# THE ECOLOGY OF THE REPTILES AND AMPHIBIANS IN THE *Burkea africana* - *Eragrostis pallens* SAVANNA OF THE NYLSVLEY NATURE RESERVE

by

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## ABSTRACT

The ecology of reptiles and amphibians in the *Burkea africana* - *Eragrostis pallens* savanna is discussed in relation to population size and biomass. Aspects of reptile and amphibian life style with regard to food, feeding, reproduction, growth and movement are discussed.

Population densities and biomass fluctuate both during and between years. Snakes average 3,08/ha with a biomass of 93,36 g/ha, lizards 62,27/ha with a biomass of 64,36 g/ha and amphibians 58,79/ha with a biomass of 593,4 g/ha.

On the Nylsvley Nature Reserve, snake, lizard and amphibian diversity is greatest in the Study Area. The combination of the three groups are termed a herpetofaunal assemblage. This assemblage is then discussed in the light of other similar studies including those concerned with origins and relations.

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# CHAPTER 1

# INTRODUCTION

The present study commenced in May 1975 as part of the first phase of the Savanna Ecosystem Project. The Ecosystem Project was initiated to investigate the structure and functioning of a Savanna Ecosystem with the eventual aim of being able to predict changes in the vegetation structure, composition and its inherent animal component, and monitor changes induced by management practices.

The Savannas are widespread in Africa and were formed under varying degrees of aridity, temperature and edaphic conditions. As with most semi-arid regions, they are very fragile and easily disturbed by over-grazing, overburning or by changes in the animal component. They become degraded, resulting in erosion and the spread of desert. There are several types of savanna in southern Africa, which can broadly be divided into broad-leaved deciduous and microphyllous savannas. The ecosystem study at Nylsvley is located in an area of savanna dominated by Burkea africana trees with Eragostis pallens as the main grass species. Interspersed in the Burkea africana savanna are areas of microphyllous vegetation usually located on disturbed areas.

The reptile and amphibian population study was part of the overall plan to identify major components and pathways within the ecosystem and therefore formed part of the consumer component.

The objectives of this study were basically three fold:

1. To determine the species diversity and distribution of reptiles and amphibians on the Nylsvley Nature Reserve and the Ecosystem study area in particular. Chapter 4.
2. To determine population size and biomass of reptiles and amphibians in the Ecosystem study area. Chapter 4.
3. To determine the inter-relationship between the reptiles and amphibians and their physical and biotic environment. This included an understanding of food and feeding movement, reproduction, growth and biomass. Chapters 4, 5, 6 and 7.

A checklist of the vertebrate fauna, excluding the avifauna, was completed in 1977 (Jacobsen 1977) and served to indicate the diversity of animal life on the Nylsvley Nature Reserve. A total of 29 snakes, 24 lizard, 17 amphibian, 4 chelonian and 62 mammal species was described. This represents an estimated 95% of the terrestrial vertebrate species likely to be found. Of this total, 11 amphibian, 41 reptile and 43 mammal species are to be found in the _Burkea africana_ - _Eragrostis pallens_ savanna. This made estimates of populations exceedingly difficult. From the initial survey it was apparent that only a relatively small number of species dominated the herpetofaunal community. These included two snake species, four lizard species and three amphibian species. The most abundant snakes in this instance were _Thelotornis capensis_ (vine snake) and _Psammophis sibilans brevirostris_ (short-snouted sand snake). The lizards included _Ichnotropis capensis_ (Cape rough-scaled lizard), _Lygodactylus capensis_ (Cape dwarf gecko), _Mabuya varia_ (variable skink) and _Panaspis wahlbergi_ (snake-eyed skink). Of the amphibians the most abundant were _Bufo garmani_ (northern mottled toad), _Kassina senegalensis_ (bubbling kassina) and _Breviceps adspersus_ (common short-headed frog) (Figure 1).

Population estimates from mark-recapture samples with which this study was involved have several inherent drawbacks or assumptions which question the reliability of results, particularly if a low recapture rate is experienced. Previous investigations in the Study Area showed all forms of animal life to be depauperate and other methods of population estimation not practical. Total sampling as used by Barbault (1971, 1973, 1974a) at Lamto was not possible due to inadequate labour and finance. The use of line transects to estimate populations, Western (1974), Eberhardt (1978) was also not feasible owing to the paucity of animals. Mark-recapture methods were resorted to as the only method available under the conditions pertaining at Nylsvley. The drawbacks to this are mainly concerned with three basic assumptions which had to be made:

That no emigration or immigration occurred during the period of study.

Mortality and natality are assumed to have balanced out during the period of study.

The chance of capturing marked and unmarked animals was equal.

Figure 1 The main reptile and amphibian species of the *Burkea africana* - *Eragrostis pallens* Savanna Study Area

(a) *Ichnotropis capensis*
(b) *Mabuya varia*
(c) *Panaspis wahlbergi*
(d) *Lygodactylus capensis*
(e) *Psammophis sibilans brevirostris*
(f) *Thelotornis capensis*
(g) *Bufo garmani*
(h) *Breviceps a adspersus*
(i) *Kassina senegalensis*

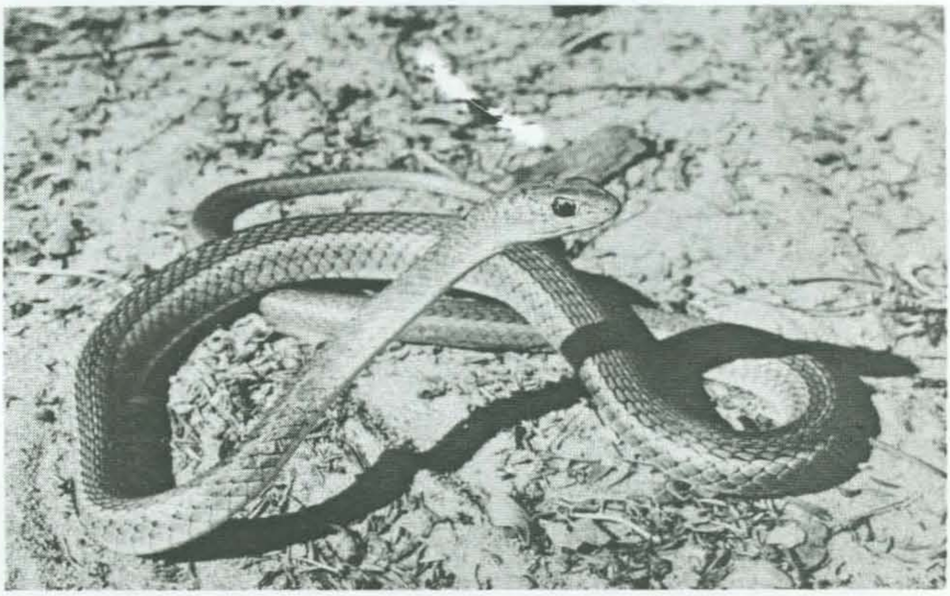
A

B

C

D

E



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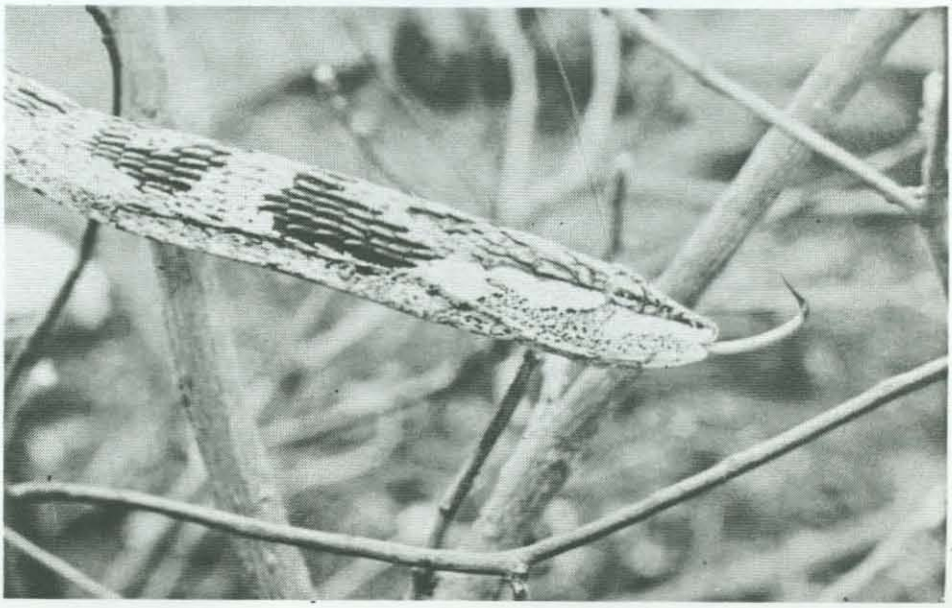

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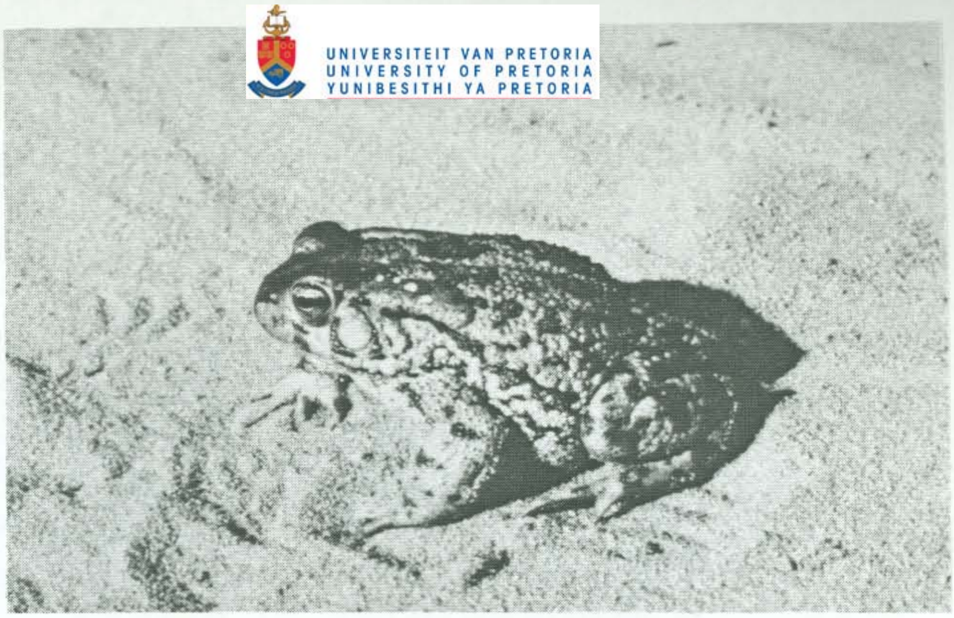

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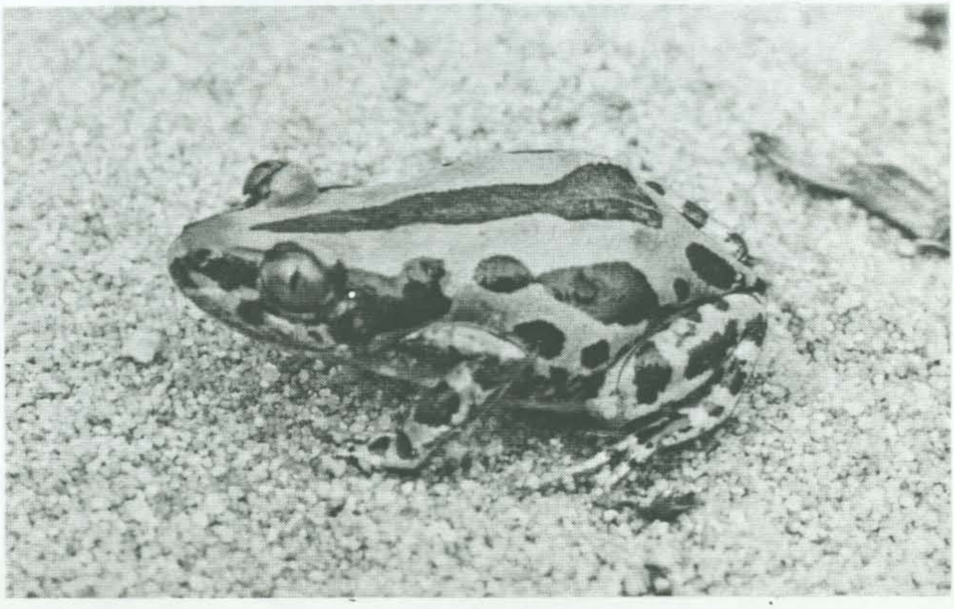


Various authors, De Lury (1951), Schaefer (1951) and Jolly (1963), have used the mark-recapture technique to determine population size. However, usually these have been used for estimating fish populations where it is possible to net a number, mark and release and, on a subsequent date, net again and determine the percentage of marked to unmarked individuals in the population.

The most simple formulas are those derived by Petersen and Lincoln and known as the Petersen and Lincoln Indices. The formula is simply as follows:-

$$N = \frac{Mn}{m}$$

where $N$ = population size
$M$ = total number of marked individuals in the population
$n$ = sample captured
$m$ = number of marked individuals in sample $n$.

This method was suitable for short periods of time but did not compensate adequately for longer intervals. This induced modifications to the existing method. One of the first was the Schnabel method which was closely followed by the Schumacher-Eschmeyer technique. The Schnabel Index is simply a summation of the existing Peterson Index as follows:-

$$N = \frac{\Sigma (M)\ (n)}{\Sigma m}$$

It is assumed that the number of recaptures follows a Poisson distribution. One of the problems of this method is that the variances are difficult to estimate. Therefore, simple straightforward tests of differences in population level, as well as confidence limits for the population estimate, are possible by using the knowledge that the number recaptured approximate a Poisson distribution, Chapman (1954).

Chapman (loc.cit) also determined that a modification of the Schnabel Index presented a nearly unbiased estimate of the total number of animals present. He therefore proposed the following equation:-

$$N = \frac{\Sigma (M)\ (n)}{\Sigma m + 1}$$

Confidence limits can then be calculated using the method of Chapman and Overton (1966). Eberhardt (1969) mentions that the usual capture - recapture methods may seriously underestimate population density, particularly as they all assume probability of capture is the same for all members of the populations. However, trapping results and estimates based thereon during this present study indicate the contrary.

The population study took place over an area of 64 ha of a section of the area demarcated for the ecosystem study and one which would remain relatively undisturbed by other researchers. The preliminary survey of the number and distribution of species involved indicated that the animals were divided into different strata within defined habitats. Thus, there were arboreal, terrestrial, rupicolous and fossorial species.

Very little research has been done on total populations within a specific area. The one most comparable and to which repeated reference is made, is that of R. Barbault under the auspices of the Laboratoire de Zoologie de l'Ecole Normale Superieure, Paris at Lamto on the Ivory Coast, Barbault (1971, 1973, 1974a, b, 1975, 1976a, b, c, d). This is an area of tropical humid savanna subjected to annual fires except where protected under experimental conditions and it is with this section in particular that some comparison will be made.

Other authors, Dargan & Stickel (1949), Degenhardt (1966), Alcala and Brown (1967), Bauerle (1971) and Western (loc.cit.,) used various sampling techniques to determine population sizes but most were difficult to apply to local conditions. The method finally decided on approximated closely that of Dargan and Stickel (loc.cit.) and Bauerle (loc.cit.)

As there are few reptiles which show sexual dimorphism, the sexing of captured reptiles followed the method of Szidat (1968). Various papers deal with the marking of individuals for later recognition. Among these methods are scale clipping, Blanchard and Finster (1933), Spellenberg (1977); tatooing, Woodbury (1948, 1956); toe clipping, Woodbury (1956): notching the carapace of chelonians, Woodbury (1956). An improved method of marking snakes involved the use of an electric soldering iron with a fine point to cut through the scales at their base, Weary (1969). This effectively produced a permanent identifiable mark. Other methods of marking which are often used during fish studies include injecting dye under the skin or into the dermis, which allows the colour to show through, Dunn and Coker (1951), Al-Hamid (1954) and Kelly (1967).

This has the advantage of recognizing animals without handling them. Finally, Radiotelemetry was used by Fitch & Shirer (1971), and snakes were made to swallow packages containing transmitters which worked with varying success and for different lengths of time. This method opens up many possibilities, particularly for relatively short-term studies.

Few population or detailed autecological studies have been carried out on African reptiles. Such studies are still largely in their infancy with most research being taxonomical, Broadley (1976). This makes any detailed study so much more important and at the same time increases our knowledge of a hitherto largely neglected group of lower vertebrates. The present study is, therefore, a contribution to our understanding of African reptiles and amphibians and their interaction with the environment, both physical and faunistic.

# CHAPTER 2

## THE ENVIRONMENT AND STUDY AREA

A number of papers have been published on the Nylsvley Ecosystem, Hirst (1975), Lubke, Clinning and Smith (1975) van der Meulen, Zwanzinger, Gonsalves and Weisser (1976), Huntley (1977, 1978), Harmse (1977) and Jacobsen (1977). These authors report on various aspects of the ecology of the area and provide descriptions of the climate, soil, vegetation and fauna. However to elucidate the position of the present study within the context of the Ecosystem Project, the various aspects are discussed in more detail.

### The physical and botanical characteristics

The savannas of Nylsvley (24°29' S; 28°42' E), lie in the Mixed Bushveld, Acocks (1953), of the central Transvaal, approximately 10 km south of the town of Naboomspruit (Figure 2). The elevation of the area varies between 1 080 m and 1 140 m a.s.l. and there is a small, seasonal river (the Nyl river), flowing across the reserve from SW to NE along a strip of marshy lowland. On account of the very low drainage elevation from one end of the Reserve to the other (7 m), extensive flooding results during the rainy season. Prominent hills are Maroelakop (1 140 m) in the south and Stemmerskop (1 090 m) further to the north west. The southern elevations are mainly underlain by sandstone and conglomerate bands of the Waterberg system, while the northern elevations are underlain by felsites of the Bushveld Igneous Complex. Several soil series occur associated with differences in geology and topography. The higher lying areas have relatively sandy soils and carry mostly a broad-leaved deciduous savanna as opposed to the lowlands, where the soil is largely calcareous clay with microphyllous deciduous thorn savanna. Both areas exhibit a marked seasonality with regard to the grass layer.

Termitaria are a feature of the northern elevation of the felsites, as well as along the edge of the Nyl floodplain. The area experiences a moderately low summer rainfall with a dry frosty winter period.

In the past, the area was used mainly for cattle ranching and was conserved as far as possible. Small areas of lowlands have been ploughed, while disturbed areas of abandoned bantu settlements are still present on the

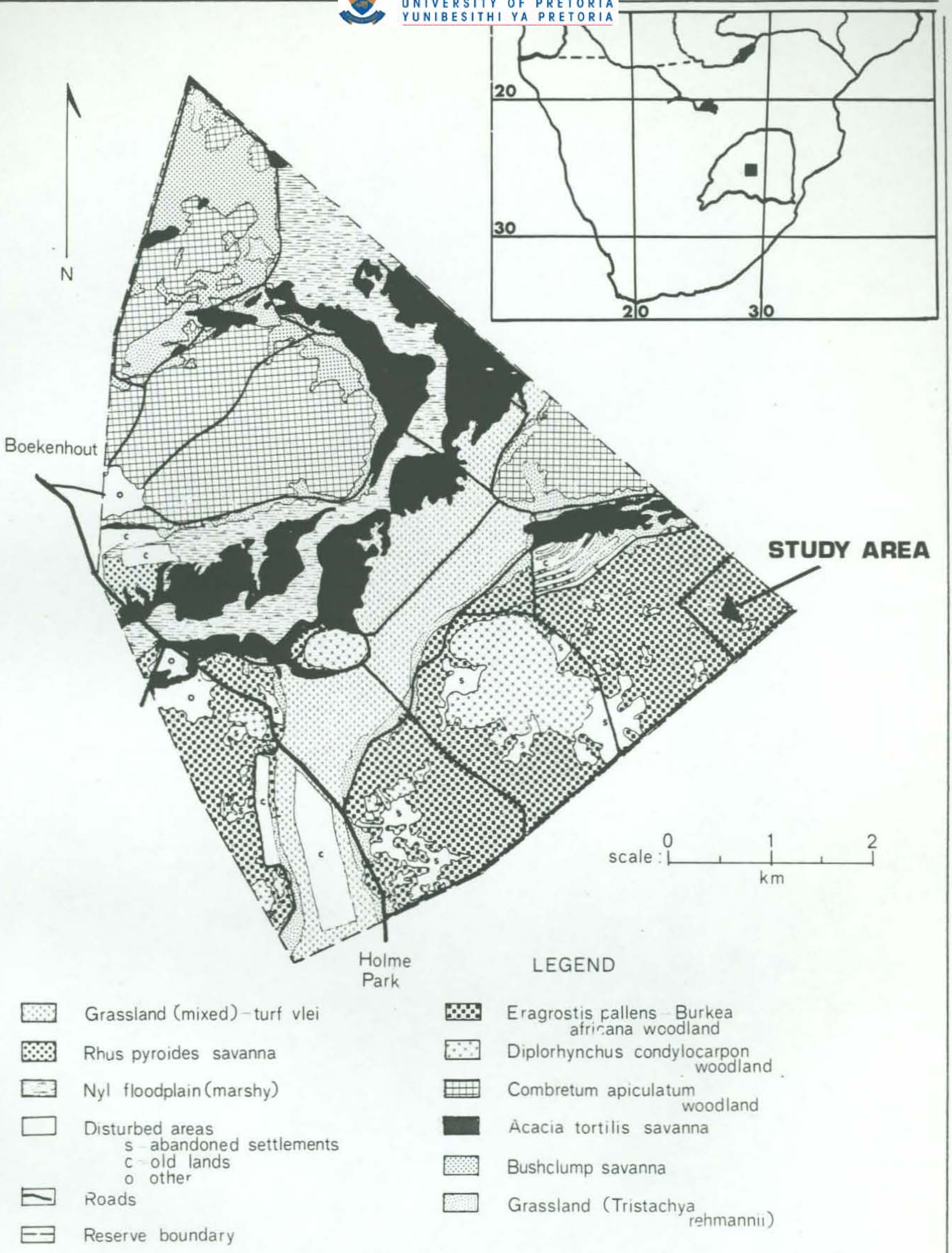


Fig. 2. VEGETATION OF NYLSVLEY NATURE RESERVE.
(modified from Coetzee et al (1977))
Showing the vegetation types and the locality of the study area.

sandstone elevations of the south, forming patches of microphyllous vegetation within the broad-leaved deciduous savanna. The use of the area as a cattle ranch has permitted a wide variety of vertebrate species to maintain viable populations, Jacobsen (1977).

