/ha. They therefore contribute substantially to the total snake biomass which ranges from a low of 57,49g/ha during winter, with a peak of 515,49g/ha during summer.

Lizards

A total number of 2142 lizards, comprising 16 species, was captured. This is double the number of species recorded for the savanna at Lamto. However, several species, notably Mabuya capensis and M. striata punctatissimus, were recorded on single occasions and can be excluded from the following calculations. The majority of captures of terrestrial species consisted of three species, while the arboreal gecko (Lygodactylus capensis), makes up the fourth. Figure 22 shows the rate of capture of all terrestrial species over the two-year observation period. The considerable fluctuations involved can be attributed, particularly during December/January, to mortality amongst individuals of one of the more abundant species, Ichnotropis capensis. The fact that very few adults are seen during January support this, although on one occasion, an adult was captured as late as May. Broadley (1967), discusses this annual lizard and shows how it avoids competition with a sympatric sibling species, Ichnotropis squamulosa, occurring only as juveniles while the latter is adult and vice versa. While both species did occur in the study area, Ichnotropis squamulosa was recorded on a single occasion and then in the more densely grassed area in variation (b), that is the Eragrostis pallens - Setaria perennis variation of the Burkea savanna and competition appears to be minimal, if not non-existent, at Nylsvley. It would also appear that many of the other lizards show similar tendencies, although there is not quite the same degree of population turnover as is experienced by Ichnotropis capensis. Figure 23 compares the rate of capture

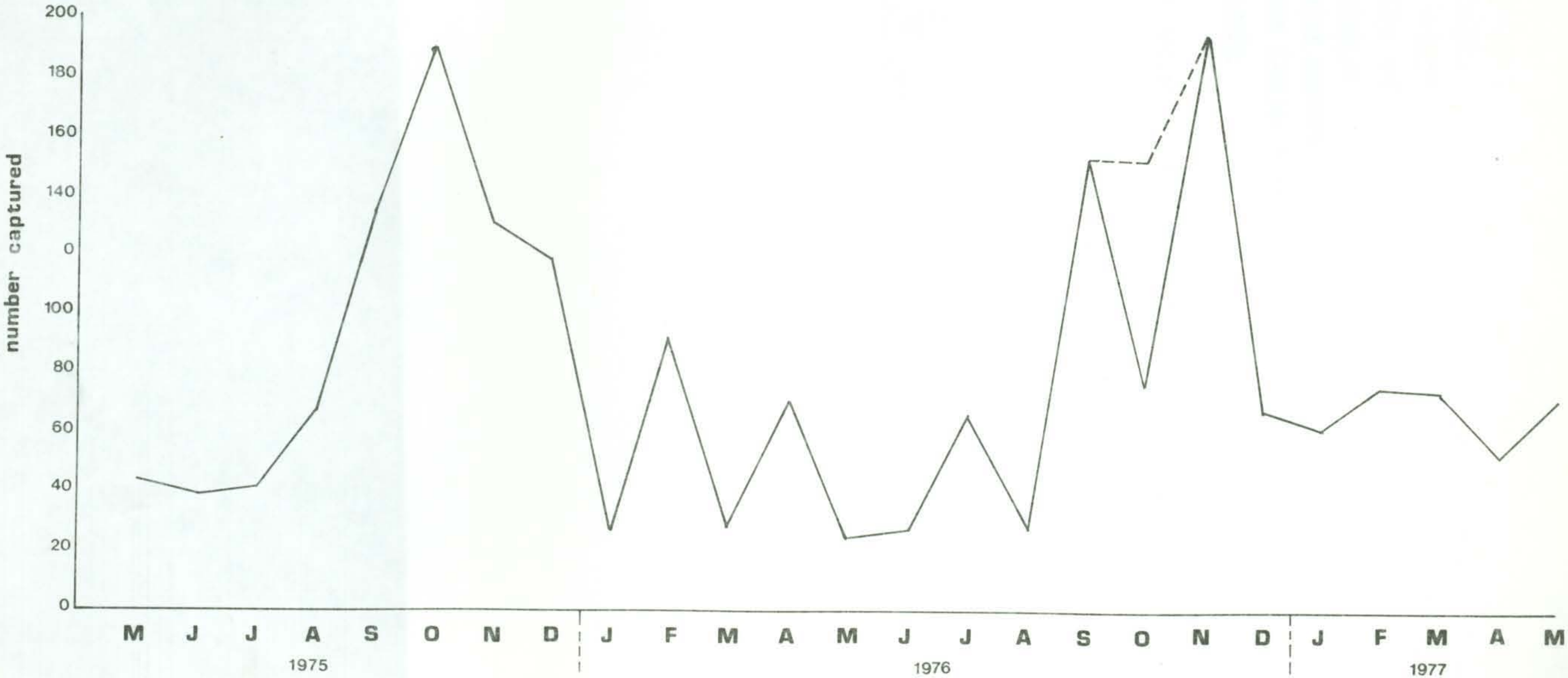


Figure 22. Total number of lizards captured per month in the Study Area, excluding Lygodactylus capensis, May 1975 to May 1977. (———— = extrapolation as census period shortened).

Figure 23. Monthly rate of capture of lizard species in the Study Area: May 1975 to May 1977 (excluding Lygodactylus capensis).