## The soils

The soils on Nylsvley may be grouped into five broad categories, Harmse (1977):-

(a) litholitic soils;
(b) non-calcareous, well-drained sandy soils;
(c) non-calcareous, poorly-drained sandy soils;
(d) calcareous, alluvial soils;
(e) calcareous, vertic black clay soils.

Of these, only the first two are present in the study area, and the first only in the isolated rocky outcrops found in the upper elevated areas. They are characterised by unconsolidated material or hard rock with a minimum of soil particles.

The majority of the area is covered by non-calcareous, well-drained sandy soils, including in this category on the more elevated areas, well-drained sandstone mainly of the Hutton and Mispah forms with isolated rocky outcrops. The sandy soil is medium to coarse with red B-horizons. Lower down the slope the Clovelly form also originating from the Waterberg sandstone predominates. This soil is also sandy but has a yellow B-horizon. It tends to be more water-logged than the soil higher up the slope. However, several series are distinguished and together form a topo-sequence. This sequence from upper to lower slopes consists of dystrophic, mesotrophic and eutrophic Hutton soils, followed by dystrophic and mesotrophic Clovelly soils. The well-drained soils of the elevated areas of the study site provide a habitat for many animals which are not found elsewhere. This is also no doubt due to the small amount of clayey material found in the B-horizon, while the sand is considerably coarser, promoting faster drainage, as well as allowing easier access for burrowing reptiles and amphibians, particularly during the winter months. The area is also favourable to the incubation of the eggs of reptiles which are subject to fungal attacks if too much moisture persists. Moreover, this is the only habitat of the Hottentot golden mole (Amblyosomus hottentotus), which probably feeds mainly on burrowing lizards (*Lygosoma sundevallii*) and amphisbaenians (*Monopeltis capensis*), which are also restricted to this habitat.

## The vegetation

As mentioned previously, the vegetation of the study area consists of broad-leaved deciduous savanna with smaller areas of microphyllous savanna established on areas of disturbed soil, such as old kraal sites. The communities of the elevated sandstone regions grow in shallow to deep non-calcareous soils which may be litholitic. Frosts are relatively mild and the soils well-drained.

On the elevated slopes, a tree savanna is more apparent, with a gradual change in structure to a grass savanna lower down the slopes with impeded drainage. The upper slopes of the study area therefore are covered by the *Eragrostis pallens* -*Burkea africana* tree savanna, Coetzee *et al.* (1976). This community occurs on the non-litholitic, sandy soils. These soils have a low nutrient status and consequently the ground cover is relatively open with *Eragrostis pallens*, the dominant grass. The topography is flat to very gently sloping, usually less than 2°. Occasionally, sandstone outcrops occur. There is usually a 5-10% cover of plant litter, mainly leaves from *Burkea africana* and *Ochna pulchra* but twigs and grass also form a part. Dead trees are occasionally found lying on the ground and provide food and shelter for many invertebrates, as well as reptiles such as *Lygosoma sundevallii*, *Lygodactylus capensis* and *Mabuya varia*.

This community is differentiated by a number of tree and shrub species, including *Grewia flavescens*, *Strychnos pungens*, *S. cocculoides*, *Lannea discolor* and *Securidaca longepedunculata*. In the field layer, the grasses *Eragrostis pallens*, *Aristida congesta* and *A. stipitata* predominate, while herbs such as *Vernonia poskeana*, *Limeum viscosum*, *Cleome rubella* and *Dichapetalum cymosum* are characteristic. While this community is broadly defined, it actually consists of three variations, Coetzee *et al.* (1976).

(a) *Eragrostis pallens* - *Dombeya rotundifolia* variation found mainly on the middle and upper slopes of the study area and making up two-thirds of the reptile and amphibian study area. This variation is found on the Hutton and Mispah soil forms. Total tree cover varies from 20 to 60% and the trees range in height from seedlings to 15 m with *Burkea africana*, *Terminalia sericea* and *Combretum molle* dominant, while *Grewia flavescens* and *Ochna pulchra* are the main shrubs. The grass and forb cover varies from 15 to 65%. Structurally, this variation can also be differentiated from the other two variations because some woody species are taller here than elsewhere. Such species include *Strychnos pungens*, *Lannea discolor*, *Ochna pulchra* and *Terminalia sericea*. In the other two variations these species occur as coppicing shrubs with emergent dead twigs, possibly caused by cold air accumulation or impeded drainage.

This area is characterized by the faunistic component of which *Amblyosomus hottentotus*, *Xenocalamus bicolor australis*, *Monopeltis capensis* and *Psammobates oculifer* are endemic while others such as *Lygodactylus capensis*, *Ichnotropis capensis*, *Thelotornis capensis* and *Lygosoma sundevallii* are most common.

Most dead wood occurs in this variation and the area is characterized by large accumulations of leaf litter around the bases of *Ochna pulchra* and *Grewia flavescens* clumps,providing good foraging areas for lizards such as *Panaspis wahlbergi* and *Ichnotropis capensis*. The preponderance of *Grewia flavescens* shrubs and *Strychnos pungens* trees are of importance to the vine snake (*Thelotornis capensis*) population, as will be discussed later.

In winter, the area tends to have large areas bare of vegetation and by August most trees have shed their leaves. Only *Strychnos pungens* and *Euclea crispa* appear to be evergreen. The leaf litter and grass among and at the base of shrubs therefore are important in providing cover for insects and termites, which are the main food item of many species of reptiles and amphibians.

### (b) *Eragrostis pallens* - *Setaria perennis* variation

This is the variation found on the lower third of the study area and is mainly in association with the dystropic Clovelly soils (Mosdale series). It differs from (a) above in that it is characterized by *Faurea saligna* trees which may be up to 10 m tall. The dominants in the tree and shrub layers are *Burkea africana*, *Terminalia sericea* and *Ochna pulchra*, while in the field layer *Eragrostis pallens* occupies the higher lying areas and *Setaria perennis* the lower slopes. The mean number of trees per unit area is half of variation (a) and total tree cover is less than 50%. The shrub cover is less than 10% but the field layer of up to 1,8 m high covers 30-75%. This is mainly due to the presence of Setaria perennis and Elionurus muticus. The soil appears less well-drained than that of (a) and therefore permits a more vigorous field layer.

The faunistic component of these lower slopes is consequently more depauperate but some species occur here but not, or only very rarely in (a). Such species include Ichnotropis squamulosa, Cryptomys hottentottus, Bitis arietans, Otomys angoniensis and Rhabdomys pumilio. The vine snake (Thelotornis capensis) only visits here irregularly during the summer months, but the Egyptian cobra (Naja haje annulifera) is most common. This is probably connected with the greater abundance of small mammals here than in (a).

(c) Eragrotis pallens - Trachypogon spicatus variation

This vegetation, found on the coarse mesotrophic Clovelly soils is found to the west of Maroelakop and therefore not in the reptile study area. It is characterized by a similar presence of trees as in the previous variation. Terminalia sericea has generally a higher cover at heights of over 4 m than Burkea africana. Total tree cover can reach 20%. Common woody species include Terminalia sericea and Burkea pulchra, while Ochna pulchra, Burkea africana, Terminalia sericea and Combretum molle dominate the lower tree layer. The main shrub species include Ochna pulchra, Burkea africana and Terminalia sericea. The field layer is dominated by Trachypogon spicatus and Eragrostis pallens with a height of 1,75 m and a total cover of 30-50%.

The faunistic component resembles that of the previous variation although there is a general paucity of species in this vegetation type.

Amongst the woody savanna typified by Burkea africana are small rocky outcrops of Waterberg sandstone. These, in particular the larger ones, have a vegetation characteristic of the large sandstone elevations such as Maroelakop and Stemmerskop. The soils are litholitic and rocks cover 10-60% of the area. Common differential species include Diplorhynchus condylocarpon and the shrubs Barleria bremekampii and Landolphia capensis, while a variety of forbs such as Tephrosia longipes, Rhynchosia *totta*, *Corchorus kirkii* and *Indigofera comosa* are also characteristic. Other trees common to these areas include *Pseudolachnostylis maprouneifolia*, *Canthium gilfillanii* and *Croton gratissimus*.

*Schizachyrium jeffreysii* is a common grass growing in the pockets of soil collected in the hollows while *Enneapogon scoparius* grows in areas of shallow soil. The cracks, fissures and loose rock enable some of the rock dwelling reptiles to thrive there. Such species as *Pachydactylus bibronii* and *Naja mossambica* are characteristic and even the veld monitor, *Varanus exanthematicus albigularis* may reside there.

Finally, we have the communities found on disturbed areas of abandoned settlements. These were sites of old bantu settlements and the soil is eutropic and of the Hutton series, with a high phosphate content. Tall *Sclerocarya caffra* trees, occasionally dotted around the settlements are characteristic, while thorn trees, *Acacia tortilis* and to some extent *A nilotica* predominate. The grass layer is formed mainly by *Eragrostis lehmanniana* which may form up to 80% cover. *Solanum delagoense* and *Crotalaria pisicarpa* are forbs characteristic of the area. There is a notable absence of rotting woody material lying on the ground and therefore little cover for reptiles which are not burrowers as well as arboreal species, although the boomslang, *Dispholidus typus*, may occur. This area is noteworthy for the virtual absence of the Cape dwarf gecko, *Lygodactylus capensis*, which is abundant in the surrounding *Burkea africana* - *Eragrostis pallens* savanna. The main reason for this is the paucity of loose bark and holes in which it can seek shelter. The lack of dead wood is no doubt due to the relatively recent removal of these settlements and this vegetation is presumably transitional.

## Fire

The study area has been subject to periodic fires prior to the start of the survey and evidence of this is still discernible on the tree trunks and other charred logs and stumps in the area. Fire has a considerable impact on the vegetation as well as on the fauna. This is easily seen in areas which are repeatedly burnt every second year as fire breaks. Such areas have scanty vegetation cover which, in particular on the higher slopes, does not regrow fast enough to be able to burn after one season's growth. Similarly, although at this stage not quantitatively assessed, the reptiles are also affected by the paucity of cover. Fire, in addition, kills off numbers of animals, in particular geckos, as they are usually found inhabiting logs lying on the ground and which burn very easily. Other animals shelter under piles of vegetation and are also incinerated. Several tortoises examined on Nylsvley bore signs of having been in a veld fire.

Barbault (1971, 1973, 1974a) mentions that the animals do not flee over great distances during a veld fire but instead move into areas not burnt or into holes and other hideouts. He shows that there is a drastic decline in the number of reptiles per hectare. For instance, the density of snakes dropped from 3,0/ha just prior to the fire, to 0,7/ha afterwards.

In a comparison between burnt and unburnt savanna, Barbault (loc.cit.) showed that the density of snakes and lizards was twice as great in unburnt savanna, than that of these animals in savanna which was regularly burnt. Some changes in species composition were also apparent and were directly related to an increase in cover in the unburnt savanna.

Fires in the savanna usually occur during the winter months when the animals are hiding up in thick vegetation or in holes and in rotting logs. They hibernate at this time and are therefore very sluggish and unable to make an escape.

Barbault (loc. cit.) showed that a rapid recovery rate is possible, but whether this is also the case at Nylsvley, is not known, and considered unlikely owing to the pronounced seasonality of the climate and, therefore, the reptile populations. Lamto experiences a tropical climate where animals are active throughout the year. Both temperature and moisture are considerably more favourable.

## Historical background and land use

As mentioned previously, the reserve was utilised for beef production from 1945 until the purchase of the property and its proclamation as a Nature Reserve in 1974. This started off with approximately 700 head of cattle, but was subsequently reduced to about 500 head, representing a stocking rate of one large stock unit/six hectares. The farm (3 120 ha), was divided into 25 paddocks, of which the main ones ranged in size from 200-250 ha. Water was available from the Nyl river and two boreholes, while seasonally inundated pools, scattered in other low-lying areas, contributed to the supply. Rotational grazing was practiced and the whole farm was grazed as determined by water availability and rainfall. Overgrazing was avoided and the vegetation was periodically rested. The Ecosystem study area of 750 ha was grazed from mid-January to mid-May. The area was divided into four paddocks, which were grazed by two herds of cattle of approximately 150 head each. The poisonous plant, Dichapetalum cymosum, prevented the use of these paddocks at other times of the year. This system was continued during the present study period, i.e. from May 1975 to May 1977 after which the cattle were removed.

Various other animal species inhabited the study area, among them 11 amphibian, 41 reptile and 43 mammal, Jacobsen (1977). The latter include kudu (Strepsiceros strepsiceros), impala (Aepyceros melampus), reedbuck (Redunca arundinum), warthog (Phacochoerus aethiopicus), duiker (Sylvicapra grimmia) and steenbok (Raphicerus campestris), among the larger animals; while monkeys (Cercopithecus pygerethrus), porcupines (Hystrix africae-australis) and springhares (Pedetes capensis) also occur. Of importance to the reptiles and amphibians are the small carnivores, such as mongooses, genets and black-backed jackal (Canis mesomelas), which are predators of lower vertebrates. Slender (Herpestes sanguineus), and banded (Mungos mungo) mongooses are particularly active and can smell prey as far down as 20 cm in the soil. Raptors, such as the black-breasted snake eagle (Circaetus gallicus pectoralis), lizard buzzard (Kaupifalco monogrammicus) and martial eagle (Polemaëtus bellicosus), are important reptile predators, while numerous insectivorous birds are found, many of which feed on the smaller reptiles.

## The climate

### Temperature

During the course of the study, climatic data were routinely collected. Three sites were simultaneously monitored in the Ecosystem study area, named stations 1, 2 and 3. Station 1 was located in Paddock 1, which was my study area (Figure 3). The data recorded were as per Table 1. Unfortunately, during the initial stages of the project, considerable error was experienced in the weather recording at station 1. Also because soil temperatures as well as humidity were only measured at station 2, this station's data are also included.

The climate of the area is semi-arid with distinct seasons; a hot, wet season from October to April, followed by a cool, dry season from May to

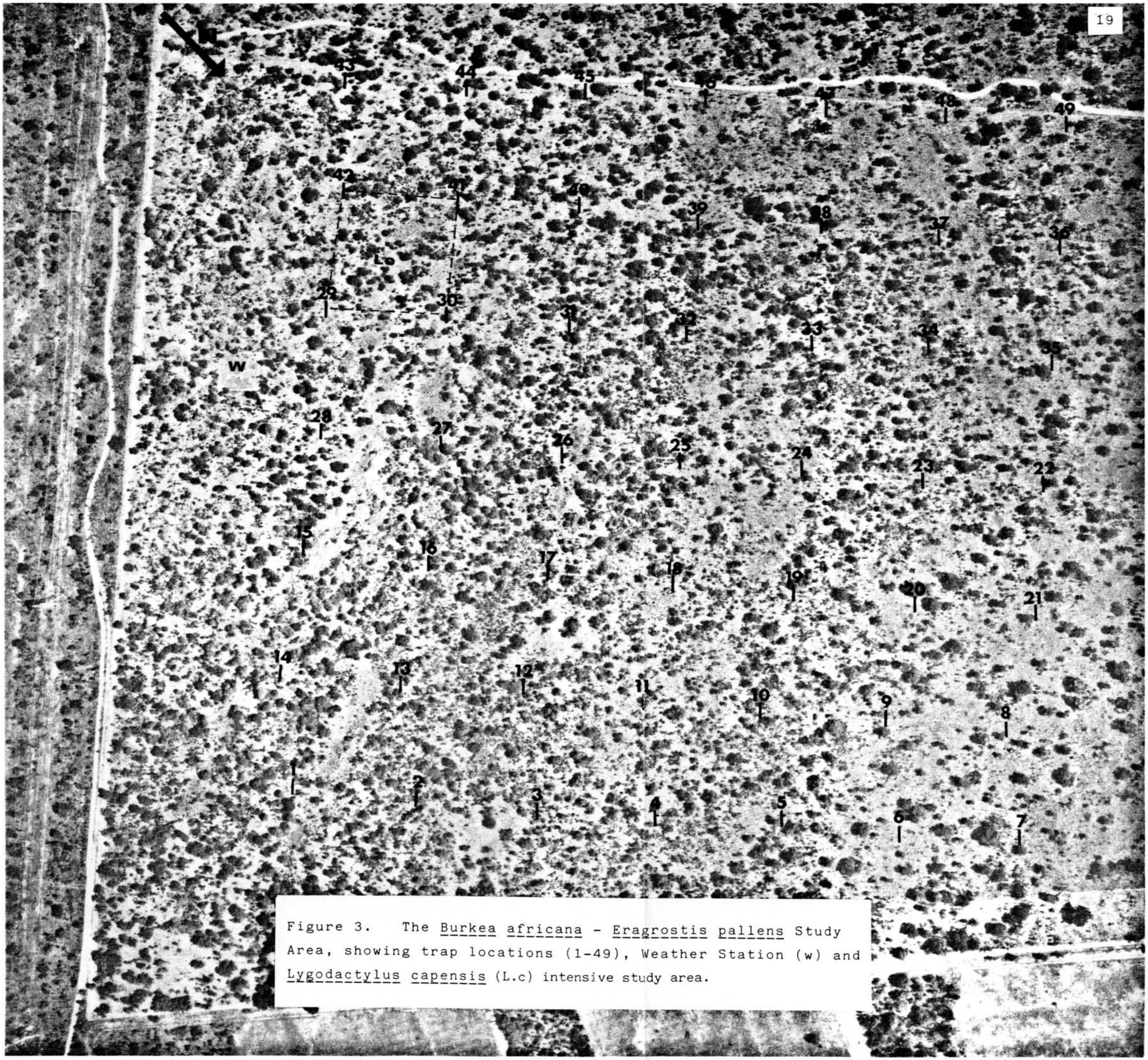


Figure 3. The <u>Burkea</u> <u>africana</u> - <u>Eragrostis</u> <u>pallens</u> Study Area, showing trap locations (1-49), Weather Station (w) and <u>Lygodactylus</u> <u>capensis</u> (L.c) intensive study area.

Table 1. Climatic data measured at two stations, four kilometres apart, over the period May 1975 to December 1977, in the Ecosystem Study Area.

| | 1975 | | 1976 (Station 1) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dec. | Nov. | Jan. | Feb. | Mar. | Apr. | May. | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
| Mean temperature | 20,6 | 22,3 | 21,9 | 18,2 | 20,9 | 18,6 | 13,4 | 12,7 | 12,8 | 14.6 | 19.4 | 20,2 | 20,9 | 23,1 |
| Mean max. temperature | 27,4 | 29,6 | 27,7 | 24,1 | 26,5 | 24,6 | 21,9 | 21,2 | 22,0 | 23,7 | 27,8 | 28,4 | 27,8 | 30,5 |
| Mean min. temperature | 15,4 | 15,0 | 16,1 | 14,2 | 15,4 | 12,6 | 6,3 | 4,2 | 3,6 | 5,6 | 11,0 | 12,0 | 14,1 | 15,7 |
| Mean rainfall | 6,2 | 1,9 | 5,0 | 6,3 | 4,9 | 1,2 | 0,4 | 0 | 0 | 0 | 0,3 | 4,3 | 4,2 | 1,9 |
| Total rainfall | 191,0 | 56,7 | 159,9 | 181,5 | 151,4 | 37,0 | 13,0 | 0 | 0 | 0 | 9,9 | 134,8 | 127,2 | 58,0 |
| Maximum raindall | 62,9 | 15,2 | 84,0 | 62,9 | 62,9 | 28,0 | 5,5 | 0 | 0 | 0 | 7,9 | 62,9 | 35,1 | 13,4 |
| Minimum rainfall | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Daily mean relative humidity | 0 | 0 | 0 | 0 | 0 | 47,2 | 72,8 | 58,7 | 48,5 | 47,8 | 41,1 | 47,0 | 55,3 | 53,6 |
| Daily mean max. humidity | 0 | 0 | 0 | 0 | 0 | 98,0 | 98,0 | 98,4 | 99,4 | 98,5 | 85,5 | 89,5 | 98,0 | 86,5 |
| Daily mean min. humidity | 0 | 0 | 0 | 0 | 0 | 65,0 | 36,0 | 37,0 | 21,5 | 23,0 | 17,0 | 24,5 | 18,0 | 28,5 |
| 0800 Mean humidity | 0 | 0 | 0 | 0 | 0 | 49,8 | 82,8 | 72,1 | 61,7 | 64,8 | 56,3 | 60,5 | 62,7 | 63,7 |
| 14,00 Mean humidity | 0 | 0 | 0 | 0 | 0 | 44,6 | 62,9 | 45,3 | 35,3 | 30,8 | 25,9 | 33,4 | 48,0 | 43,5 |
| No. of rain days | 19 | 11 | 9 | 11 | 9 | 3 | 4 | 0 | 0 | 0 | 2 | 8 | 11 | 9 |

Table continued/...

Table 1 continued

| | 1977 (Station 1) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
| Mean tempterature | 24,3 | 21,7 | 19,8 | 19,7 | 15,9 | 14,0 | 13,2 | 16,0 | 19,4 | | | |
| Max. mean temperature | 31,8 | 28,4 | 25,2 | 27,0 | 24,6 | 22,9 | 22,0 | 24,4 | 26,8 | | | |
| Min. mean temperature | 17,1 | 16,1 | 14,5 | 12,4 | 7,2 | 5,1 | 4,4 | 7,5 | (10,7)<br>(13,1) | | | |
| Min. mean temperature | 17,1 | 16,1 | 14,5 | 12,4 | 7,2 | 5,1 | 4,4 | 7,5 | 12,0 | | | |
| Mean Rainfall (mm) | 2,9 | 3,2 | 5,9 | 0,1 | 0,1 | 0 | 0 | 0,7m | 1,0 | | | |
| Total rainfall(mm) | 89,2 | 90,1 | 183,6 | 5,9 | 4,6 | 0,2 | 0 | 20,6 | 29,4 | | | |
| Max. rainfall (mm) | 30,1 | 31,2 | 51,7 | 2,8 | 4,2 | 0,2 | 0 | 19,3 | 11,1 | | | |
| Min. rainfall (mm) | 0 | 0 | 0 | 0 | 0,4 | 0 | 0 | 1,3 | 1,6 | | | |
| Daily mean relative humidity | 53,7 | 63,4 | 67,9 | 59,5 | 45,9 | 44,6 | 46,5 | 43,6 | 53,8 | | | |
| Daily mean max. humidity | 86,5 | 82,0 | 98,9 | 92,0 | 67,0 | 68,0 | 61,0 | 70,5 | 96,0 | | | |
| Daily mean min. humidity | 26,5 | 46,0 | 39,0 | 37,0 | 26,5 | 25,5 | 30,5 | 24,5 | 21,5 | | | |
| 0800 Mean humidity | 64,5 | 76,4 | 79,6 | 75,8 | 63,4 | 63,3 | 64,9 | 58,6 | 69,2 | | | |
| 1400 Mean humidity | 43,0 | 50,3 | 56,2 | 43,2 | 28,5 | 25,9 | 28,1 | 28,5 | 38.3 | | | |
| No. of rain days | 11 | 8 | 11 | 3 | 2 | 1 | 0 | 2 | 6 | | | |

Table continued.

Table 1 continued

Weather Data - Nylsvley

Station 2

May 1975 - December 1977

| Month | Soil temperature |  |  |  |  |  |  |  |  |  |  |  | MMT | MMT | Mean | R mm | RD | M. RH. | 0800 | 1400 | Wind km/day | Sunshine |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 10 cm |  |  | 20 cm |  |  | 30 cm |  |  | 60 cm |  |  |  |  |  |  |  |  |  |  |  | Act. h/d | Poss. |
| 1975 | 0800 | 1400 | A | 0800 | 1400 | A | 0800 | 1400 | A |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| May | 13,8 | 24,7 | 19,3 | 15,7 | 20,4 | 18,1 | 16,2 | 21,8 | 19,0 | 20,2 | 19,9 | 20,0 | 24,1 | 8,3 | 16,2 | 5,7 | 5 | 8,4 | 9,0 | 7,8 | 0 | 0 | 10,8 |
| June | 10,4 | 20,8 | 15,6 | 12,6 | 16,7 | 14,7 | 13,0 | 18,1 | 15,6 | 17,5 | 17,2 | 17,4 | 20,6 | 4,5 | 12,6 | 10,6 | 3 | 9,2 | 6,6 | 11,8 | 0 | 0 | 10,5 |
| July | 10,2 | 20,3 | 15,3 | 12,7 | 16,1 | 14,4 | 12,3 | 18,0 | 15,4 | 16,9 | 16,9 | 16,9 | 21,0 | 3,1 | 12,0 | 0 | 0 | 5,4 | 6,1 | 4,7 | 0 | 0 | 10,6 |
| Aug. | 12,8 | 23,2 | 18,0 | 15,5 | 19,1 | 17,3 | 15,7 | 20,8 | 18,2 | 18,6 | 18,5 | 18,6 | 23,7 | 6,4 | 15,1 | 4,5 | 1 | 4,4 | 5,8 | 3,1 | 0 | 0 | 11,1 |
| Sept. | 18,8 | 30,7 | 29,6 | 20,9 | 24,1 | 22,4 | 20,9 | 26,4 | 23,6 | 22,6 | 22,4 | 22,4 | 27,8 | 11,7 | 19,8 | 0,2 | 1 | 4,4 | 6,0 | 2,8 | 0 | 0 | 11,8 |
| Oct. | 20,7 | 33,0 | 26,7 | 22,3 | 27,0 | 24,5 | 22,3 | 28,2 | 25,1 | 24,3 | 24,1 | 24,2 | 28,9 | 13,0 | 21,0 | 22,3 | 5 | 5,4 | 5,0 | 5,6 | 0 | 0 | 12,6 |
| Nov. | 22,0 | 33,9 | 28,0 | 24,6 | 33,4 | 29,0 | 22,7 | 29,6 | 26,2 | 25,0 | 24,8 | 24,9 | 29,4 | 15,5 | 22,4 | 57,7 | 13 | 49,9 | 62,4 | 37,4 | 0 | 0 | 13,2 |
| Dec | 21,5 | 33,3 | 27,5 | 0 | 0 | 0 | 22,1 | 28,4 | 25,3 | 24,1 | 24,2 | 24,2 | 27,6 | 16,0 | 21,7 | 203,4 | 18 | 62,8 | 75,3 | 50,2 | 0 | 0 | 13,5 |
| 1976 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Jan. | 22,5 | 33,3 | 27,9 | 0 | 0 | 0 | 23,2 | 28,2 | 25,7 | 25,1 | 25,1 | 25,1 | 27,9 | 16,5 | 22,2 | 102,6 | 11 | 62,5 | 71,1 | 53,8 | 0 | 0 | 13,3 |
| Feb. | 20,9 | 30,8 | 25,8 | 0 | 0 | 0 | 22,4 | 27,6 | 25,0 | 24,5 | 24,3 | 24,5 | 27,8 | 16,3 | 22,1 | 149,7 | 9 | 68,3 | 81,6 | 53,5 | 0 | 0 | 12,8 |
| Mar. | 20,0 | 28,9 | 24,4 | 0 | 0 | 0 | 21,5 | 26,4 | 23,9 | 23,9 | 23,9 | 23,9 | 26,4 | 15,4 | 20,9 | 81,9 | 8 | 70,5 | 85,0 | 56,1 | 0 | 0 | 12,1 |
| Apr. | 17,5 | 26,9 | 22,2 | 19,5 | 23,5 | 21,5 | 19,3 | 24,1 | 21,7 | 22,1 | 21,9 | 22,0 | 29,6 | 11,5 | 18,0 | 34,1 | 4 | 65,9 | 85,6 | 46,2 | 0 | 0 | 11,4 |
| May. | 12,2 | 21,8 | 17,0 | 19,9 | 18,4 | 16,7 | 14,7 | 19,6 | 17,2 | 19,1 | 18,6 | 18,9 | 21,6 | 6,8 | 14,2 | 15,1 | 4 | 65,8 | 85,4 | 46,0 | 0 | 0 | 10,8 |
| June | 10,2 | 17,4 | 14,8 | 13,0 | 15,8 | 14,4 | 12,5 | 17,5 | 15,0 | 16,6 | 16,6 | 16,6 | 20,9 | 4,4 | 12,7 | 0 | 0 | 58,0 | 81,2 | 34,8 | 0 | 0 | 10,5 |
| July | 9,2 | 18,9 | 14,1 | 12,9 | 15,7 | 14,3 | 12,2 | 17,5 | 14,9 | 16,2 | 16,2 | 16,2 | 21,8 | 3,9 | 12,8 | 0 | 0 | 49,7 | 69,7 | 29,6 | 0 | 0 | 10,6 |
| Aug. | 12,3 | 22,6 | 17,6 | 14,8 | 18,6 | 16,7 | 14,0 | 20,0 | 17,0 | 17,4 | 17,5 | 17,4 | 23,6 | 5,9 | 14,7 | 0 | 0 | 46,0 | 64,1 | 27,8 | 143,8 | 0 | 11,1 |

Table 1 continued.

Station 2 (continued)

| Month | Soil temperature | | | | | | | | | | | | MMT | MMT | Mean | R mm | RD | RH. | 0800 | 1400 | Wind km/day | Sunshine | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10 cm | | | 20 cm | | | 30 cm | | | 60 cm | | | | | | | | | | | | Act. h/d | Poss. |
| 1976 | 0800 | 1400 | A | 0800 | 1400 | A | 0300 | 1400 | A | 0800 | 1400 | A | | | | | | | | | | | |
| Sept. | 18,2 | 27,1 | 22,6 | 19,5 | 23,7 | 21,6 | 19,6 | 25,2 | 22,5 | 21,5 | 21,5 | 21,5 | 27,4 | 11,4 | 19,4 | 8,9 | 2 | 43,7 | 57,0 | 30,4 | 156,0 | 0 | 11,8 |
| Oct. | 20,3 | 30,0 | 25,1 | 21,7 | 29,4 | 25,6 | 22,2 | 26,4 | 24,3 | 24,3 | 24,2 | 24,2 | 27,3 | 16,5 | 21,9 | 35,0 | 7 | 50,3 | 65,1 | 35,6 | 161,9 | 0 | 12,6 |
| Nov. | 22,5 | 29,6 | 26,0 | 21,6 | 26,9 | 24,2 | 21,5 | 26,6 | 24,0 | 23,4 | 23,3 | 23,4 | 28,3 | 14,5 | 21,4 | 142,6 | 11 | 58,9 | 68,2 | 49,6 | 227.0 | 10.0 | 13.4 |
| Dec. | 25,6 | 32,2 | 28,9 | 24,2 | 29,7 | 27,0 | 24,2 | 27,4 | 26,9 | 26,2 | 26,0 | 26,1 | 29,7 | 15,5 | 22,6 | 71,6 | 9 | 59,4 | 79,0 | 48,8 | 136,5 | 0 | 13,5 |
| 1977 | | | | | | | | | | | | | | | | | | | | | | | |
| Jan. | 0 | 0 | 0 | 26,0 | 30,8 | 28,4 | 25,9 | 31,1 | 28,5 | 27,3 | 27,1 | 27,2 | 31,5 | 16,8 | 24,2 | 73,0 | 10 | 56,0 | 67,3 | 44,7 | 127,9 | 0 | 13,3 |
| Feb. | 22,7 | 34,6 | 28,9 | 24,3 | 29,5 | 26,9 | 24,2 | 29,0 | 26,6 | 26,2 | 26,1 | 26,2 | 28,9 | 16,3 | 22,6 | 105,2 | 8 | 63,5 | 76,6 | 50,4 | 118,3 | 7,3 | 12,8 |
| Mar. | 19,5 | 28,2 | 23,9 | 21,5 | 25,1 | 23,2 | 21,4 | 25,1 | 23,2 | 23,9 | 23,5 | 23,7 | 25,2 | 15,2 | 20,2 | 178,7 | 120 | 73,5 | 85,6 | 61,4 | 107,9 | 5,8 | 12,1 |
| April | 18,6 | 27,7 | 23,2 | 21,4 | 24,2 | 22,8 | 20,9 | 25,7 | 23,3 | 23,3 | 23,2 | 23,3 | 26,2 | 12,8 | 19,5 | 1,2 | 2 | 62,5 | 79,8 | 45,2 | 2776,0 | 8.3 | 11.4 |
| May | 12,8 | 22,7 | 17,8 | 17,1 | 19,5 | 18,3 | 16,0 | 21,9 | 19,0 | 20,3 | 20,2 | 20,2 | 24,2 | 7,2 | 15,7 | 3,1 | 2 | 47,4 | 65,9 | 29,0 | 3542,0 | 9,6 | 10,8 |
| June | 9,6 | 19,6 | 14,6 | 14,3 | 16,2 | 15,2 | 13,1 | 19,1 | 16,1 | 17,5 | 17,5 | 17,5 | 22,5 | 4,9 | 13,7 | 0,3 | 1 | 45,7 | 65,2 | 26,2 | 3135,0 | 9,7 | 10,5 |
| July | 8,2 | 20,5 | 14,3 | 13,3 | 15,5 | 14,4 | 12,3 | 18,7 | 15,5 | 16,5 | 16,5 | 16,5 | 21,7 | 3,9 | 12,8 | 0 | 0 | 47,4 | 67,0 | 28,0 | 3283,0 | 10,2 | 10,6 |
| Aug. | 11,3 | 24,6 | 17,9 | 15,9 | 18,7 | 17,3 | 15,0 | 21,0 | 18,0 | 18,1 | 18,1 | 18,1 | 24,0 | 7,9 | 16,0 | 25,3 | 2 | 41,8 | 60,4 | 27,6 | 4263,0 | 9,3 | 11,1 |
| Sept. | 16,2 | 28,3 | 22,3 | 19,3 | 22,5 | 20,9 | 19,0 | 24,0 | 21,5 | 21,2 | 21,1 | 21,1 | 25,9 | 12,0 | 18,9 | 49,7 | 6 | 58,2 | 70,8 | 44,9 | 4489,0 | 8,2 | 11,8 |
| Oct. | 20,2 | 35,5 | 27,8 | 22,1 | 28,1 | 25,1 | 22,4 | 28,3 | 25,4 | 24,2 | 23,9 | 24,1 | 30,2 | 14,2 | 22,2 | 52,2 | 7 | 48,3 | 60,3 | 36,3 | 4690,0 | 10,1 | 12,6 |
| Nov. | 22,5 | 38,2 | 30,4 | 24,6 | 30,3 | 27,4 | 24,8 | 29,3 | 27,1 | 26,0 | 26,0 | 26,0 | 28,2 | 15,4 | 21,8 | 24,6 | 7 | 51,8 | 63,3 | 40,4 | 4561,0 | 8,5 | 13,2 |
| Dec. | 22,6 | 35,8 | 29,2 | 24,5 | 28,8 | 26,7 | 25,0 | 26,9 | 26,0 | 25,8 | 25,7 | 25,8 | 29,6 | 16,8 | 23,2 | 122,0 | 10 | 58,2 | 68,6 | 47,9 | 4500,0 | 7,5 | 13,5 |

September. The mean annual [illegible] st (1975), Mean annual temperature is 18,6°C. Figure 4 summarises the general climate of the Study Area in the form of climate diagrams for stations 1 and 2.

The summer months are characterized by hot days and warm nights, particularly during the period September to December, after which the increasing rainfall introduced a cooling effect. There are variations, depending on the frequency and occurrence of the rainfall (Figure 5). Maximum and minimum temperatures can be seen in Table 1. It may be pertinent here to point out the differences in climate between stations 1 and 2, although they are only about 2 km apart.

During winter, however, temperatures are moderate during the day and cold at night, while clear skies associated with this time of the year permit extensive radiation of heat into the atmosphere. This accounts for the large daily range in temperature, especially during the months of June, July and August, reaching as much as 17,5°C between the mean maximum and mean minimum. Daily ranges may even be greater as temperatures may drop to as low as -5°C at night and rise to 24°C during the day. Ground frosts are experienced nightly in the lower lying areas of the Reserve, but are rare in the Study Area.

Fluctuations in mean monthly temperature and rainfall are shown in Figure 5, including the mean monthly ranges in temperature. As can be seen, the greatest ranges occur during the winter months, and the smallest during the fluvial season. This effect is enhanced along drainage lines, as mentioned previously.

Soil temperatures do not fluctuate as much as ambient temperatures, as shown in Figure 6, with temperatures recorded at depths ranging between 10 and 60 cm. Greater fluctuations are apparent at 10 cm depth, but from 20 cm downwards, the range between mean maximum and mean minimum temperatures is not very great and in the order of 5°C, with the greatest differences occurring in summer and the least in winter. This is in direct opposition to that of the ambient temperatures. At 30 cm depth, a temperature difference of 10°C is recorded between winter and summer. This large difference is, no doubt, partly responsible for the hibernation of reptiles at Nylsvley, as the cooler soil will enhance the effect of a depressed ambient temperature, and reptiles will remain in a torpid state until the heat of the sun penetrates the soil during September. Rise in temperature, therefore, will assist in activating the reptiles even when 30 cm below the surface.

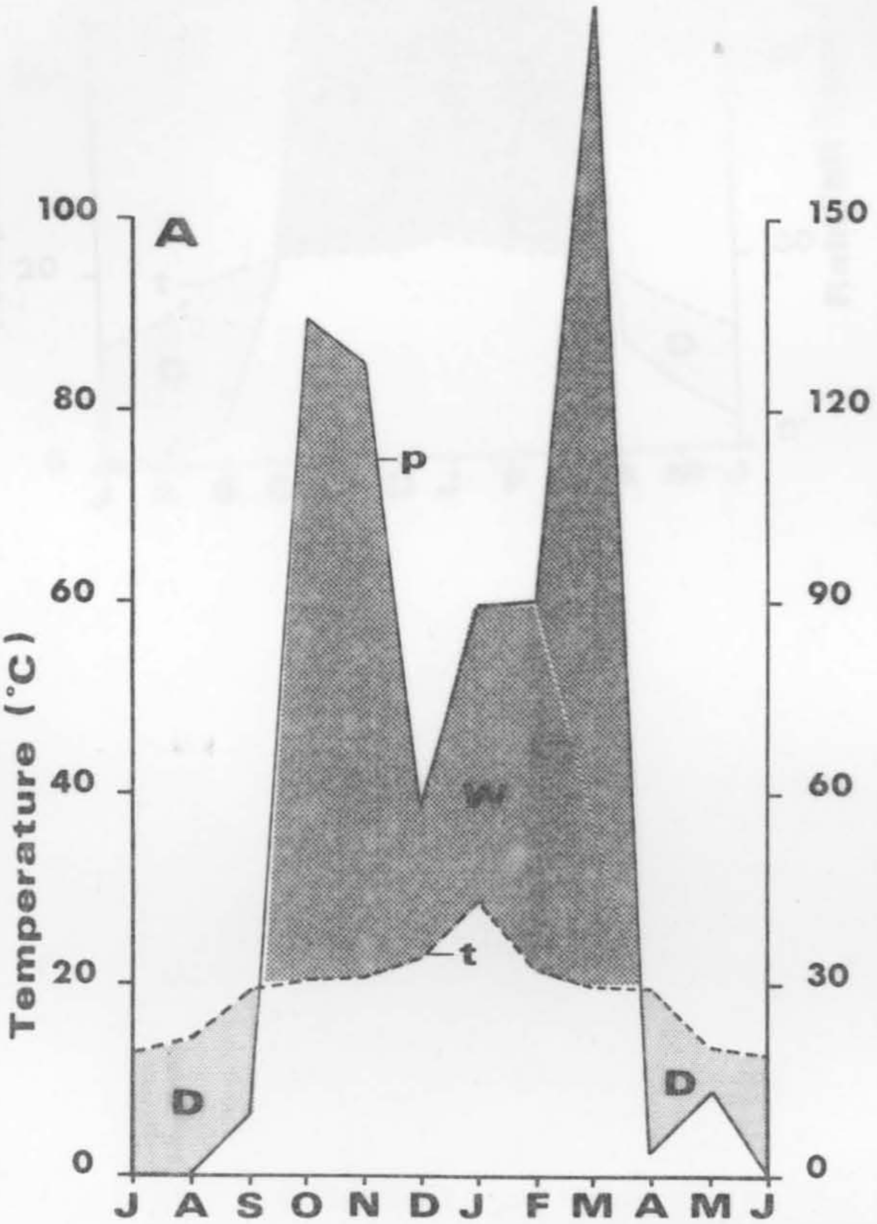
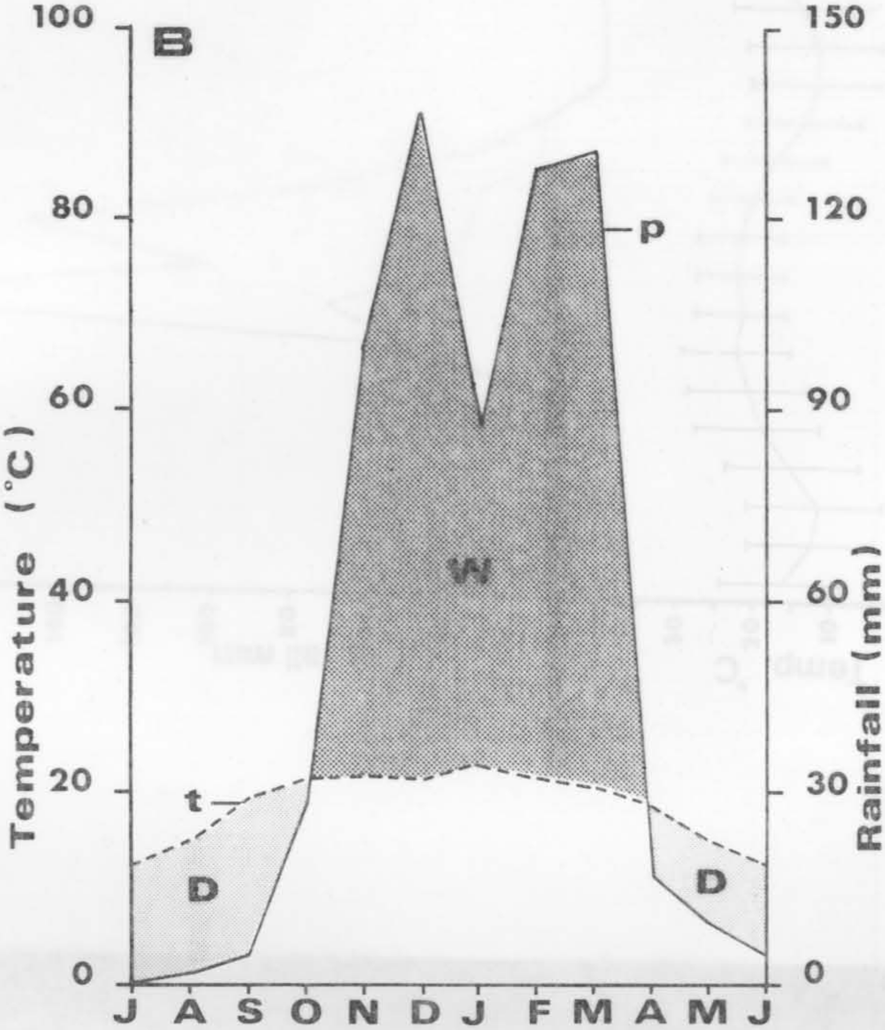


Figure 4. Climograph of two weather stations within the Ecosystem Study Area, showing the difference in climate over the period May 1976 to April 1977 (A) Station 1 and May 1975 - May 1977, (B) Station 2. p = mean monthly rainfall, t = mean monthly temperature, D = arid period, W = humid period.