A Ichnotropis capensis

B Mabuya varia

C Panaspis wahlbergi

D Lygosoma sundevallii

E Nucras intertexta

F Pachydactylus bibronii

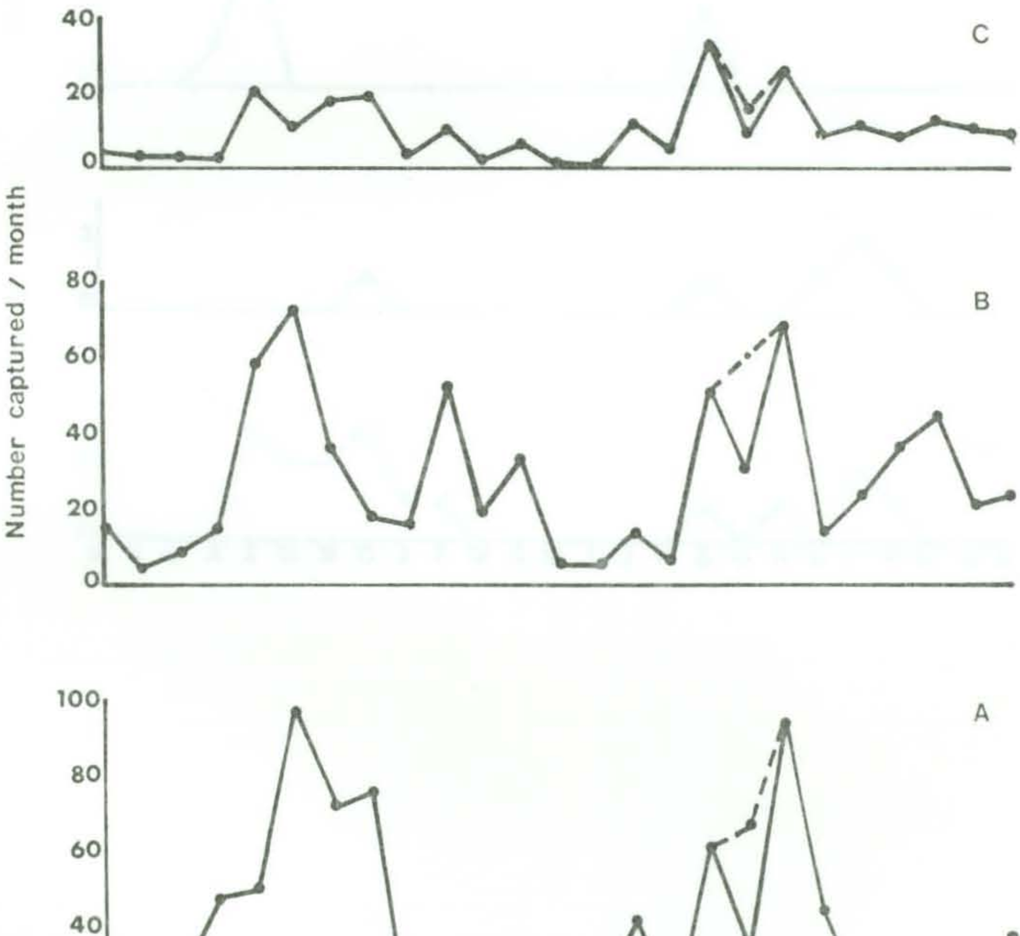
G Agama atricollis

H Pachydactylus capensis

I Gerrhosaurus flavigularis

J Agama aculeata

--------- extrapolation, as census period was of shorter then normal duration.


C
B
A
Number captured / month
40
20
0
80
60
40
20
0
100
80
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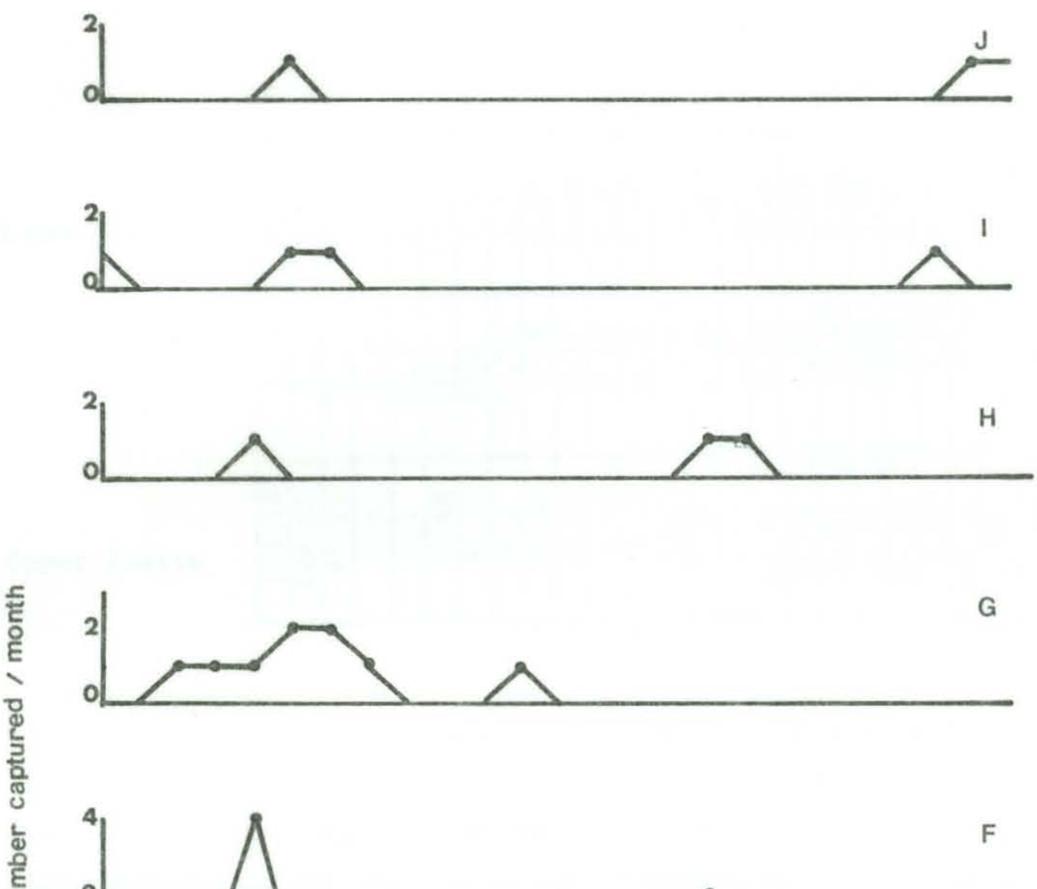
M J J A S O N D J F M A M J J A S O N D J F M A M


J
I
H
G
F
E
D
Number captured / month
0
2
4
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

of the various species of the most important terrestrial lizards in the snake trapping grid. It is apparent that those species which were most commonly captured exhibited a considerable decline at this time of the year. Additional suppressive effects are those of rainfall and cool, cloudy weather, as mentioned previously.