B
Temperature (°C)
100
80
60
40
20
0
Rainfall (mm)
150
120
90
60
30
0
p
t
W
D
D
J
A
S
O
N
D
J
F
M
A
M
J

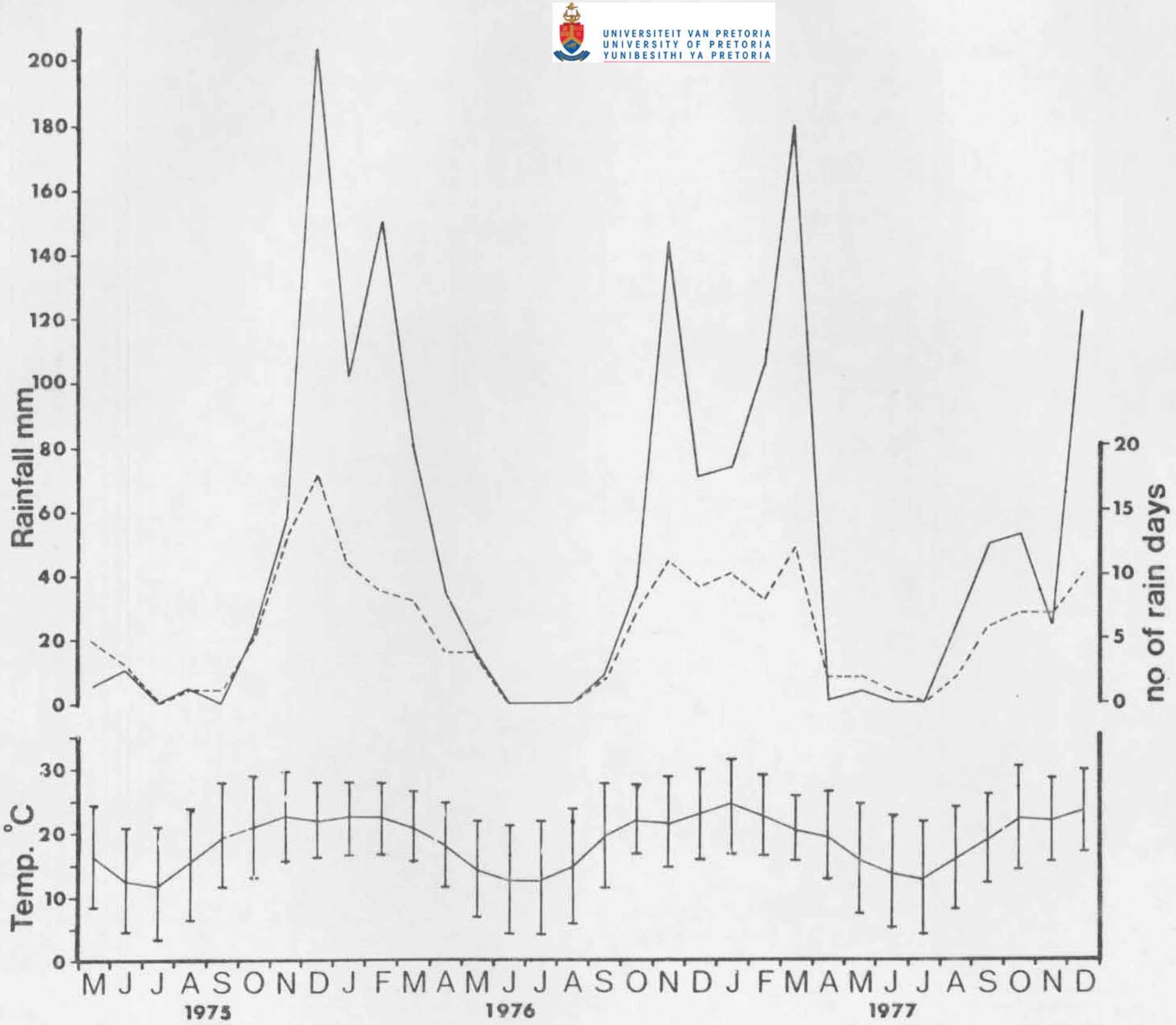


Figure 5. Mean monthly rainfall and temperature in the *Burkea africana* - *Eragrostis pallens* savanna, May 1975 - May 1977.

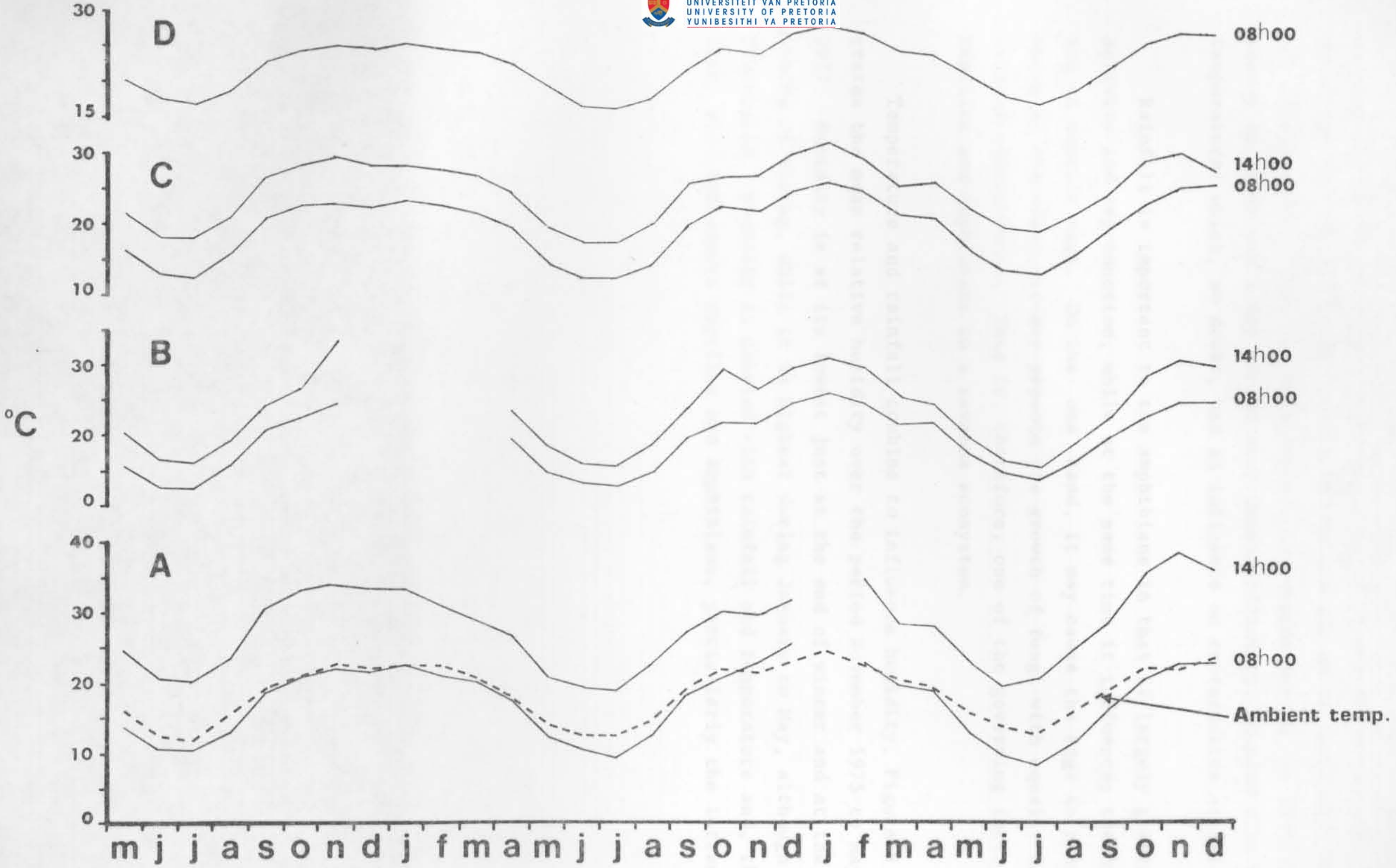


Figure 6. Mean soil temperatures in the *Burkea africana* - *Eragrostis pallens* Savanna: May 1975 - May 1977.

A = 10 cm B = 20 cm. C = 30 cm. D = 60 cm.

Rainfall is variable and concentrated mainly between five and six months of the year. Rain falls most frequently in the form of diurnal thunderstorms of relatively short duration. Figure 5 shows the variation in mean monthly rainfall and the number of rainy days per month over the period May 1975 to December 1977. It can be seen that there are at least two to three months in which absolutely no rain falls. Note the difference in rainfall at stations 1 and 2 over the period November 1975 to May 1977, as seen in Figure 7. It can be seen that station 1 experienced, on average, more rainy days than did station 2.

Occasional hailstorms occur but do not appear to affect reptile or amphibian numbers, apart from a cooling effect similar to that of rainfall. Considerable fluctuations in rainfall occur from year to year and, although the mean of 630 mm, Hirst (loc. cit.), gives an indication, the two years 1975 and 1976 experienced 686 mm and 618 mm respectively, which came erratically. This was particularly pronounced during the 1976/77 season as there was a dry period over December/January, coupled with high temperatures which, no doubt, had an influence on reproductive activity.

Rainfall is important to the amphibians in that it largely governs activity and reproduction, while at the same time it influences the hatching of reptile eggs. On the one hand, it may cause the eggs to dehydrate, while on the other, it may promote the growth of fungi with equally disastrous consequences. This is, therefore, one of the governing factors of reptiles and amphibians in a savanna ecosystem.

Temperature and rainfall combine to influence humidity. Figure 8 illustrates the mean relative humidity over the period November 1975 to May 1977. Humidity is at its lowest just at the end of winter and at the beginning of spring, while it is highest during January to May, although it fluctuates. Humidity is coupled with rainfall and temperature and, therefore, also influences reptiles and amphibians, particularly the latter.

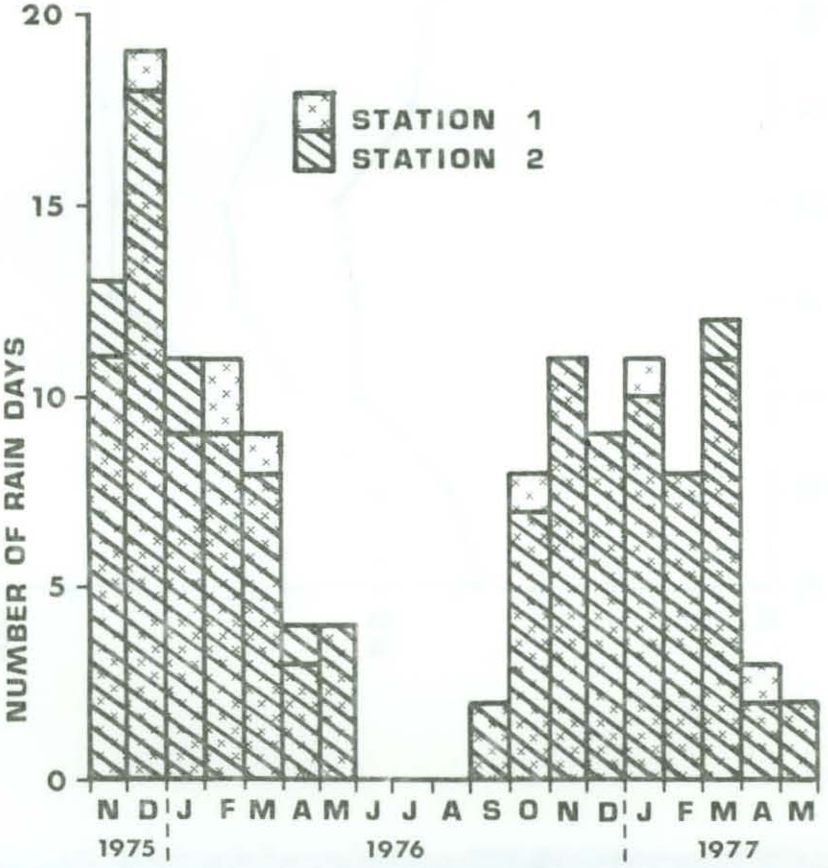


Figure 7. Occurrence of rain at Station 1 (November 1975-May 1977) and Station 2 (November 1975 - May 1977) in the *Burkea africana* Savanna

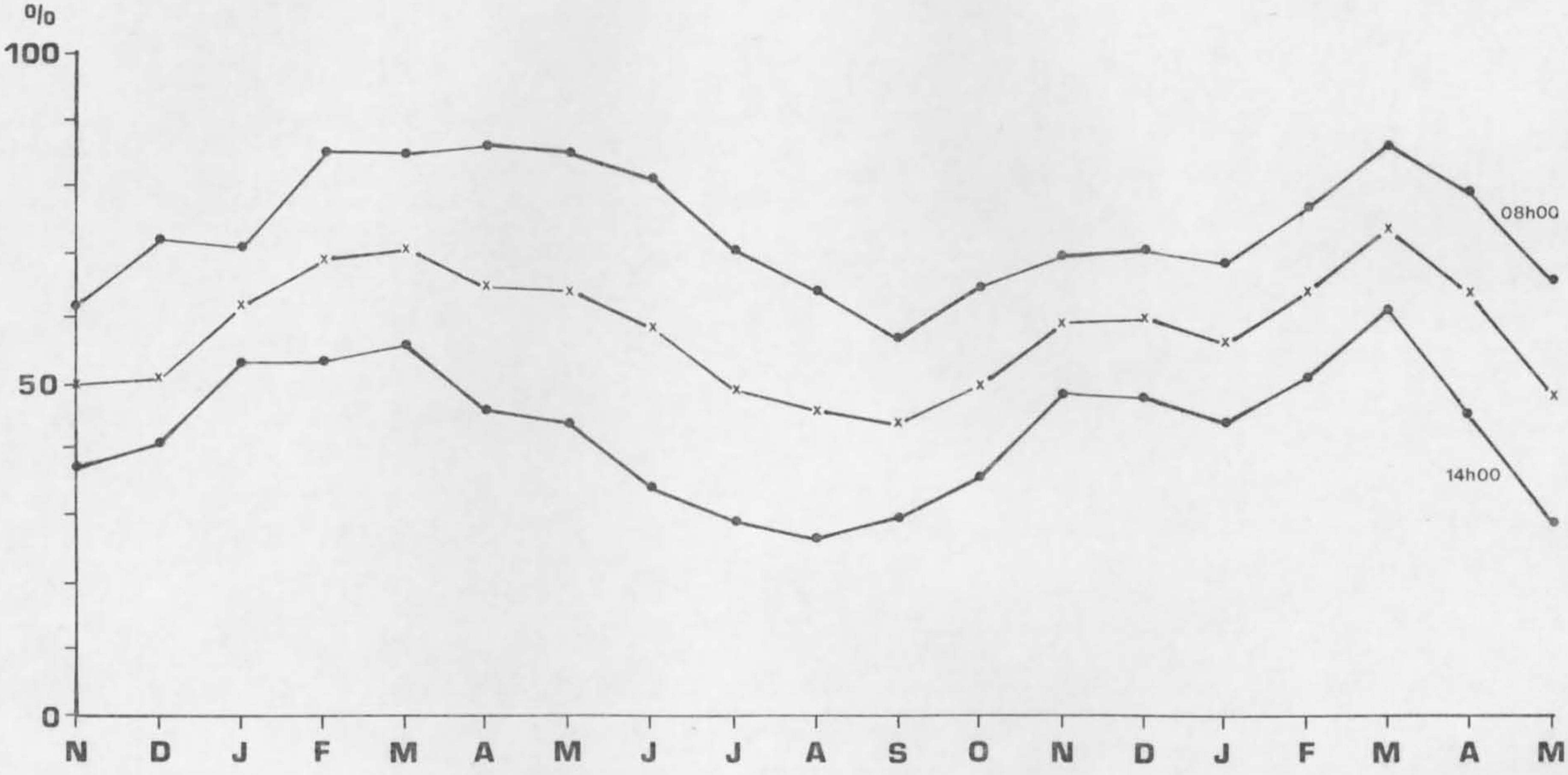


Figure 8. Mean relative humidity in the *Burkea africana* Savanna - November 1975 to May 1977.

# CHAPTER 3

# MATERIAL AND METHODS

In order to assess the size of the various reptile and amphibian populations, different methods of marking and capture were attempted. In a study such as this, where the species are so diverse and inhabit different strata within a community, a variety of methods must be applied in order to be able to assess the populations. Also, in most populations of mixed species, there are those which are common and could possibly be considered as density dependent, while on the other hand, there are many more which are rare and, therefore, density independent. It is these that are difficult to sample adequately, particularly when it comes to mark - recapture techniques.

This diversity coupled with the pronounced seasonality of the climate results in large scale fluctuations in animal visibility, particularly reptiles and amphibians, and made this study a difficult one.

## Trapping and census techniques

The main method of capturing snakes and terrestrial lizards, was by continuous trapping for a period of ten days each month, using funnel traps and drift fences, Dargan & Stickel (1949). The drift fences were constructed out of tempered masonite strips, which together were nine metres long and 30 cm high. This barrier was supported by eight gauge galvanised wire stakes placed at the ends and to which the strips were attached. Other supporting stakes were placed at intervals along the fence as the masonite tended to warp and buckle, particularly when on uneven ground. These strips were placed on either side of the funnel trap, the funnels of which were divided in two by a wedge-shaped piece of masonite, so that the animals could not go around the end of the drift fence, but had to move into the trap.

Each trap consisted of a rectangular cage, constructed from welded wire mesh 50 mm x 50 mm, covered over with gauze screening. The trap is 1,2 m long, 60 cm wide and 30 cm high, (Figure 9). A door placed in the roof facilitated the removal of trapped animals. Some difficulty was experienced with small species as they had a habit of squeezing in under the funnel and were difficult to extract. Large poisonous snakes also presented a problem until one is able to take hold of the tail and extract them slowly,

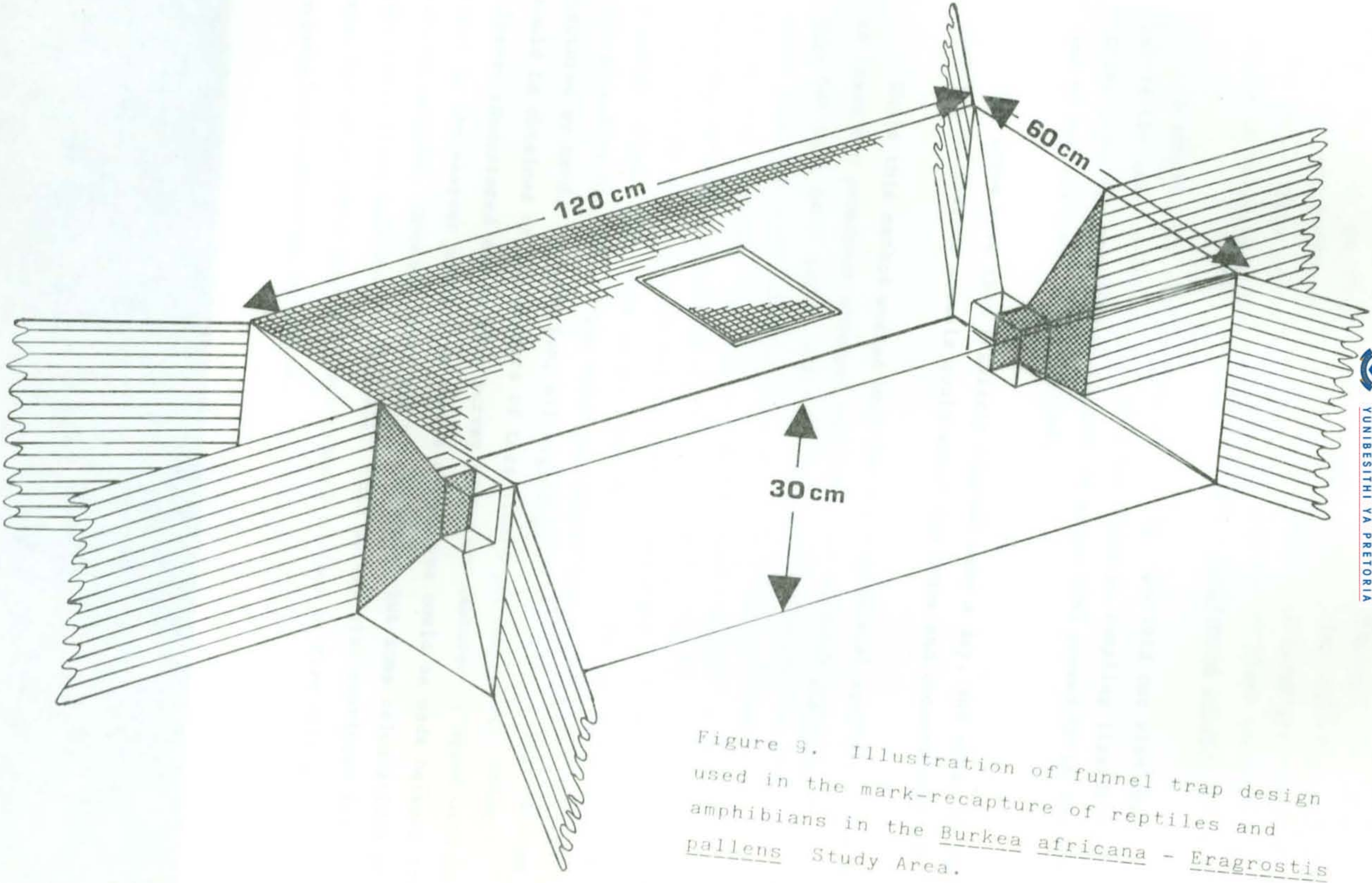


Figure 9. Illustration of funnel trap design used in the mark-recapture of reptiles and amphibians in the Burkea africana - Eragrostis pallens Study Area.

although they tended to twist in and out of the welded wire mesh and could only be removed gradually. The traps were then covered over with grass or sacking on the tops and on one side, to prevent the animals dying from dehydration and sunstroke, particularly in summer.

These traps were then spaced 100 m apart in a grid of 7 traps by 7 traps in order to obtain a representative random sample. They are located over an area of 49 ha, although their influence possibly extended over an area of 64 ha. This plot was located in Paddock 1 (Figure 3), along grid lines laid out over the whole Ecosystem study area. They therefore occupied the area between grid points $B_3$ to $B_9$ inclusive, and along grid lines B to H inclusive. This area encompassed the majority of plant community variations to be found in the Burkea africana - Eragrostis pallens savanna.

A second, but smaller, area of 0,36 ha was laid out with smaller traps, but of the same construction. This was aimed at sampling lizards (terrestrial), but the area and the number of traps (36) proved to be too small and no results could be calculated.

The traps were then regularly checked once a day, and after 10 days upended, so that no animals could enter the traps and consequently die.

While this method worked well for the terrestrial species, there were at least two prominent arboreal reptiles, one of which Lygodactylus capensis, the Cape dwarf gecko, had to be surveyed differently as they rarely cross extensive areas of ground and were not likely to be fully represented in the trap captures. In order to census these reptiles, a one hectare area was delimited between grid points $F_3$ and $F_4$ (Figure 2). All of the trees, shrubs and logs were marked with a galvanised iron disc stamped with a number (Figure 10). The object then was to systematically walk through the area from one side to the other and search for geckos which were then captured by hand. In addition, all sightings were noted, so that an idea could be obtained of the numbers of this lizard per unit area. Other lizards encountered during this survey were also captured or noted with respect to the nearest number, so that a comparison could be made between the various methods. However, this was not possible, but some calculations of home range sizes were made. Initially, this survey also continued for 10 days, but after three months it was reduced to four or five days as the disturbance was considered excessive.

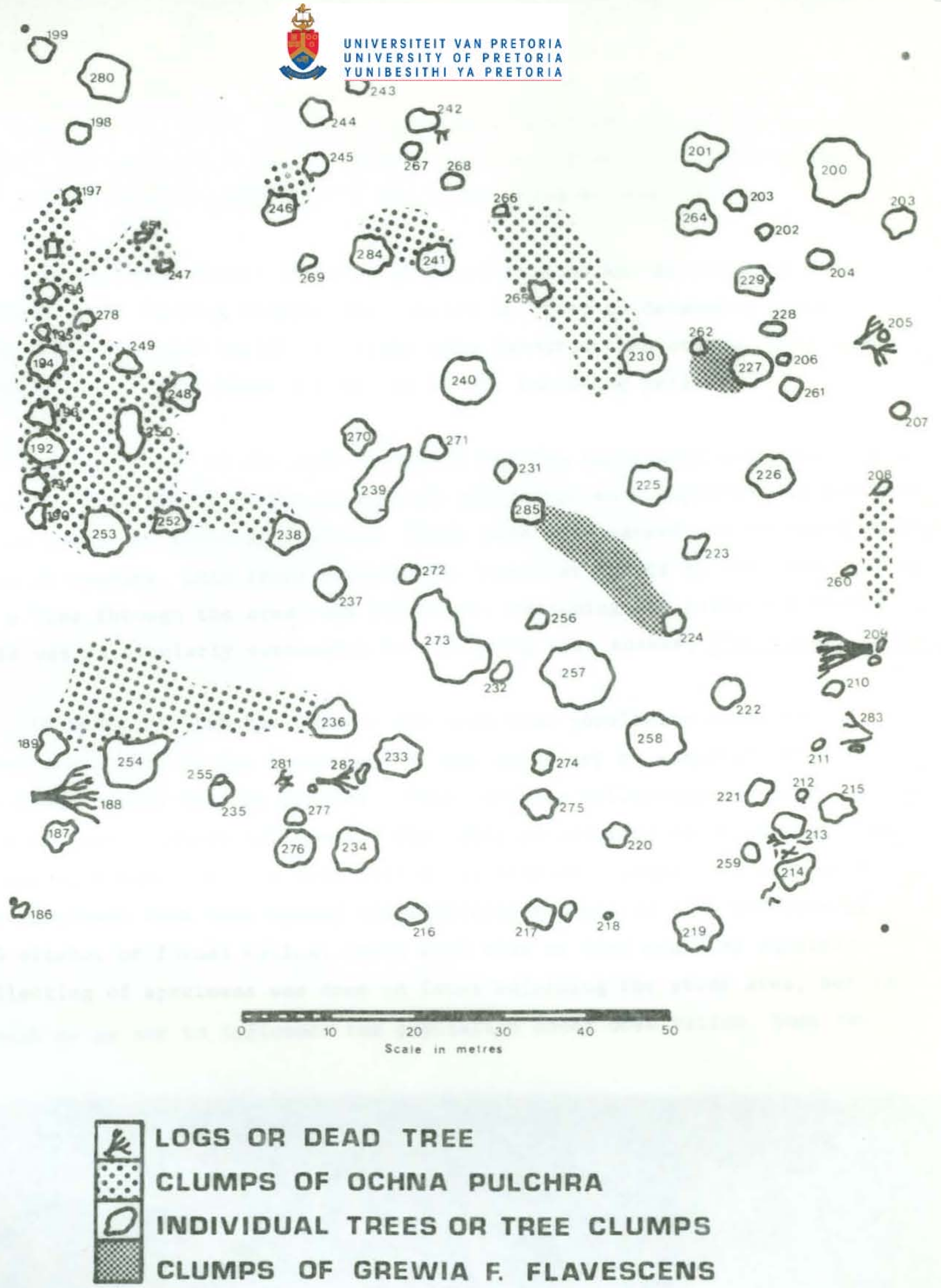


Figure 10. Diagram of the Lygodactylus capensis intensive study area.

In order to establish [illegible]orial species, an area of one hectare was demarcated and iron fencing droppers were used to mark a grid of 10 points x 10 points. These droppers were numbered and at each point a square metre of soil was dug up, to a depth of approximately 30 cm and sifted for the presence of these animals. This method was repeated twice during the year to broadly include the seasons. Nothing was accomplished, so this method was only used during the first year. This plot was set up in Paddock 4 of the Ecosystem Study Area in the site set aside for destructive sampling.

As an aid to assess the movement of snakes into and out of the Study Area, spoor counts of these reptiles crossing the roads surrounding this area were made. This was done by two assistants perched on the bonnet or bumper of the vehicle who look for spoor, while the driver maintains a speed of approximately 10 km/h. At the same time, a bunch of branches tied behind the vehicle wiped out old spoor which had already been recorded. Snake crossings were noted as ingoing or outgoing and on occasions even the species of snake responsible for the track could be ascertained.

The distance around the area amounted to 4,44 km. At each 100 m, a numbered iron fencing dropper was located in order to determine whether there were any particular crossings more favoured than others. This spoor recording also took place during the 10 day recording period.

During visits to the area by myself and two assistants and other workers, the presence of snakes were noted and snakes were captured, if possible, so as to add to existing captures. These were also marked and released at the site of capture. This later extended to irregular counts by the team walking in a line through the area back and forth, searching the trees and shrubs. This was particularly successful for locating vine snakes, <u>Thelotornis capensis</u>.

In order to link the reptile and amphibian population study to the other components of the Ecosystem, it was necessary to ascertain what food was eaten by the various species. This involved collecting specimens of the more abundant lizards and frogs. They were obtained by shooting them with strips of rubber tube, or else with a .22 revolver loaded with dust shot. The specimens were then opened mid-ventrally and placed in a solution of 70% alcohol or formal saline, until such time as they could be examined. Collecting of specimens was done on farms adjoining the study area, but far enough so as not to influence the population under observation. Some reproductive data was also obtained from these specimens.

It was not possible to collect snakes for analysis so that feeding records were restricted to those occasions where snakes were found which had recently fed. These snakes were then palpated and forced to regurgitate their prey so that identification was possible. Road kills, round and about Nylsvley, were also collected and dissected to identify stomach contents. Apart from this, specimens killed on farms in the area were also collected, particularly on the adjoining farm.

Amphibians were mostly collected at random, but mainly derived from the population in the study area which had died from dehydration in the traps, or killed by carabid beetles and formicid ants (Camponotus sp), as well as those that died from shock and heat stroke.

## Marking, measuring and sexing.

All reptiles and amphibians were weighed, measured, sexed if possible, marked and released the following morning. Measurements taken were standard and included snout to vent and tail where applicable, as well as mass. Problems arose in the sexing of small snakes and lizards, as the normal method of everting the hemipenes did not work, except of dead specimens which were relaxed. In was, therefore, necessary to resort to probing with a liquid paraffin moistened probe, behind the vent. A deep pocket indicated the presence of inverted hemipenes following Szidat (1968). This method, however, does have its drawbacks, in that it is not always easy to insert a probe, as the hemipene may be constricted by muscles which block the entrance of the probe. In addition, the probing must be done very gently in order to avoid piercing the soft skin of the socket. Probes of various sizes were made to suit all reptiles likely to be captured.

Some lizards showed sexual di-chromatism, especially during the reproductive period while also at the same time exhibiting swollen hemipenes, so that sexing was relatively simple and provided a back check on the sexing done by the method described above.

The amphibians on the other hand, were difficult to sex when immature. Differences between the sexes when adult include dark coloured gular regions, as well as pads on the thumb in males, both of which characters were not, or only partially, developed in females. These then were the basic characters relied on.

Initially, all snakes were marked by a standard scale clip method, Blanchard & Finster (1933). This involved clipping the belly scales so that a permanent mark is made, which upon recapture can be endorsed again. In this method, the anal scale covering the vent is considered as No. 0. Moving anteriorly, the next scale is No. 1 and so forth to the 10th. The eleventh scale is No. 20, while the twentieth is No. 100 and so forth. This method allows for an indefinite number of combinations. Clipping the scales of juveniles was difficult and required a very narrow, sharp-pointed scissors, (Figure 11).

At the same time, another method of marking was also attempted, using a tattooing machine and a twelve volt battery as described by Woodbury (1948). The snakes were either marked caudally or else the ventral skin was twisted around to be against the ribs in the neck region and a number tattooed. This method was not of use on species with a dark ventral skin, as the mark is not visible. Another drawback experienced, was that the machine was too coarse for small snakes and on the other hand, not adequate enough to pierce the heavy ventral scales of the larger snakes.

However, both the above methods proved to be too laborious, and in the first mentioned method, some regrowth was seen to take place. Therefore another method, Weary (1969), was attempted. This involved the use of a fine-tipped soldering iron. The subcaudal scales are paired in most snakes and are numbered starting from the first large subcaudal on the left-hand side posterior to the vent (Figure 11). Again, a system of numbering from one to 10, 20 - 100, 200 - 1000, is used which enables an infinite number of combinations. This method proved to be particularly successful and no regrowth occurred, the marks being clearly visible four years after the animal was marked.

As all these methods involved subsequent recapturing in order to determine whether they were marked, another method of marking, namely cryobranding, was attempted, so that the mark could be seen without resorting to the capture of the animal. Two different methods were tested, one using a can of "Dust Off", produced by Falcon Safety Products, Inc., commonly used by photographic agencies. This contains freon (Dichlorodifluoromethane), which is a liquid gas which by inverting the container, is squirted onto the skin of the reptile for a few seconds. The skin is frozen in that area and

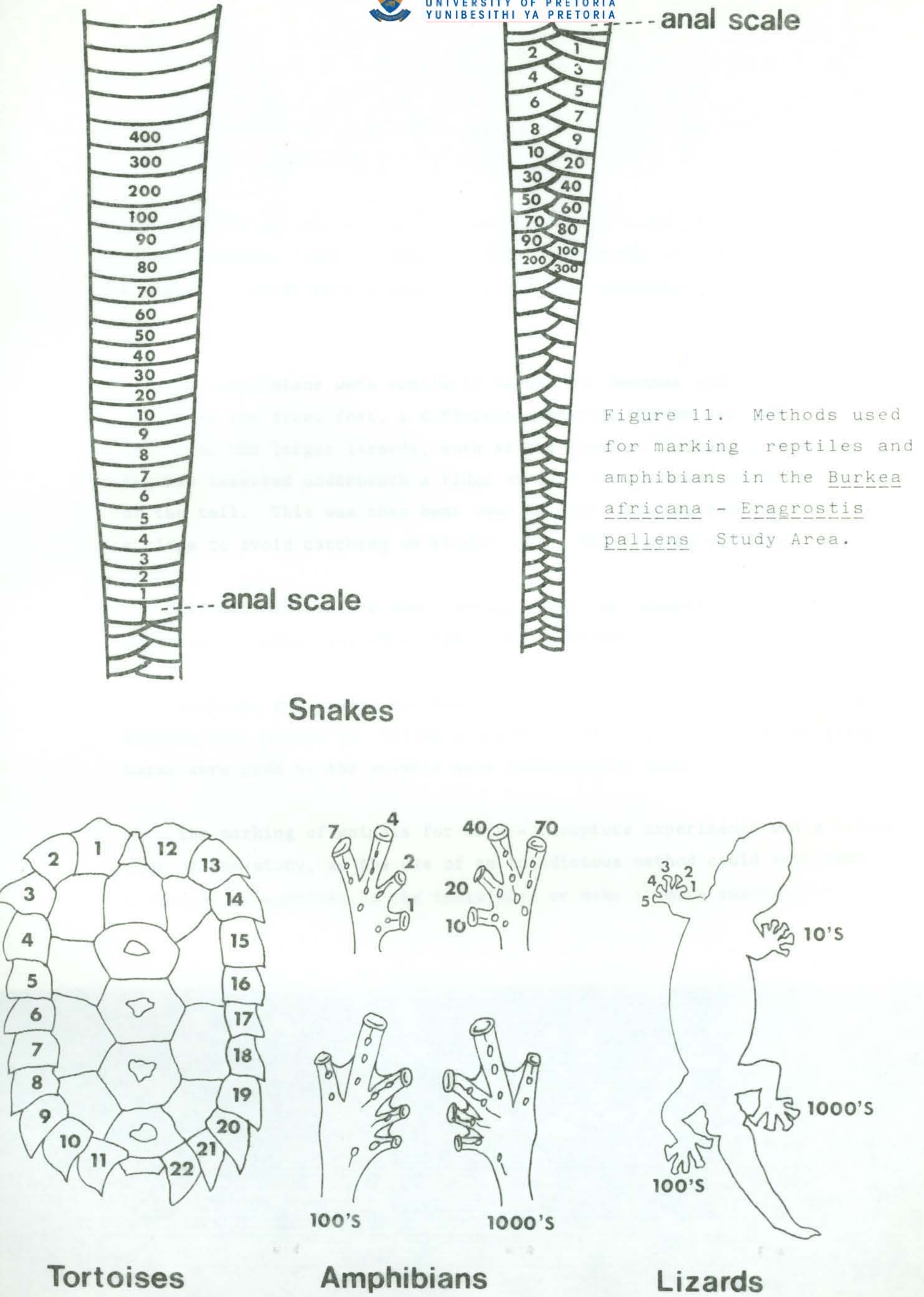


Figure 11. Methods used for marking reptiles and amphibians in the *Burkea africana* - *Eragrostis pallens* Study Area.

the pigment cells are killed so that after subsequently shedding the skin, the area is white. In this instance, a burst of five seconds proved to be too long, and although showing white initially after the first ecdysis, scar tissue formed and virtually obliterated the marks. A less lengthy exposure would possibly obtain good results.

The other method involved brass branding irons in the shape of symbols, immersed in a mixture of dry ice and methanol. The irons cool down to approximately -70°C, usually discernable when the mixture stops boiling. At this stage, the irons are removed and held firmly against the skin of the reptiles. The skin froze onto the underlying tissue and on subsequent sloughings the marks became clearly discernible. All the marks, however, only lasted one year and became less visible after each successive sloughing. With some species, such as pythons, distinctive markings on the head and tail were photographed for later recognition. This, however, is only applicable to those species having such distinctive colour variations.

Lizards and amphibians were marked in the standard toe clipping technique, Woodbury (1948). This involved the removal of the first section of a digit. Lizards were clipped on all digits according to numbers, (Figure 11).

The amphibians were similarly marked but because they only have four digits on the front feet, a different numbering system was used (Figure 11). For the larger lizards, such as the Monitor lizards, a numbered metal tag was inserted underneath a ridge of hard scales found on the dorsal side of the tail. This was then bent over so that the tag took on the shape of a ridge to avoid catching on sticks, etc. This proved very successful.

Alcohol was applied when marking, with the exception of snakes and tortoises. Infections were, therefore, avoided.

Although an attempt was made to assess the tortoise population, and animals were marked by filing a notch in the marginal scutes, no recaptures were made as the animals were infrequently seen.

The marking of animals for mark - recapture experiments was a critical part of the study, as the use of an injudicious method could seriously have affected the survival of the individual or make it more susceptible to to predation. The trauma of capture coupled with the pain of marking may also affect its subsequent catchability. With this background, a method of establishing the presence of a marked animal by means of a suitable dye should be thoroughly investigated. Although several methods were tested, none proved to last for more than the ten-day period, and had to be repeated at each visit.

# 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* |

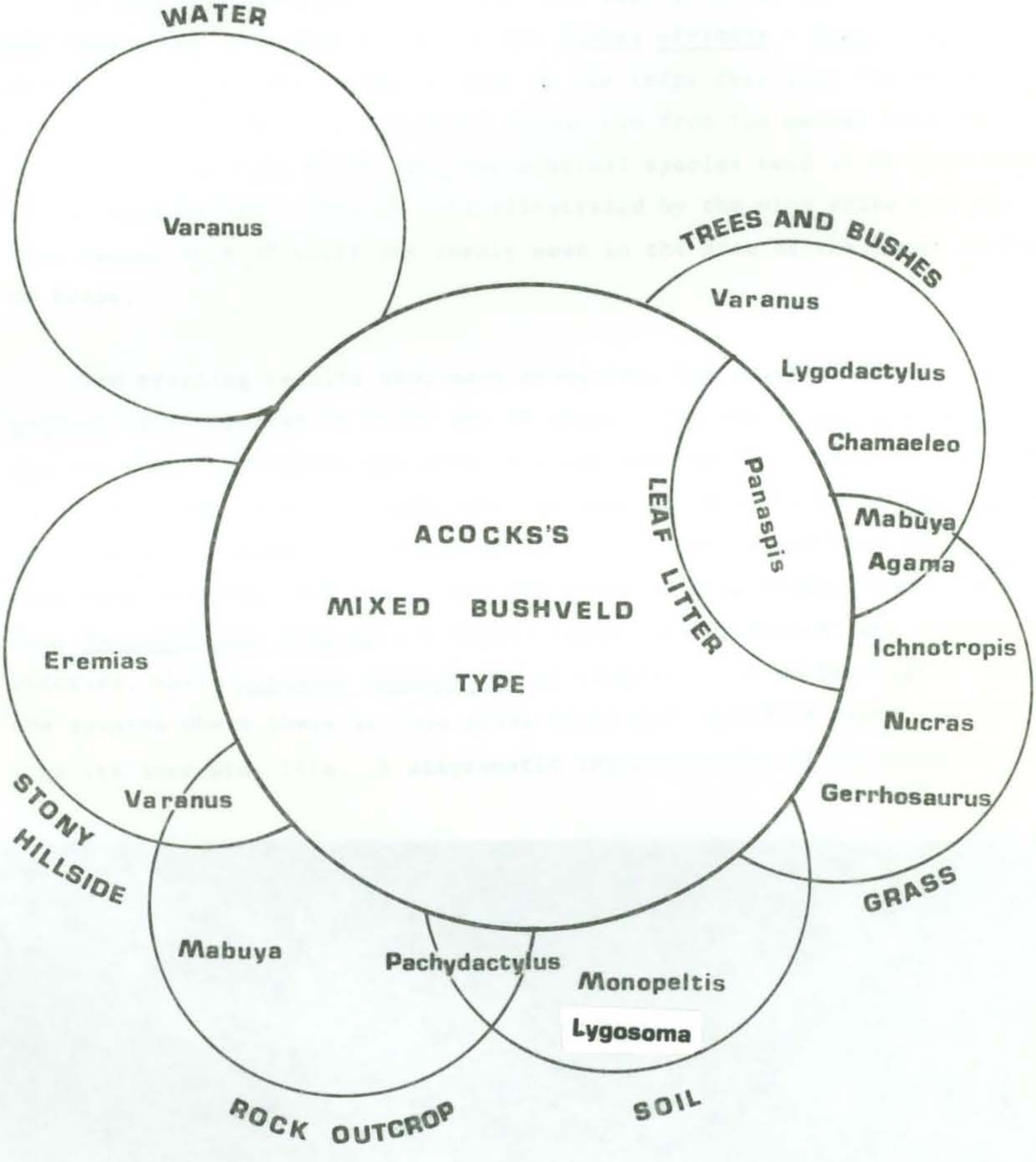


Figure 12. Habitats and microhabitats occupied by various Saurian genera on the Nylsvley Nature reserve.

| | | |
|---|---|---|
| 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 and 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.

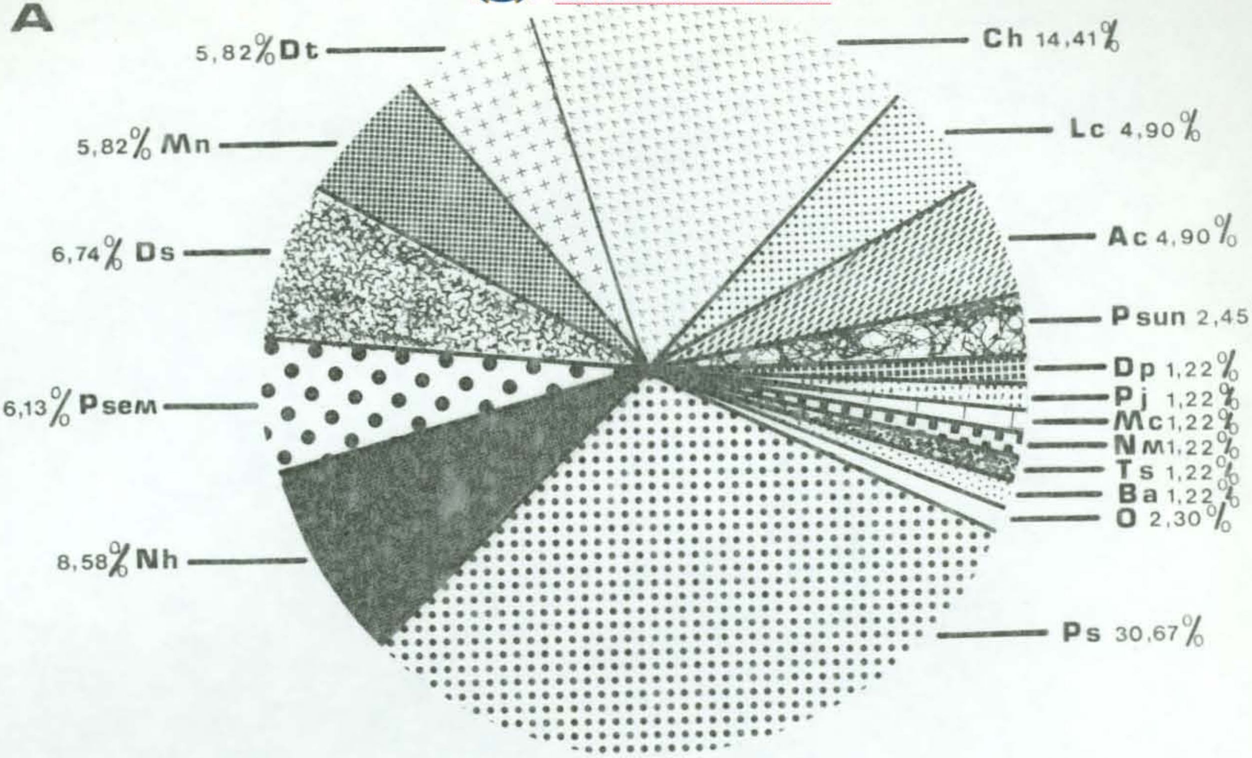
## Snakes

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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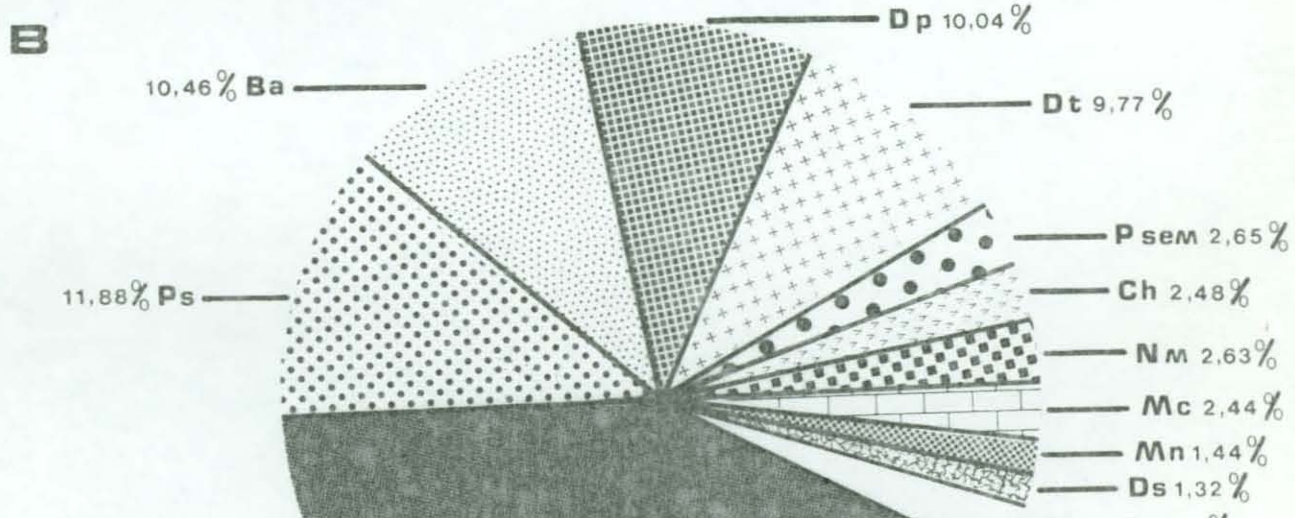


BIOMASS

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 | S/V (mm) Range | Mass (g) Mean | Mass (g) 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.