Terrestrial lizards, therefore, show a marked fluctuation in population density and biomass over the period of observation (Figure 24). Concomitant with the snakes, density of lizards in the 1975/76 summer season was high, even extending into November. Declines during January and March were also apparent for reasons previously explained. This trend was repeated during the 1976/77 season. Density ranged from a peak of 23/ha during early summer to as low as 0,18/ha during winter. These fluctuations and their confidence limits are recorded in Table 10.

Table 10. Density of lizards showing upper and lower confidence limits (No/ha).

	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
Lower Limits	0,53	0,47	0,31	1,21	7,75	10,32	7,6	5,75	0,29	1,10	0,0	0,60	0,10	0,004	0,27	0,04	0,76	6,69	5,96	1,5	0,38	0,61	0,71	0,55	0,17
D	7,3	6,6	4,37	4,37	19,7	19,3	23,6	15,97	4,08	7,17	0,18	8,39	0,68	0,06	1,25	0,63	4,93	14,29	10,6	6,8	2,45	8,43	1,97	3,59	2.45
Upper Limits	143,18	128,86	85,11	12,91	42,7	32,68	60,54	37,2	79,54	40,47	3,58	163,47	3,86	1,19	4,62	12,33	27,86	26,87	17,37	25,15	13,87	164,26	4,59	20,26	47,73

Although a reduction in density during January is attributable to a decrease in numbers of animals, it is also apparent that the biomass falls disproportionately low. This is the result of the combined effect of the loss of adult animals as well as the influx of hatchlings which emerge from eggs or are given birth to at this time of the year (See also Reproduction).

Lygodactylus capensis, the Cape dwarf gecko, is the most abundant arboreal lizard in the Burkea Savanna Ecosystem. As mentioned previously, it was not feasible to sample them by conventional trapping means. It was,

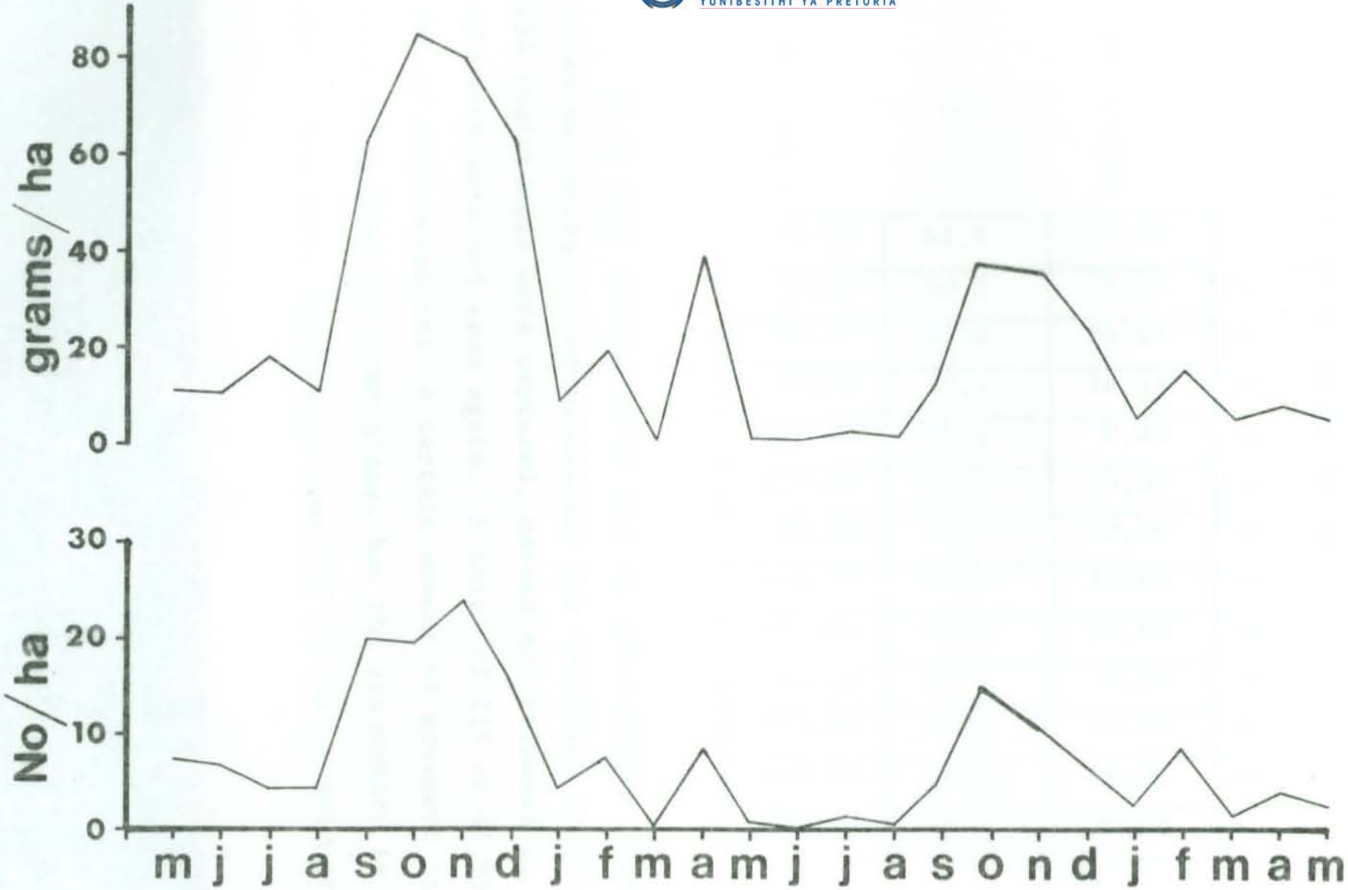


Figure 24. Density and biomass of lizards in the *Burkea africana* - *Eragrostis pallens* Study Area: May 1975 to May 1977 (excluding *Lygodactylus capensis*)

therefore, necessary to locate these lizards on foot and capture them by hand on boles of trees, rotting logs and even on the stems of shrubs. Initially censussed daily over ten days, the study was later curtailed to include up to five censusses over this period. This was necessitated because of the trauma of capture and handling, as well as the risk of injury to these small lizards which, when fully mature, may attain a mass of 1,3 g.These grey geckos move like a shadow in retreat and often scurry around from the sunlit side of the bole into the shadows where their cryptic coloration make them exceedingly difficult to see. However, it was possible ultimately to capture most of these lizards and an accumulative total of captures revealed that all available habitat (69%) of all trees, was occupied by these lizards (Figure 25). They breed throughout the year, compounding the problems of censussing a population. Table 11, therefore, expresses the density of these lizards per ha over the period of thirteen months, from June 1975 to June 1976. Confidence limits are included.