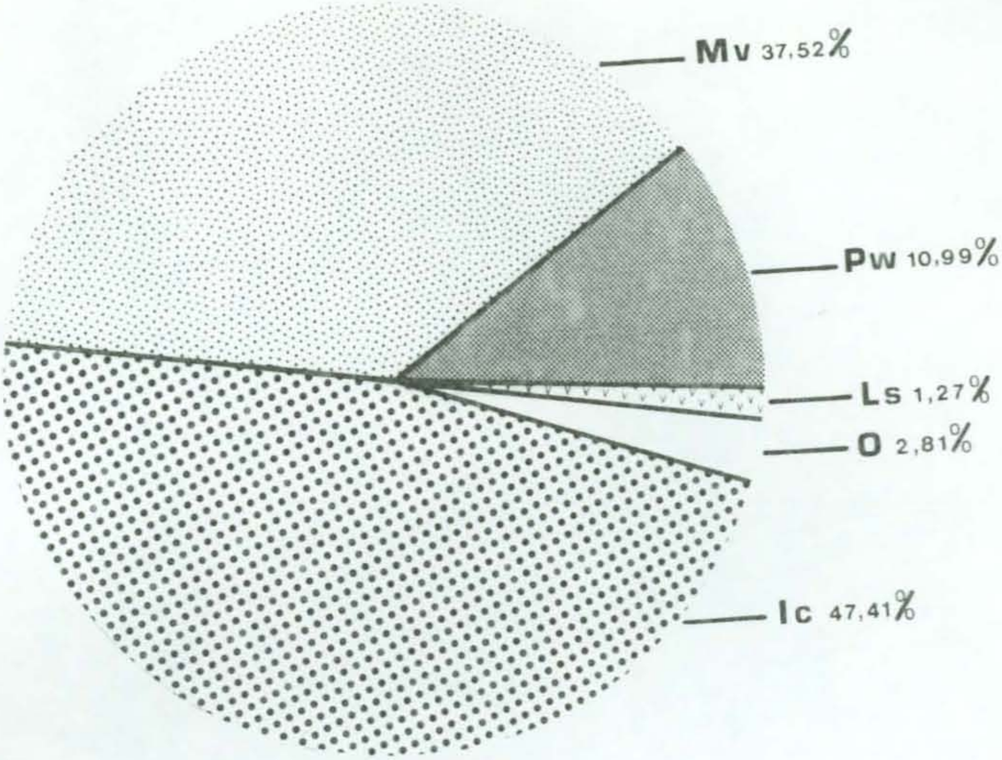
Table 5. Mean Snout-to-Vent length and Mass of lizards in the *Burkea africana* - *Eragrostis pallens* Study Area

| 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).

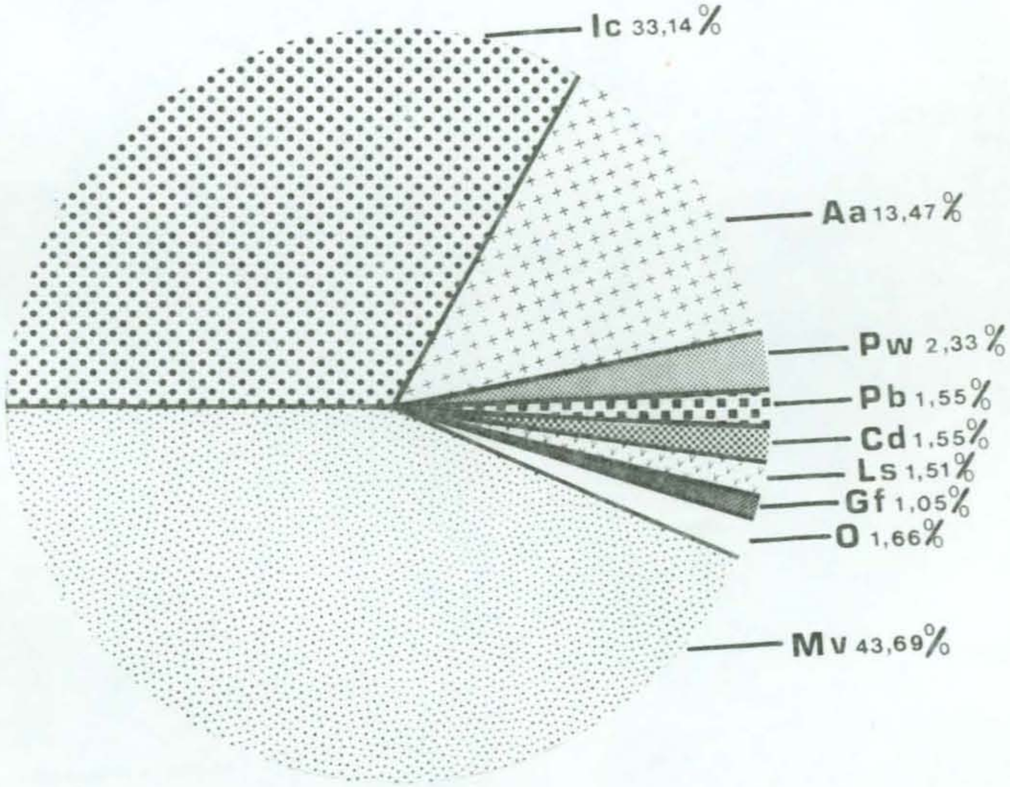
Ic = Ichnotropis capensis
Aa = Agama atricollis
Pw = Panaspis wahlbergi
Pb = Pachydactylus bibroni
Cd = Chamaeleo dilepis
Ls = Lygosoma sundevallii
Gf = Gerrhosaurus flavigularis
O = Others
Mv = Mabuya varia

A



NUMBERS

B



BIOMASS

## 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 | S/V (mm) Range | Mass (g) Mean | Mass (g) 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 |

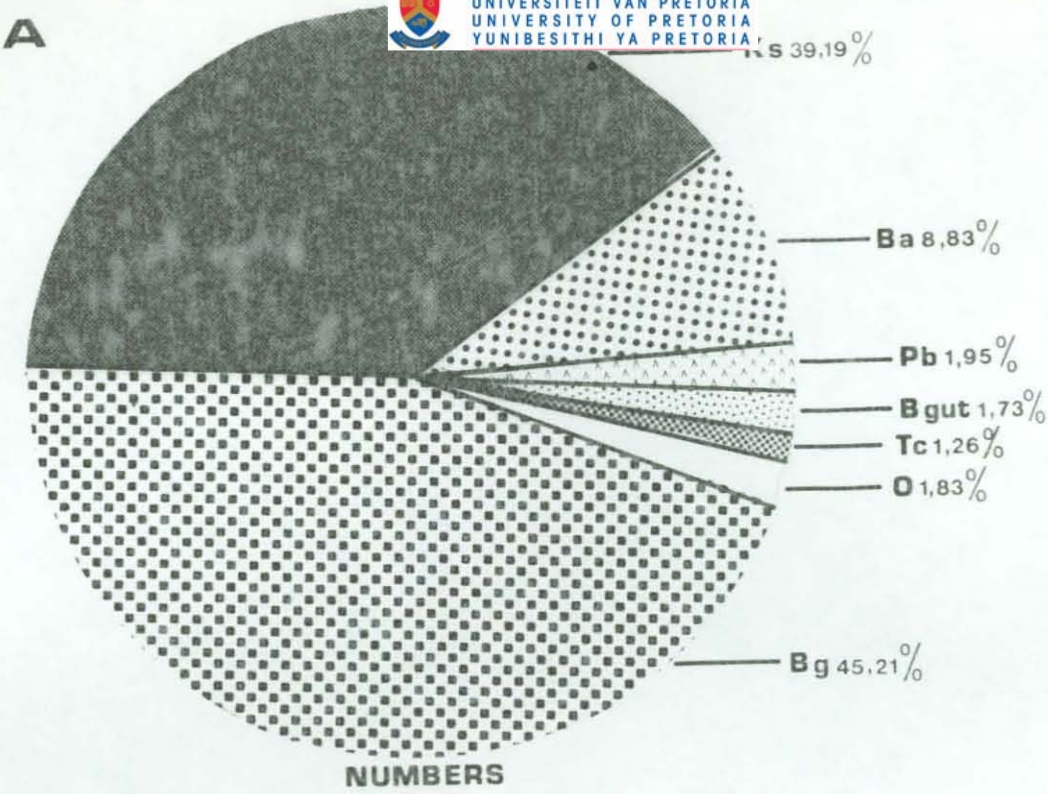
## Seasonal fluctuation of the populations

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

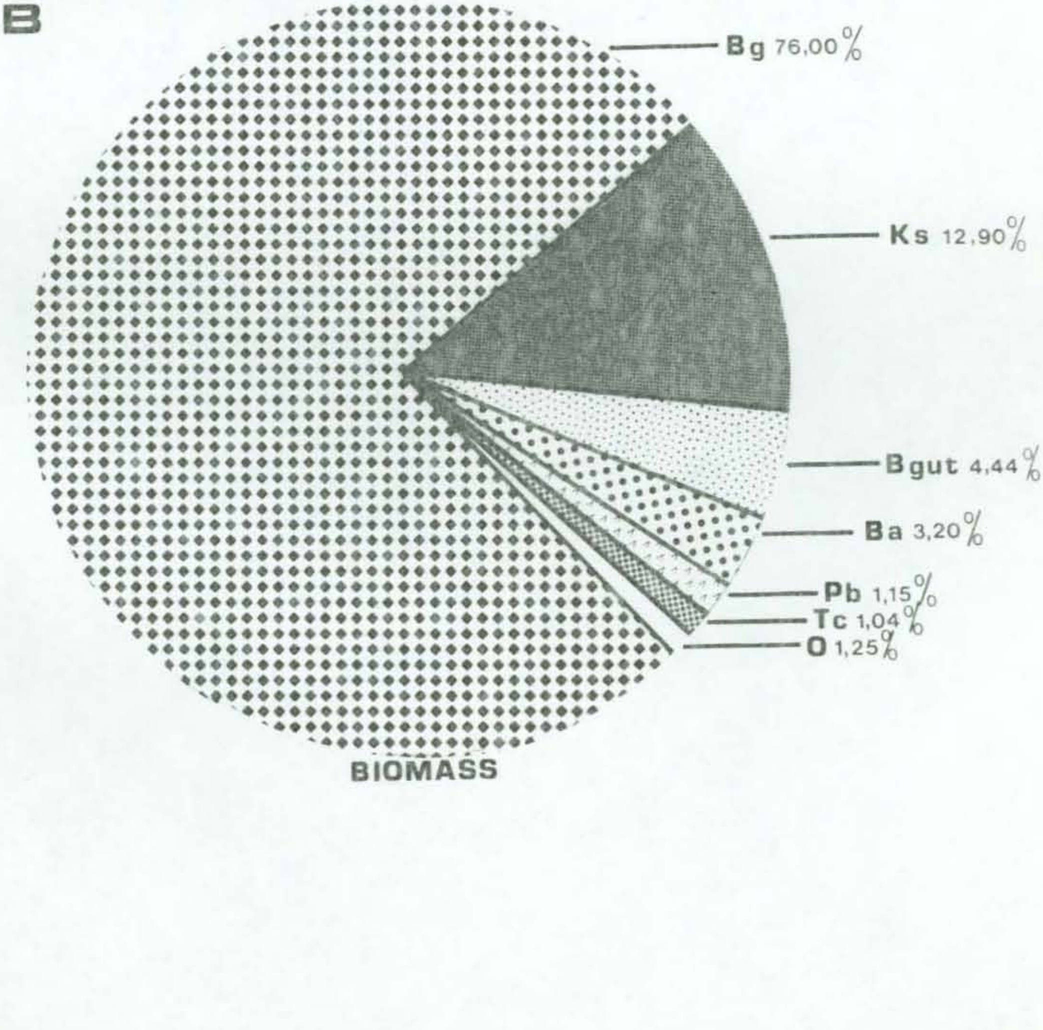
Figure 15. Spectrum of (A) Amphibian species composition and (B) proportionate biomass in the *Burkea africana* - *Eragrostis pallens* Study Area: May 1975 - May 1977

Bg = *Bufo garmani*
Ks = *Kassina senegalensis*
Bgut = *Bufo gutturalis*
Ba = *Breviceps adspersus*
Pb = *Phrynomerus bifasciatus*
Tc = *Tomopterna cryptotis*
O = Others

A


Ks 39,19%
Ba 8,83%
Pb 1,95%
B gut 1,73%
Tc 1,26%
O 1,83%
Bg 45,21%
NUMBERS

B


Bg 76,00%
Ks 12,90%
B gut 4,44%
Ba 3,20%
Pb 1,15%
Tc 1,04%
O 1,25%
BIOMASS

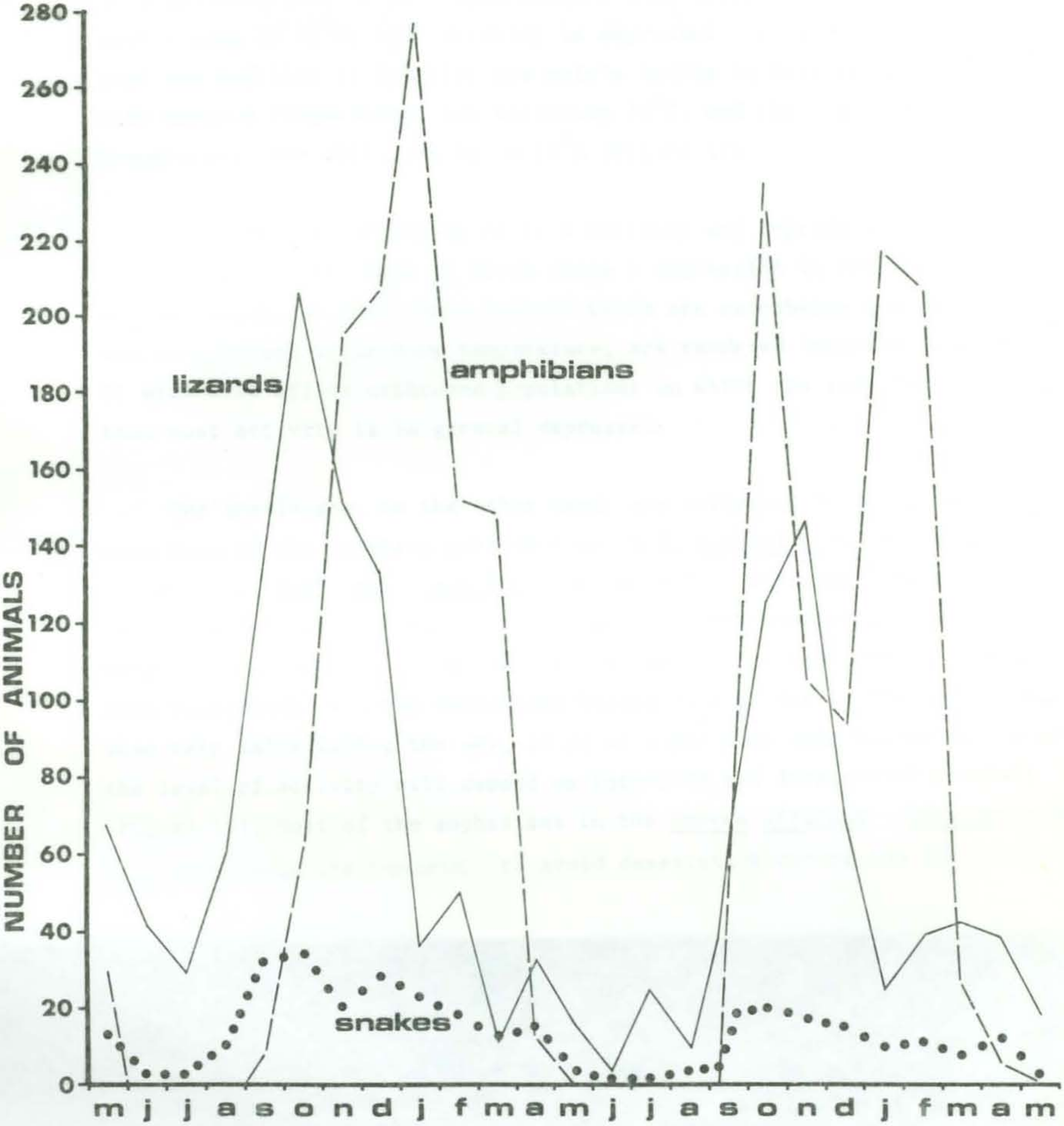


Figure 16. Number of animals captured in the trapping grid from May 1975 to May 1977 in the Burkea africana- Eragrostis pallens Study Area.

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.

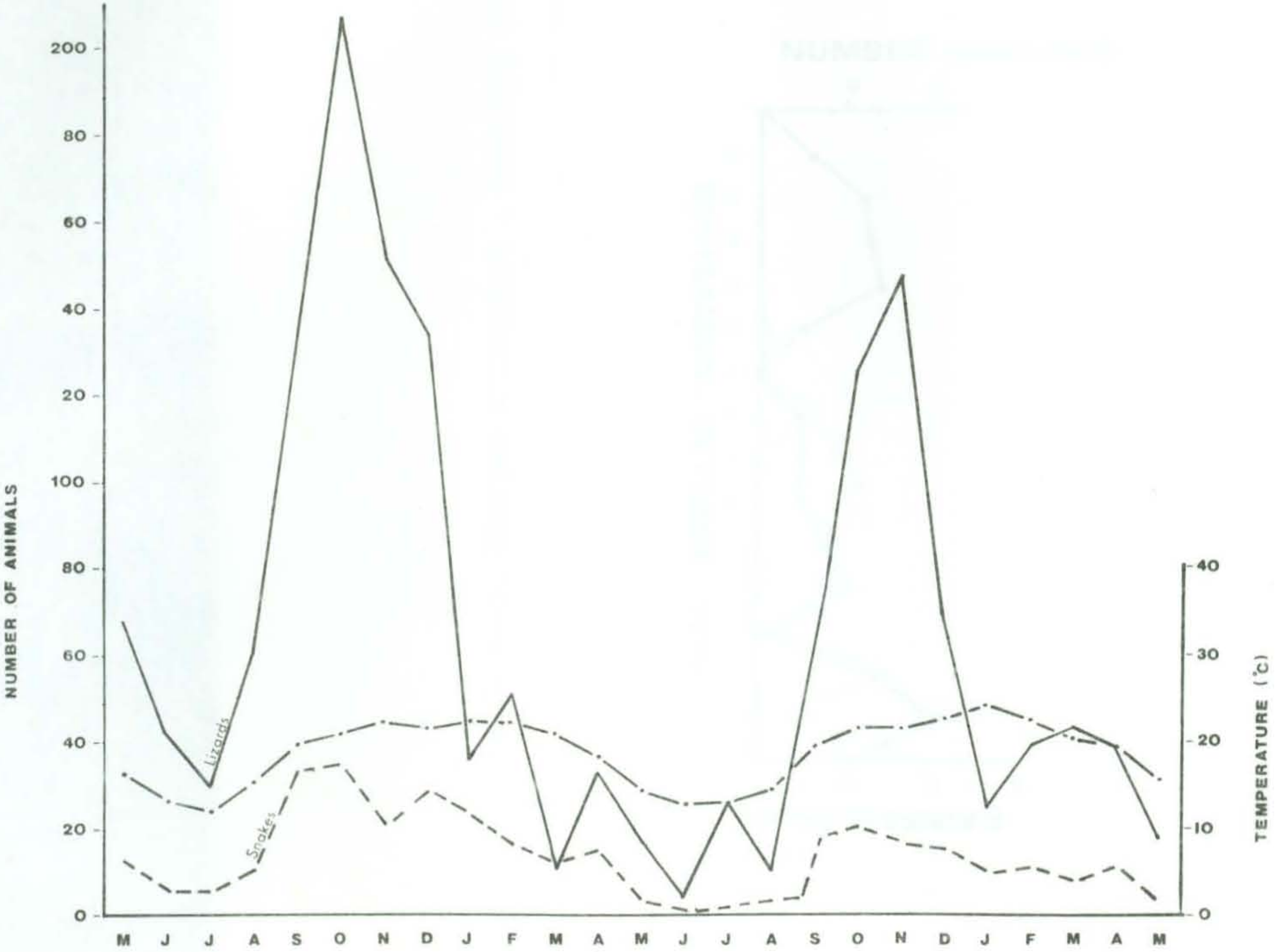


Figure 17. Effect of temperature on the activity of reptiles in the *Burkea africana* - *Eragrostis pallens* Study Area: May 1975 - May 1977.

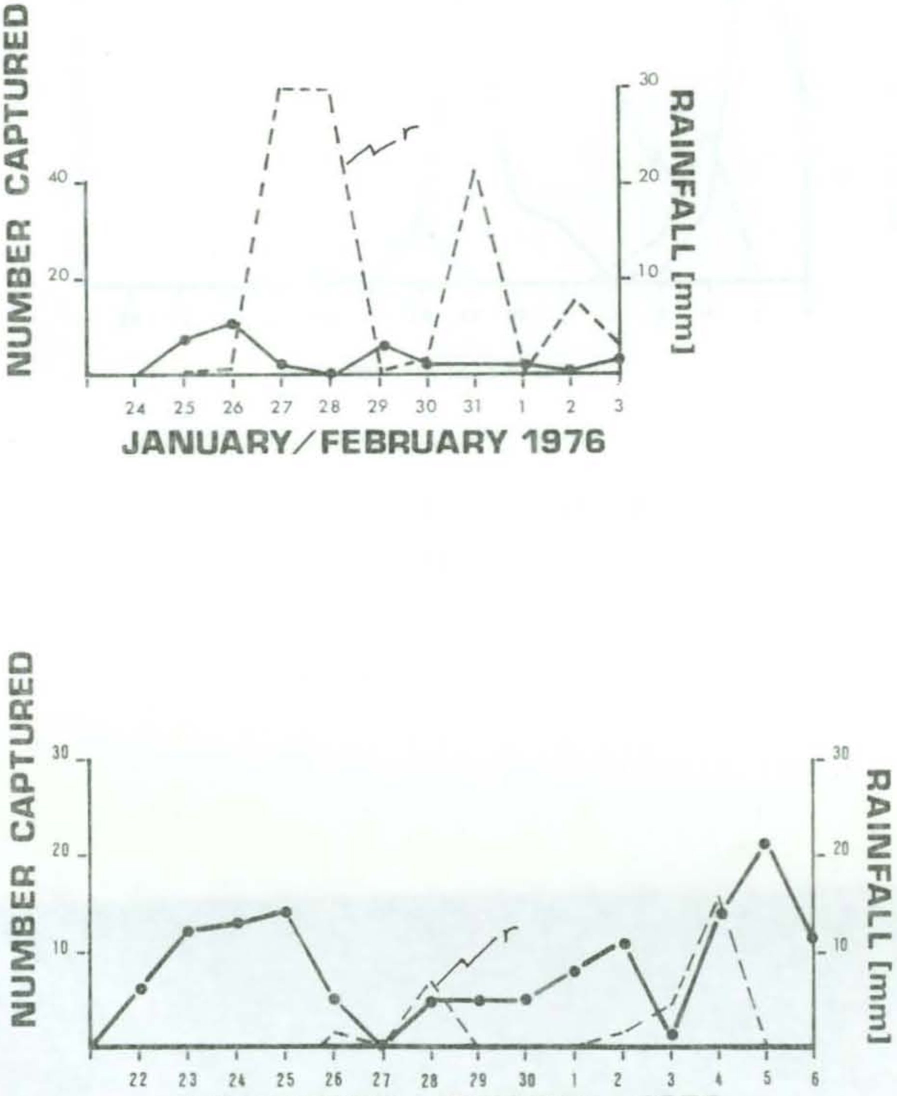


Figure 18. Effect of rainfall on the activity of lizards in the <u>Burkea africana</u> - <u>Eragrostis pallens</u> Study Area.

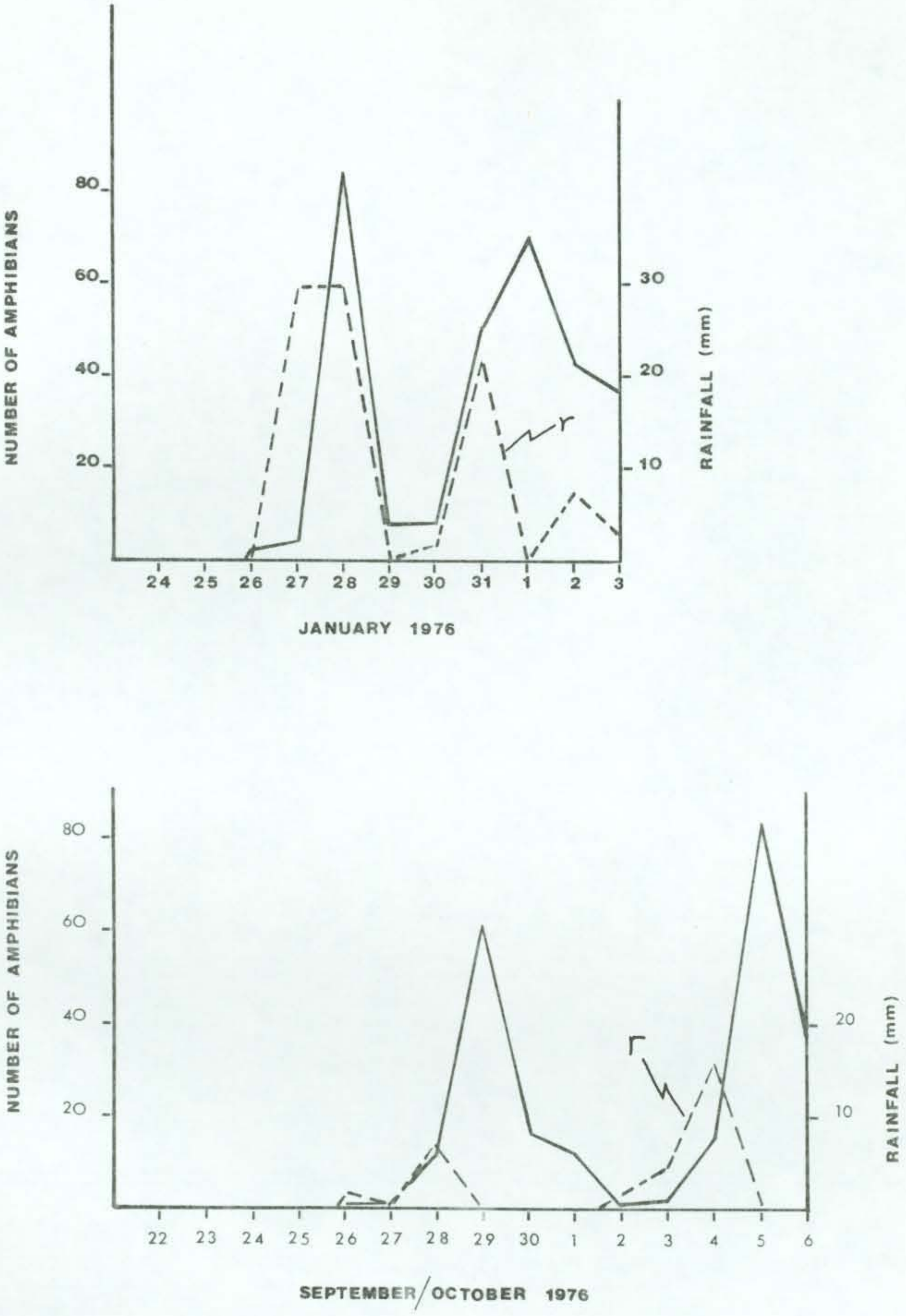


Figure 19. Effect of rainfall on the activity of amphibians in the *Burkea africana* - *Eragrostis pallens* Study Area.

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,

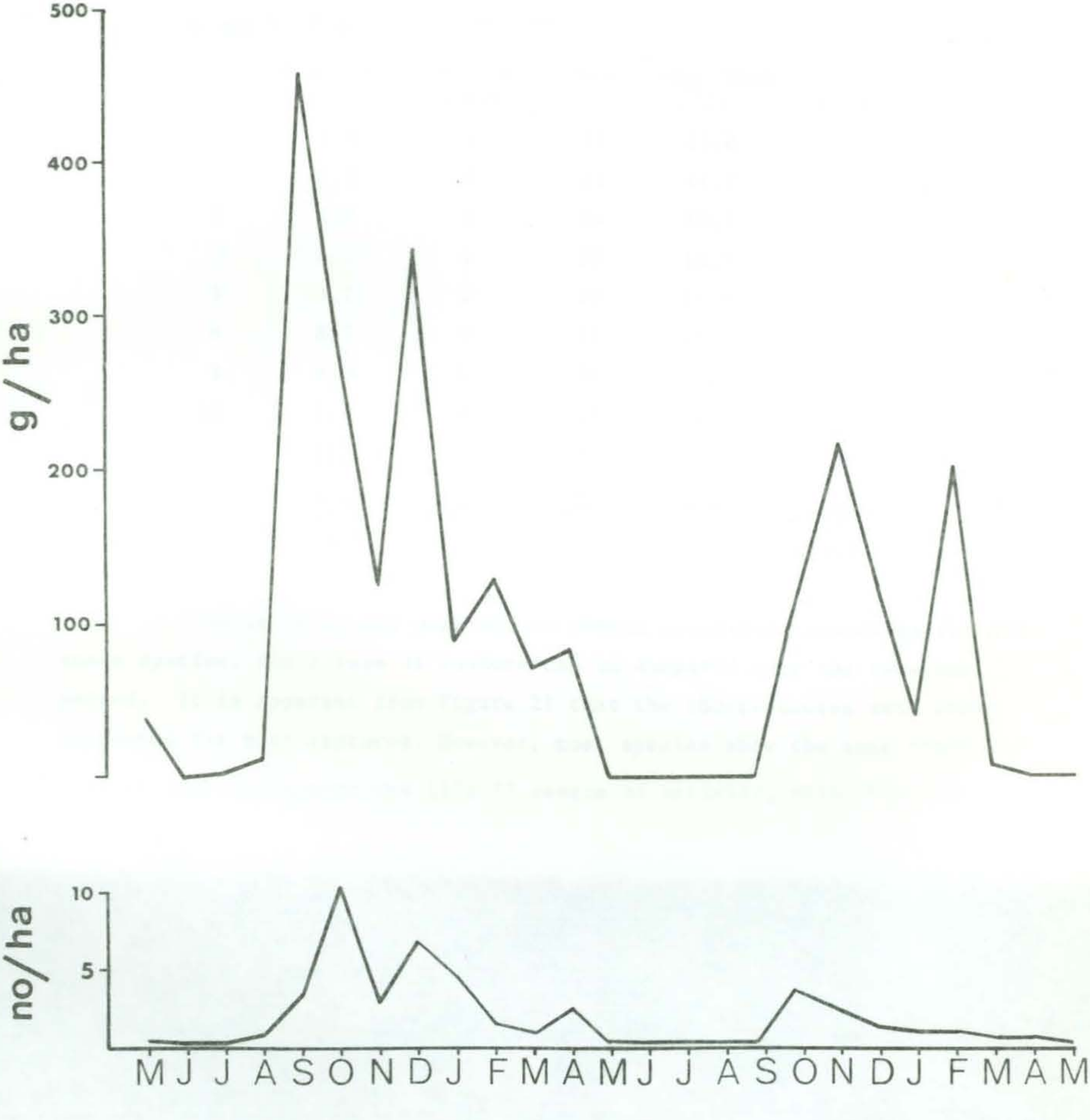


Figure 20. Density and biomass of snakes in the Burkea africana -Eragrostis pallens Study Area: May 1975 - May 1977 (excluding Thelotornis capensis)

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 $10^{\circ}$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 $12{,}6^{\circ}$C compared to $8{,}5^{\circ}$C for the previous census. Mean maximum temperatures were virtually the same during both periods, namely $26{,}12^{\circ}$C and $26{,}48^{\circ}$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 <u>Burkea africana</u> - <u>Eragrostis pallens</u> Study Area.

| | Date | Min. Temp. ($^{\circ}$C) | No. of snakes | Date | Min. Temp. ($^{\circ}$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 |

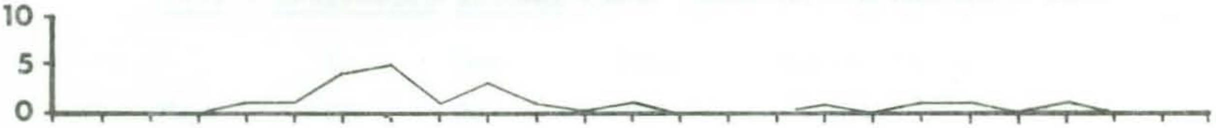
While it is not possible to obtain population estimates for all snake species, their rate of capture can be compared over the two-year period. It is apparent from Figure 21 that the short-snouted sand snake accounted for most captures. However, most species show the same trend and numbers declined during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

**LYCOPHIDION CAPENSE**

**PROSYMNA SUNDEVALLII**

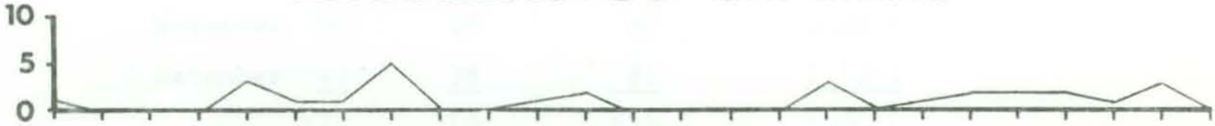
**DISPHOLIDUS TYPUS**

**PHILOTHAMNUS SEMIVARIEGATUS**

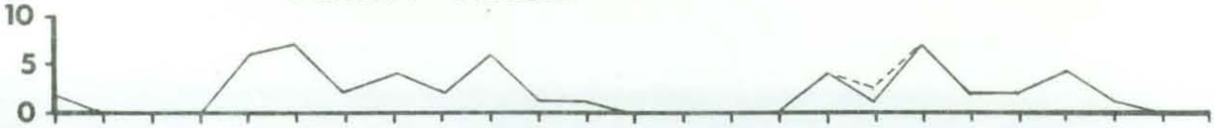


**MEHELYA NYASSAE**

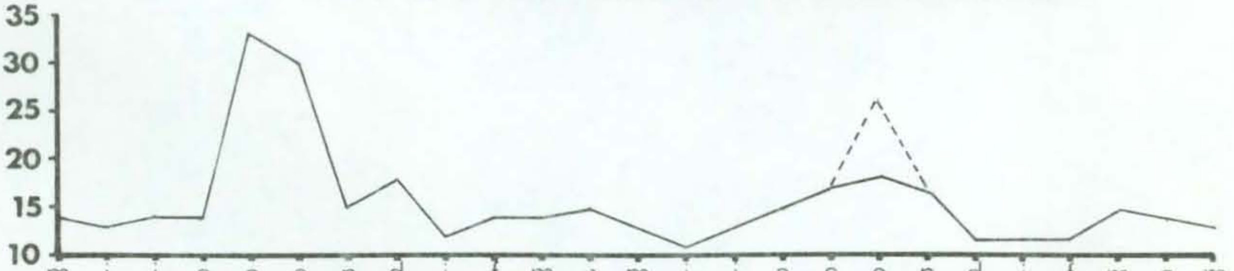
**APARALLACTUS CAPENSIS**



**NAJA HAJE**



**CROTAPHOPELTIS HOTAMBOEIA**



**PSAMMOPHIS SIBILANS**

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 <u>Burkea africana</u> - <u>Eragrostis pallens</u> 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 (<u>Coluber constrictor</u>), 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 (<u>Thelotornis capensis</u>) 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

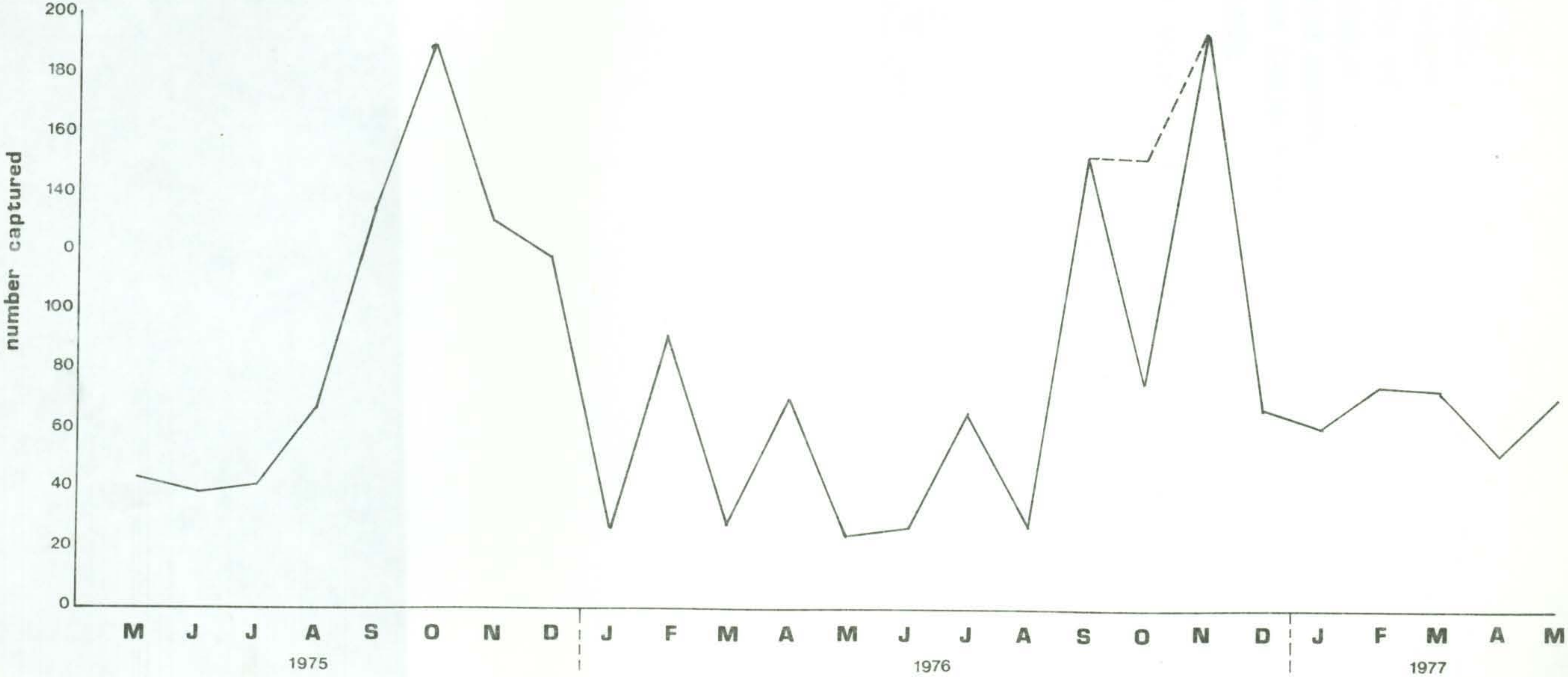
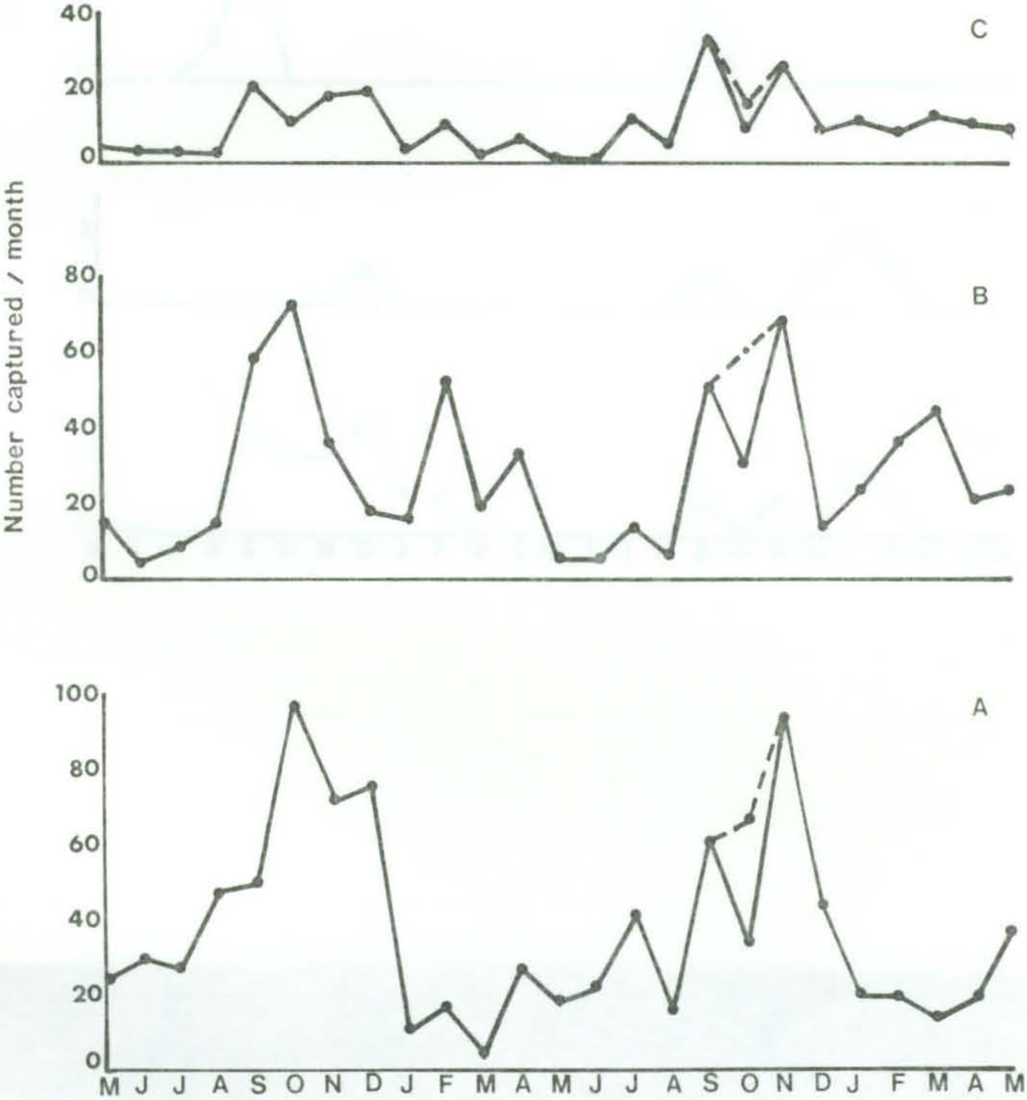


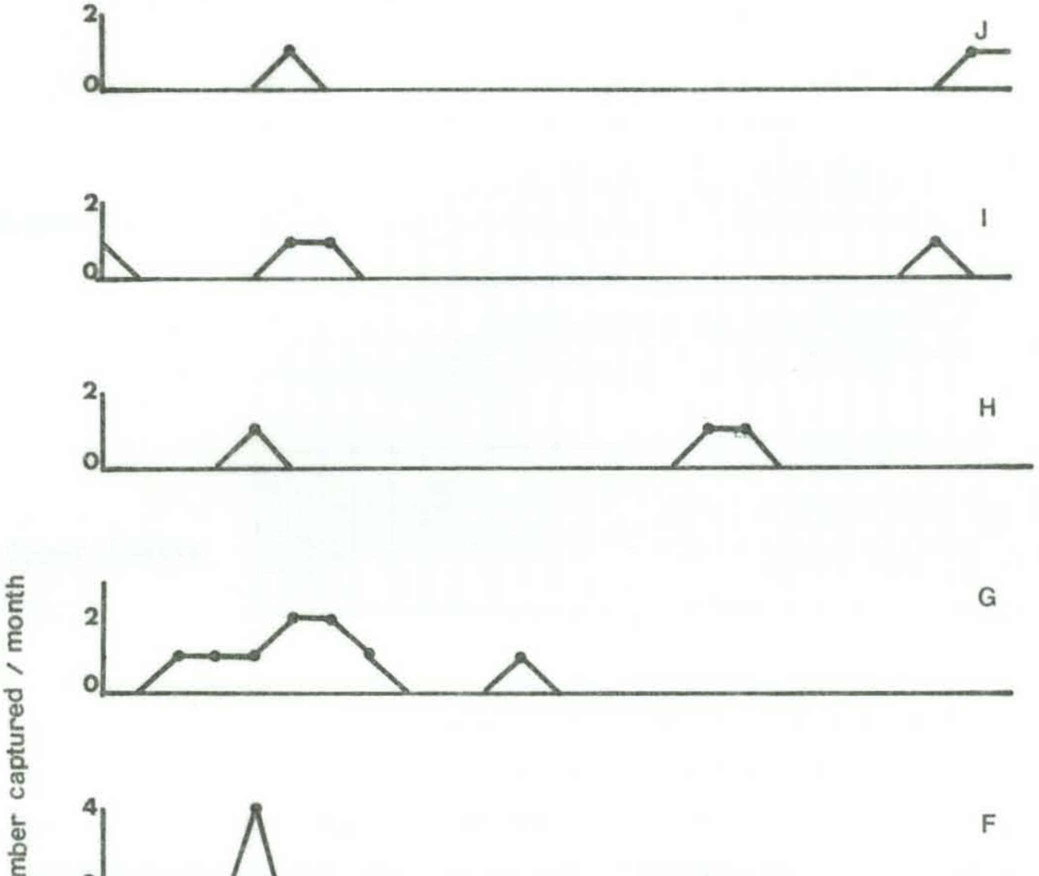
Figure 22. Total number of lizards captured per month in the Study Area, excluding Lygodactylus capensis, May 1975 to May 1977. (– – – – – – – extrapolation as census period shortened).