Table 11. Density of _Lygodactylus capensis_ in the _Burkea africana_ - _Eragrostis pallens_ Study Area, showing upper and lower confidence limits (No/ha).

	J	J	A	S	O	N	D	J	F	M	A	M	J
Lower Limits	37,38	37,29	26,68	18,96	9,29	43,07	30,66	15,84	16,64	2,30	23,30	66,81	30,26
D	61,8	50,3	47,6	38,3	64,5	71,2	50,7	41,0	72,3	10	49,2	102,5	56,9
Upper Limits	105,08	68,34	88,7	83,11	2514,08	121,05	86,18	126,20	612,66	84,63	113,41	160,64	112,69

It is only during March that an unacceptable figure for density was obtained, owing to the relatively few censusses undertaken. A total of 254 individuals were captured, marked and released in the Study Area, many of which were not seen again. A total of 119 or 46,85% were recaptured on one or more occasions. A certain amount of movement in and out of the one hectare Study Area did take place, but the assumption is made that this cancels out. Therefore, apparently over 50% of the individuals disappeared after

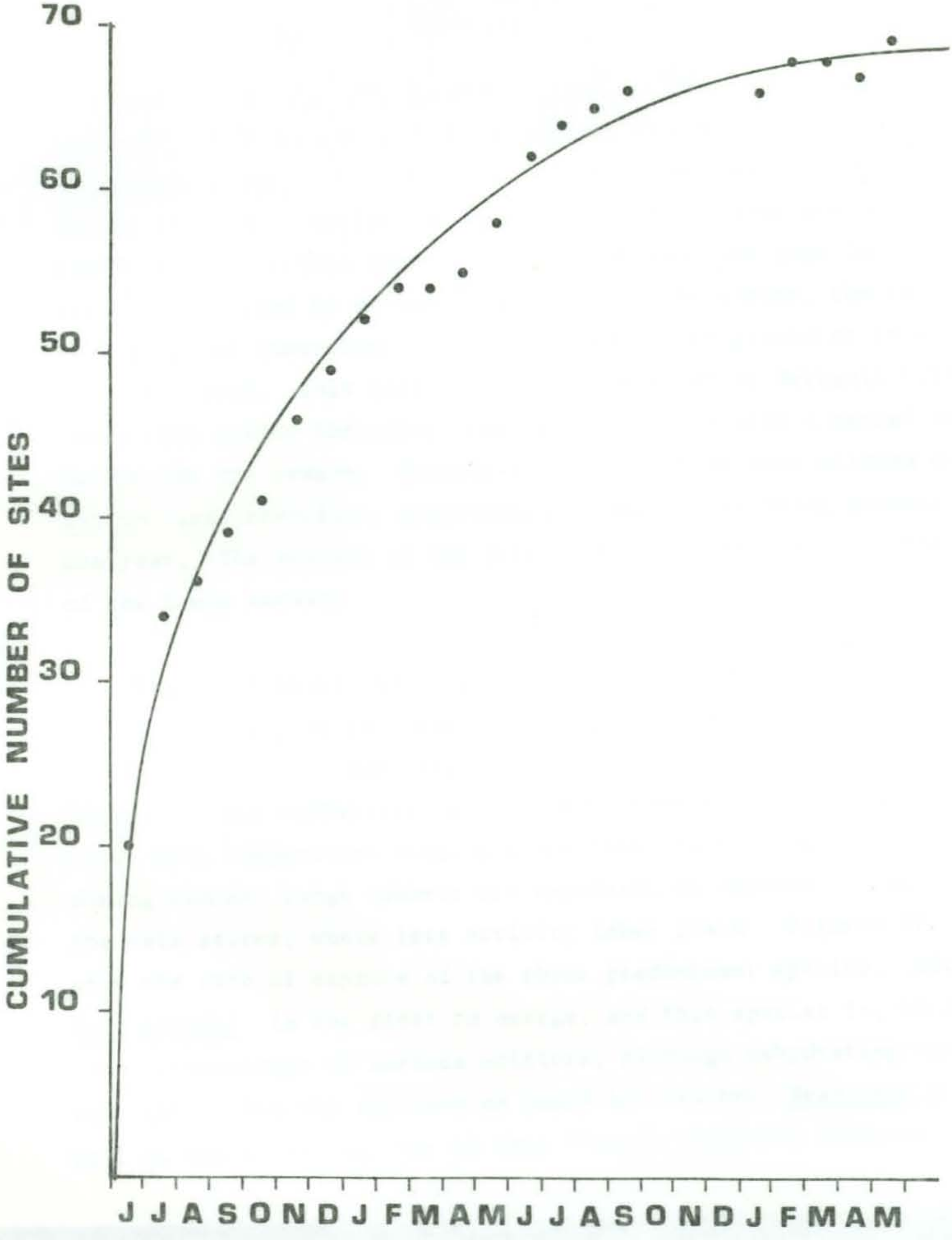


Figure 25. Cumulative number of Lygodactylus capensis capture sites, June 1975 to May 1977, in the Intensive Study Area.

they were released. Only a tiny fraction could have died from handling and so forth and, therefore, mortality must be relatively high. They breed throughout the year and are relatively long-lived lizards. From Table 11 it is apparent that there are considerable fluctuations in numbers from one month to the next, with a mean of 55,1/ha. Mean mass of Lygodactylus capensis is 0,76 g, (N = 100, SD = 0,29) which gives a mean biomass of 41,87g/ha.

A mean total lizard density, therefore, is 7,71 + 55,1 = 62,27/ha with a biomass of 22,49 + 41,87 = 64,36g/ha. The geckos, therefore, contribute substantially to the savanna community.

Amphibians

One of the greatest surprises arising from the present study was the discovery of large numbers of amphibians existing in the Burkea africana - Eragrostis pallens savanna. A total of eleven species were found here during the summer months but again only two or three predominated and could make a possible impact on the ecosystem (see page 56). Winters are characterised by no amphibian activity whatsoever, the vast majority having buried themselves or found holes in the ground or in hollow logs and even trees. This contrasted with the study by Barbault (1975), who found them active throughout the year, although with a marked depression during the dry season. Depressions in his study area allowed water accumulation and, therefore, contributed to amphibians being present throughout the year. The ecotone of the forest was also important for the amphibians of the Lamto savanna.

Figure 26 shows the total number of amphibians captured in the present study area over the two-year period. It is apparent that there is no activity from April to September, and during 1977, from the end of March. Earlier it was emphasised (p. 30) how dependent the amphibians are on moisture, with temperature playing a secondary role. Therefore, on rainy days during summer, large numbers are captured, as opposed to hot days inbetween the rain storms, where less activity takes place. Figures 27, 28 and 29 show the rate of capture of the three predominant species. After winter, Bufo garmani is the first to emerge, and this species is, to a certain extent, independent of surface moisture, although dehydrating very rapidly in sunlight. With the approach of humid hot weather, Breviceps a. adsperus will be heard calling, but as this frog is virtually independent of surface

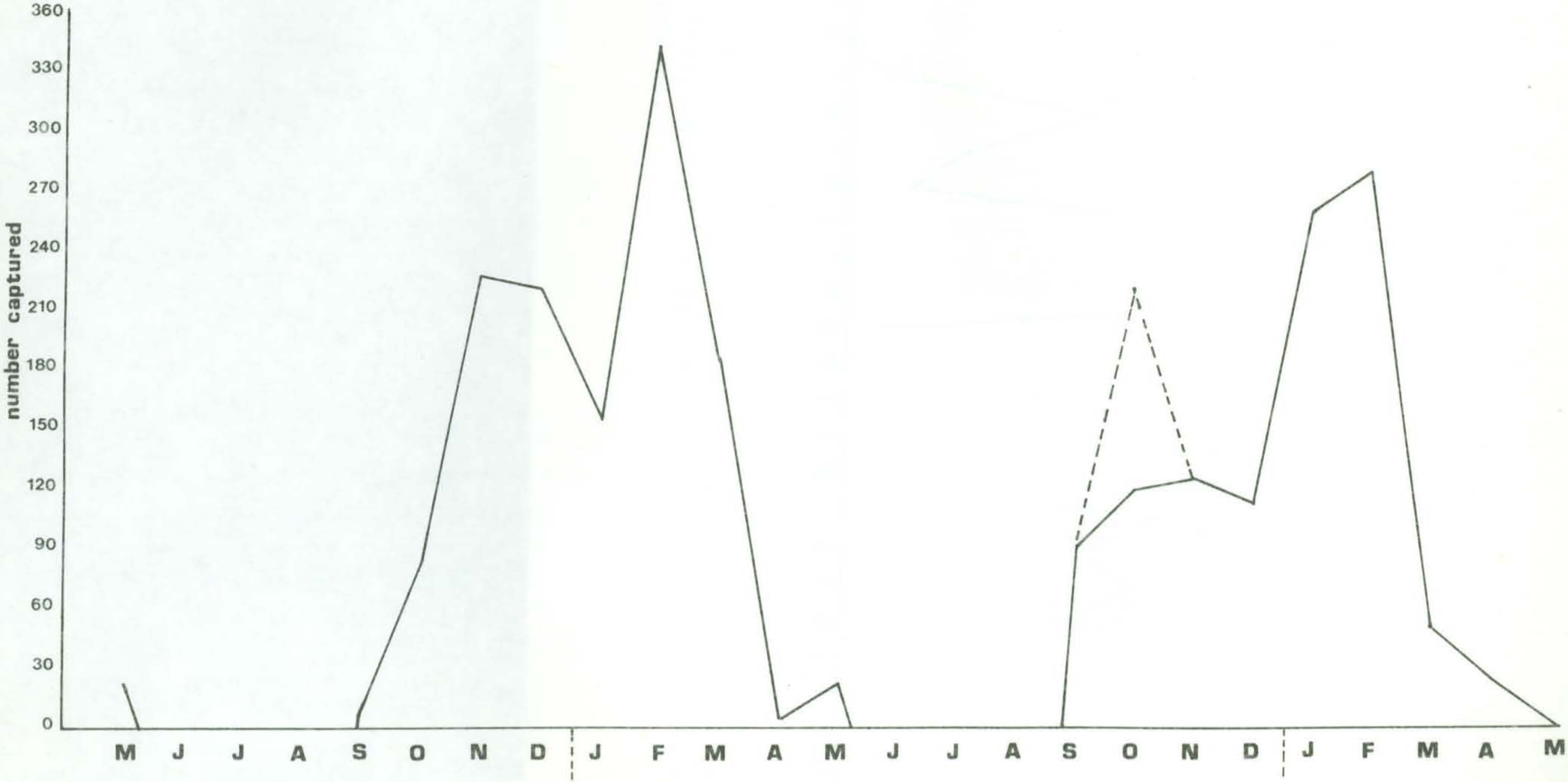


Figure 26. Total number of amphibians captured in the *Burkea africana* - *Eragrostis pallens* Study Area, May 1975 - May 1977. (------------ = extrapolation as census period shortened).

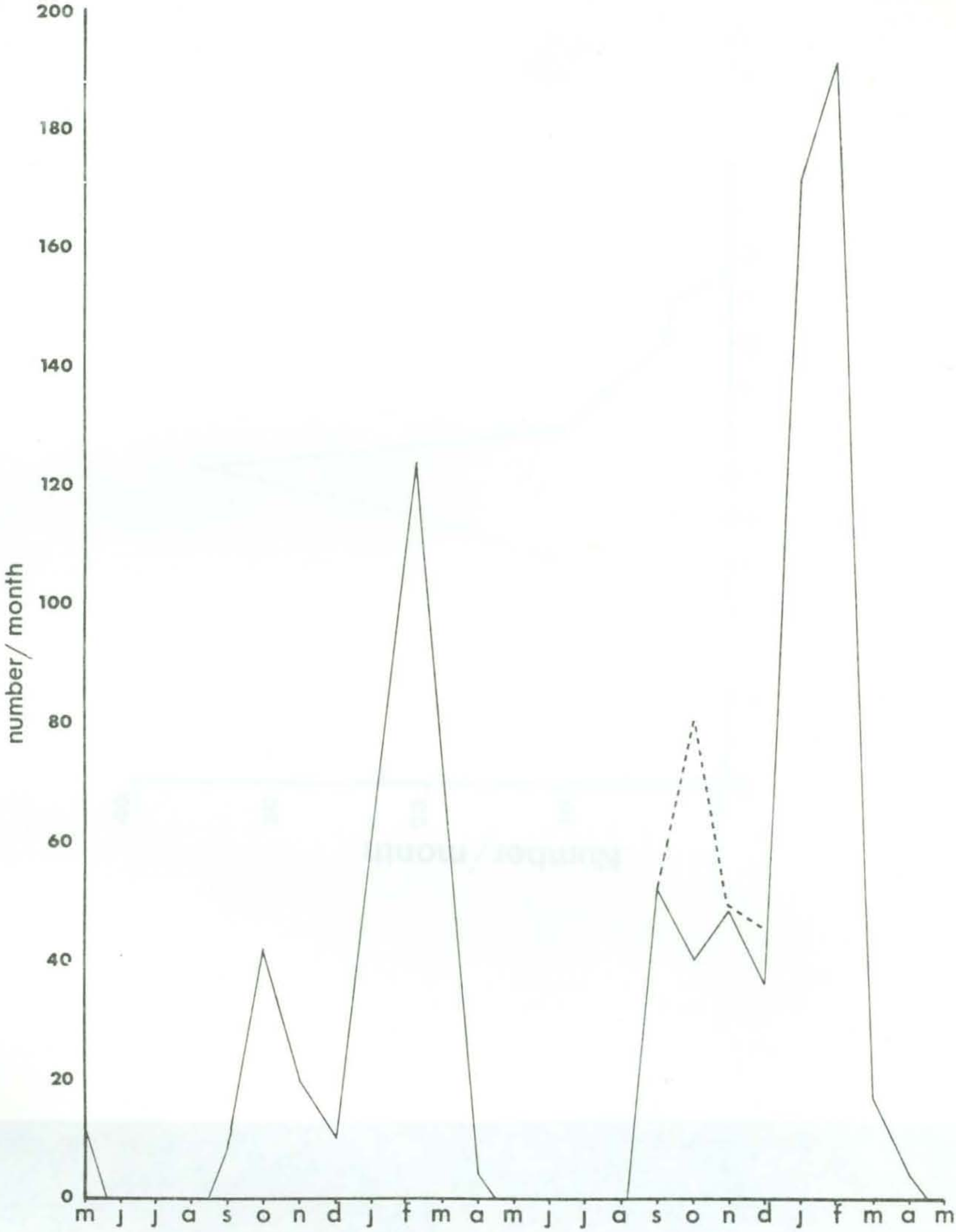


Figure 27. Monthly fluctuations of Bufo garmani captured in the Study Area, May 1975 - May 1977. (---------- = extrapolation as census period shortened).

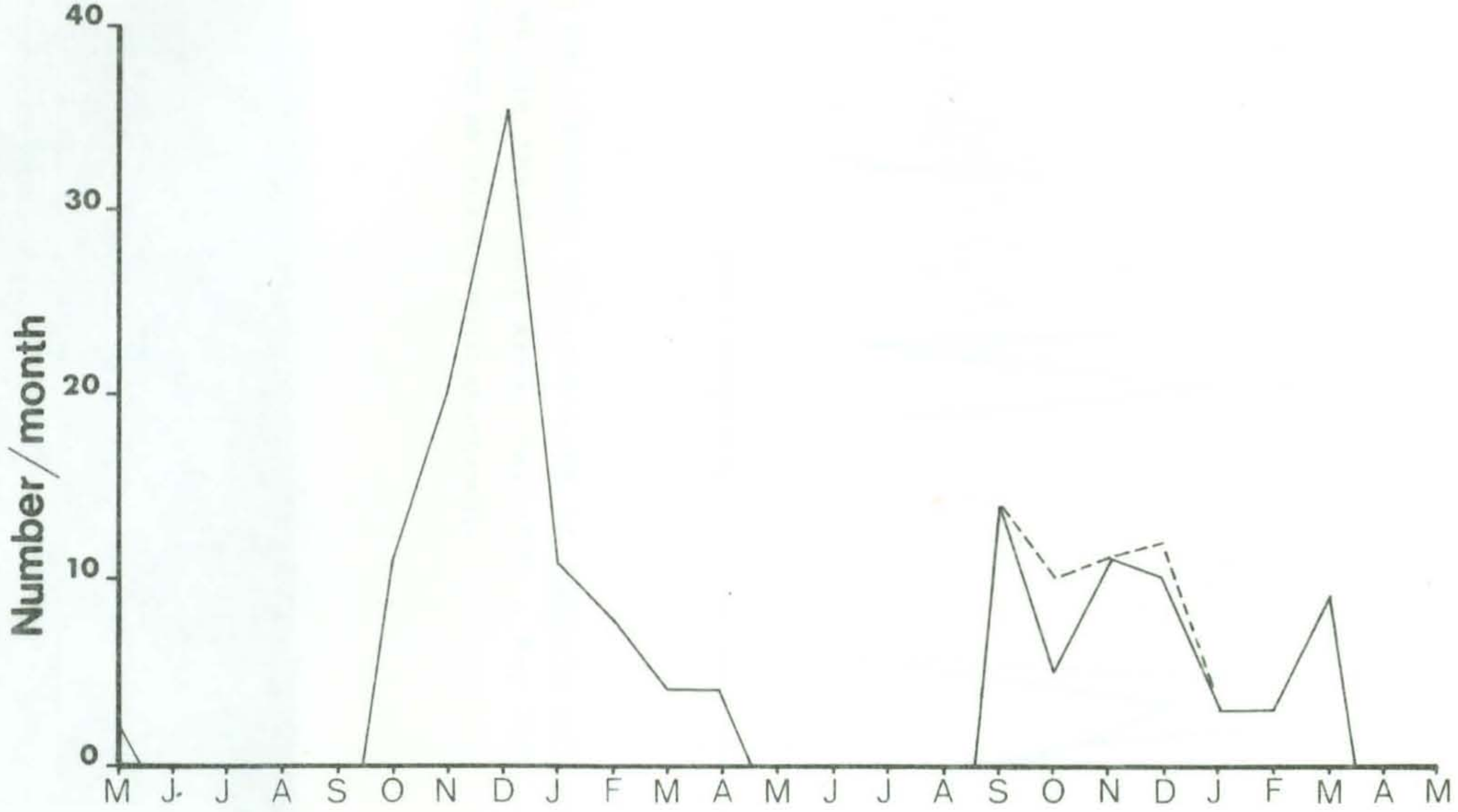


Figure 28. Monthly fluctuations of Breviceps adspersus captured in the Study Area, May 1975 - May 1977. (---------- = extrapolation as census period shortened).

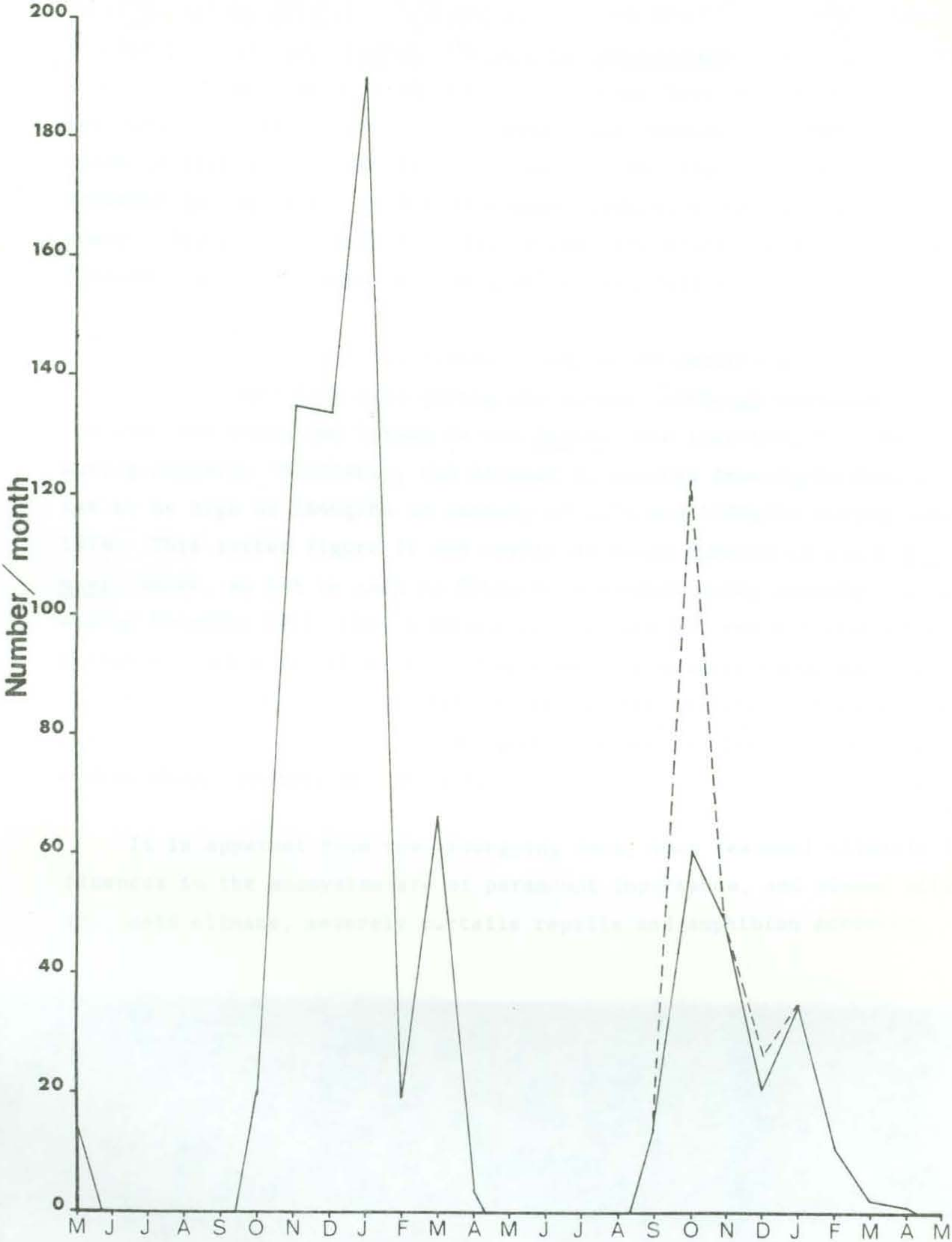


Figure 29. Monthly fluctuations of Kassina senegalensis captured in the Study Area, May 1975 - May 1977. (------------ = extrapolation as census period shortened).

water, it is widespread and found many kilometres from water. The third species, Kassina senegalensis, is completely dependent on the rains and will only emerge during and after a rain storm. They are very sensitive to heat stress and may die even if not exposed to the sun.

The notable feature of the Study Area is the sandy nature of the soil, which on the one hand permits animals to burrow easily, particularly the amphibians, and on the other it is porous and, therefore, no matter how much precipitation occurs, the water drains away. Despite the occurrence of scattered pools along the road fringing the Study Area, no breeding was observed to take place here. Therefore, adult amphibians move westwards, downslope until they reach the turfvlei where the clayey nature of the soil allows the formation of pools. The adult Bufo garmani move down prior to the Kassina's, but once rain has fallen, all the amphibians, with the exception of Breviceps, are found breeding there. This results in a large scale immigration of juveniles into the Study Area during January, particularly of Bufo garmani and Kassina senegalensis, which do not reach maturity in one season as do most of the other species, which accounts for the enormous peak of activity in January and February. Breviceps adsperus reach a peak of activity prior to that of the other species, usually during November and December, with a pronounced reduction during January and February. Troughs and peaks of activity can, therefore, be attributed to four factors, namely, emigration, immigration, rainfall and drought.

Figure 30 exhibits the trends of amphibian density and the biomass. The former ranges from zero during the winter, although technically speaking they are alive and living in the Burkea, but inactive, to 199,9/ha during January. Similarly, the biomass fluctuates from 0g/ha during winter to as high as 1640g/ha in January of 1976 and 1500g/ha during October 1976. This latter figure is the result of large numbers of adult Bufo garmani which, as can be seen in Table 6, are fairly bulky animals. It was during December 1976, that a period of low rainfall and hot weather was experienced, which is reflected in the number of animals captured, coupled with an interrupted program when the researcher was involved in another project. Table 12 refers to the density values and the confidence limits within which the data are analysed.

It is apparent from the aforegoing data, that seasonal climatic influences in the ecosystem are of paramount importance, and winter with its dry, cold climate, severely curtails reptile and amphibian activity.

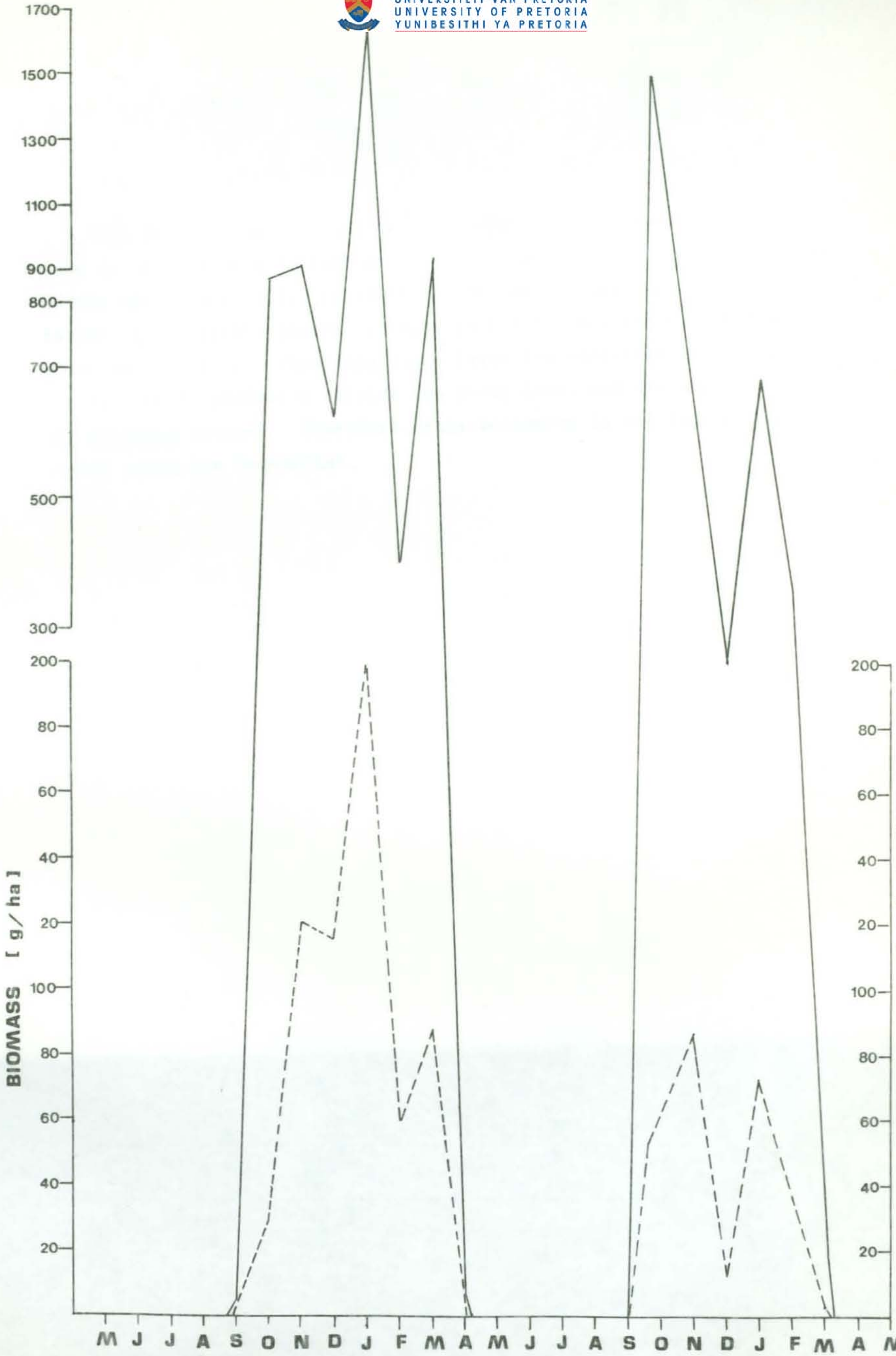


Figure 30. Density and biomass of Amphibians in the <u>Burkea</u>

Table 12. Density of amphibians in the *Burkea africana* - *Eragrostis pallens* Study Area over the period May 1975 to May 1977.

	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
Lower Limits	0,14	0,0	0,0	0,0	0,01	2,09	18,46	25,65	44,15	13,11	13,55	0,06	0,0	0,0	0,0	0,0		16,8	6,32	2,65	23,49	16,85	0,49	0,0	0,0
D	1,9	0,0	0,0	0,0	0,1	29,1	120,4	115,9	199,9	59,4	88,3	0,9	0,0	0,0	0,0	0,0		52,2	87,8	12,0	72,9	37,8	3,2	0,0	0,0
Upper Limits	38,58	0,0	0,0	0,0	2,78	567,96	679,17	427,51	437,82	219,04	498,28	17,5	0,0	0,0	0,0	0,0		133,83	1711,45	44,28	187,16	73,88	17,96	0,0	0,0

Moreover, it is also apparent, as mentioned previously, that temperature is the factor governing activity in reptiles and to a lesser extent, in the amphibians, while rainfall is the factor limiting activity in the latter, and possibly indirectly also in the former, as will be discussed under Reproduction. When amphibians leave the ecosystem to breed, they are exposed to predation outside the Study Area, and are lost to the *Burkea africana* savanna. Therefore, this ecosystem is not independent of others along its boundaries.