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.


40
20
0
C
Number captured / month
80
60
40
20
0
B
100
80
60
40
20
0
A
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


Number captured / month
J
I
H
G
F
E
D
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,

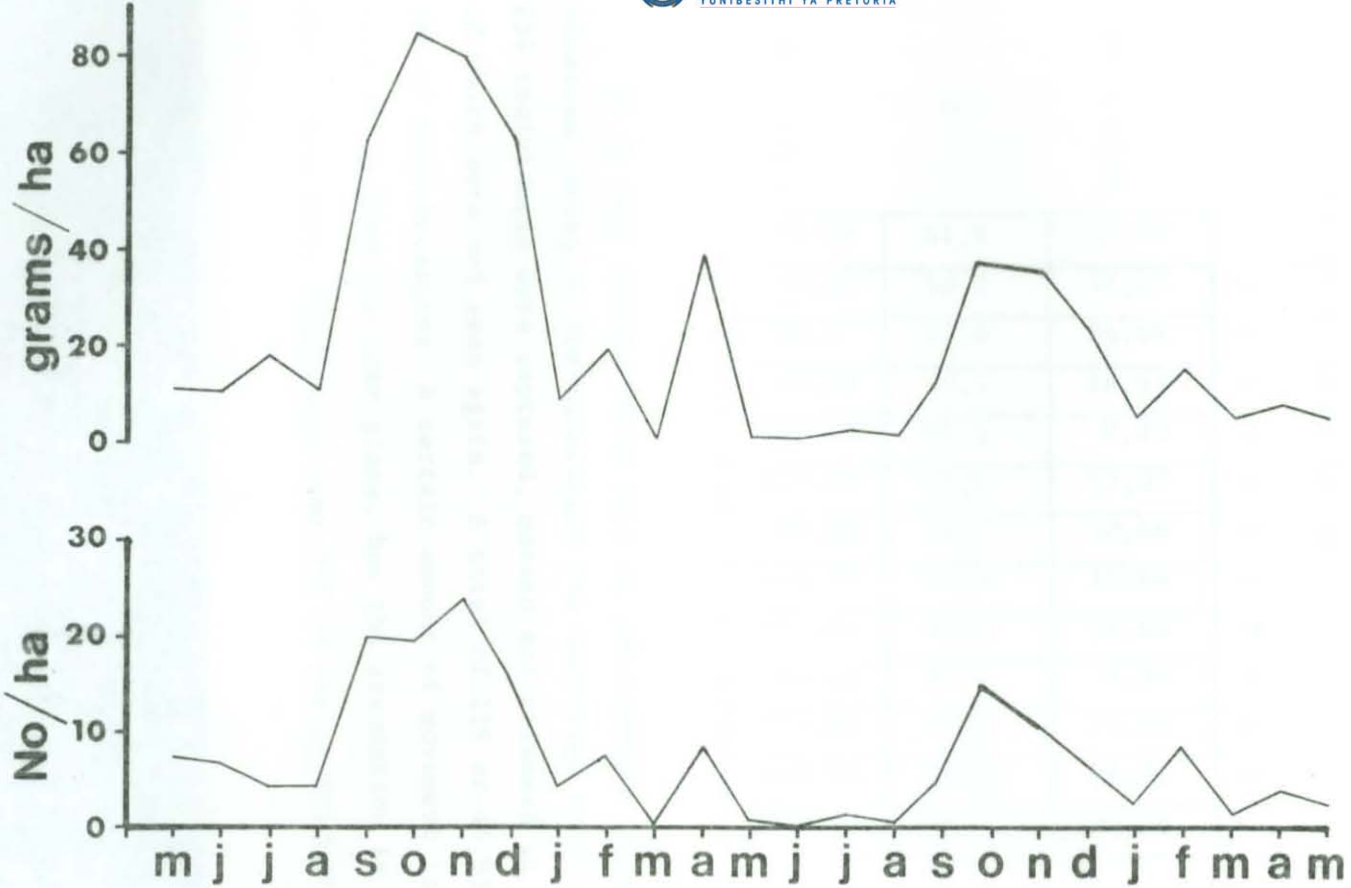


Figure 24. Density and biomass of lizards in the *Burkea africana* - *Eragrostis pallens* Study Area: May 1975 to May 1977 (excluding *Lygodactylus capensis*)

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

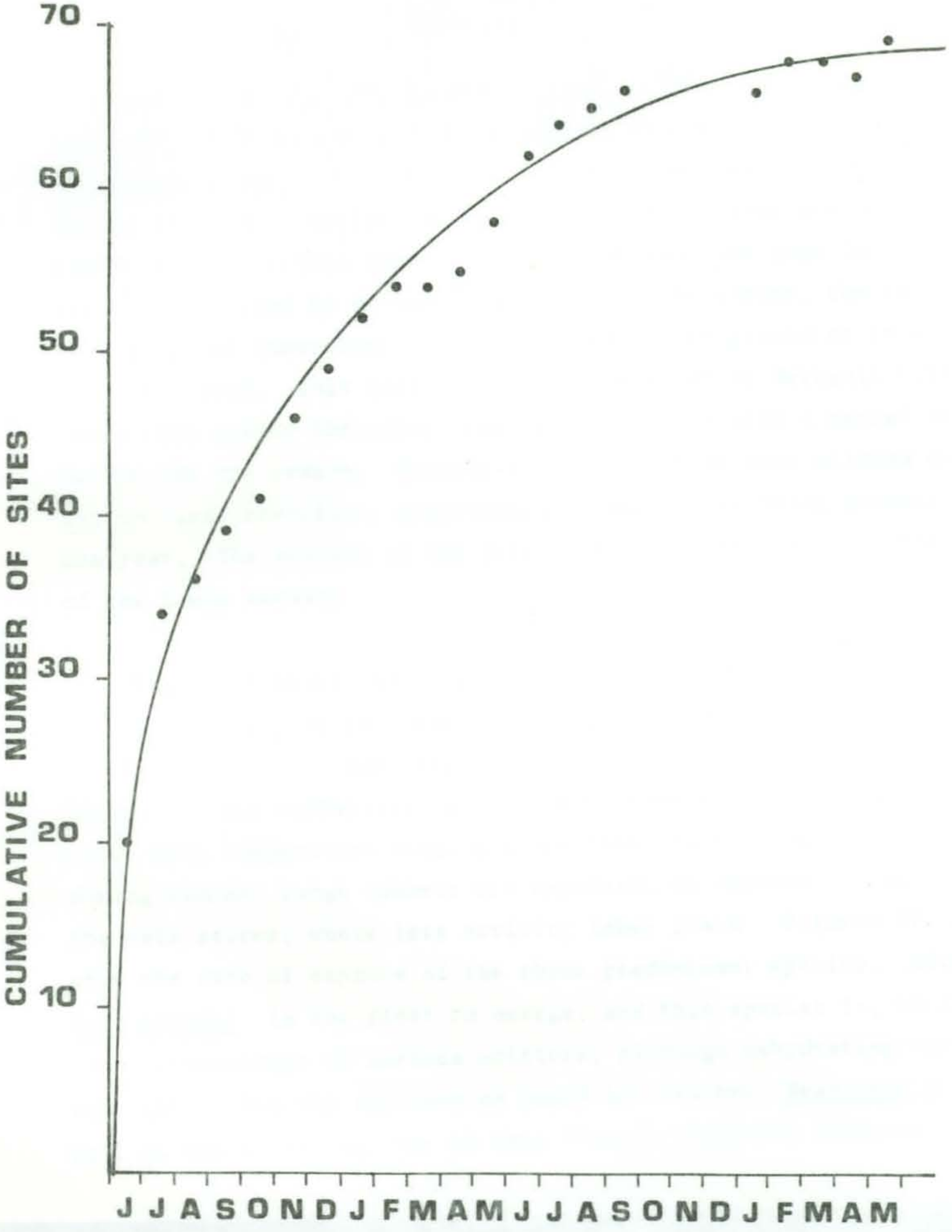


Figure 25. Cumulative number of Lygodactylus capensis capture sites, June 1975 to May 1977, in the Intensive Study Area.

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

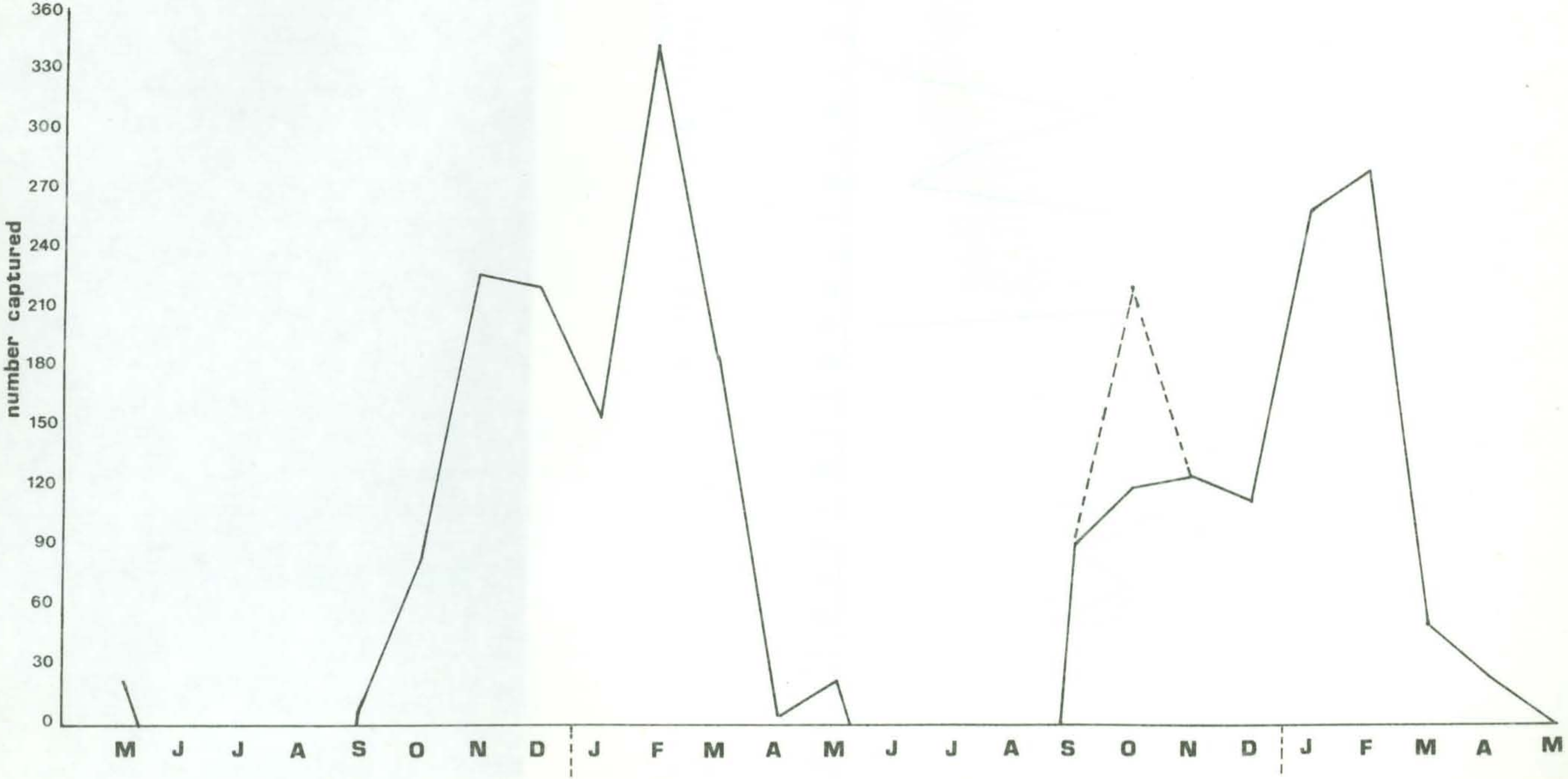


Figure 26. Total number of amphibians captured in the *Burkea africana* - *Eragrostis pallens* Study Area, May 1975 - May 1977.
(------------ = extrapolation as census period shortened).

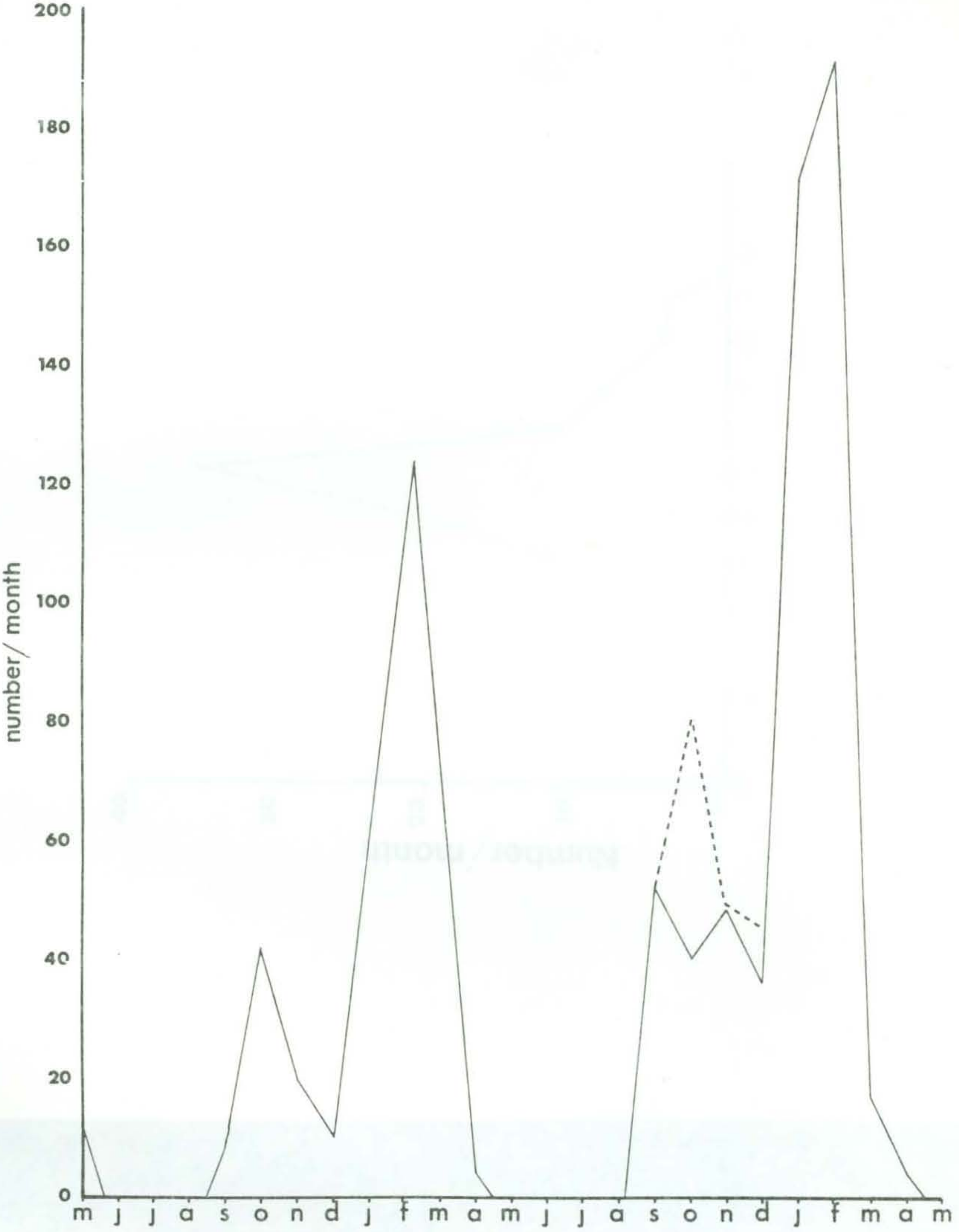


Figure 27. Monthly fluctuations of Bufo garmani captured in the Study Area, May 1975 - May 1977. (----------= extrapolation as census period shortened).

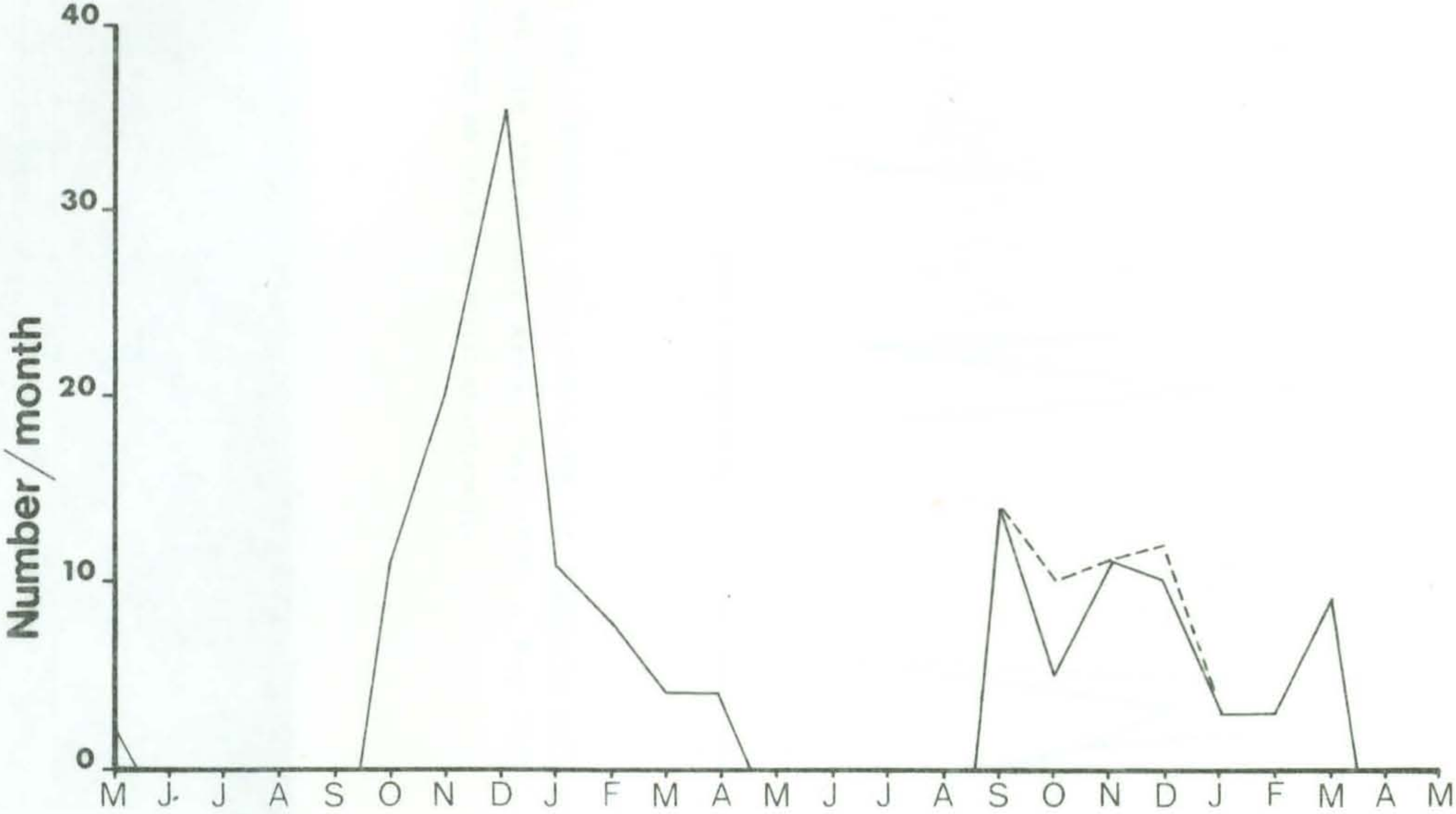


Figure 28. Monthly fluctuations of Breviceps adspersus captured in the Study Area, May 1975 - May 1977. (---------- = extrapolation as census period shortened).

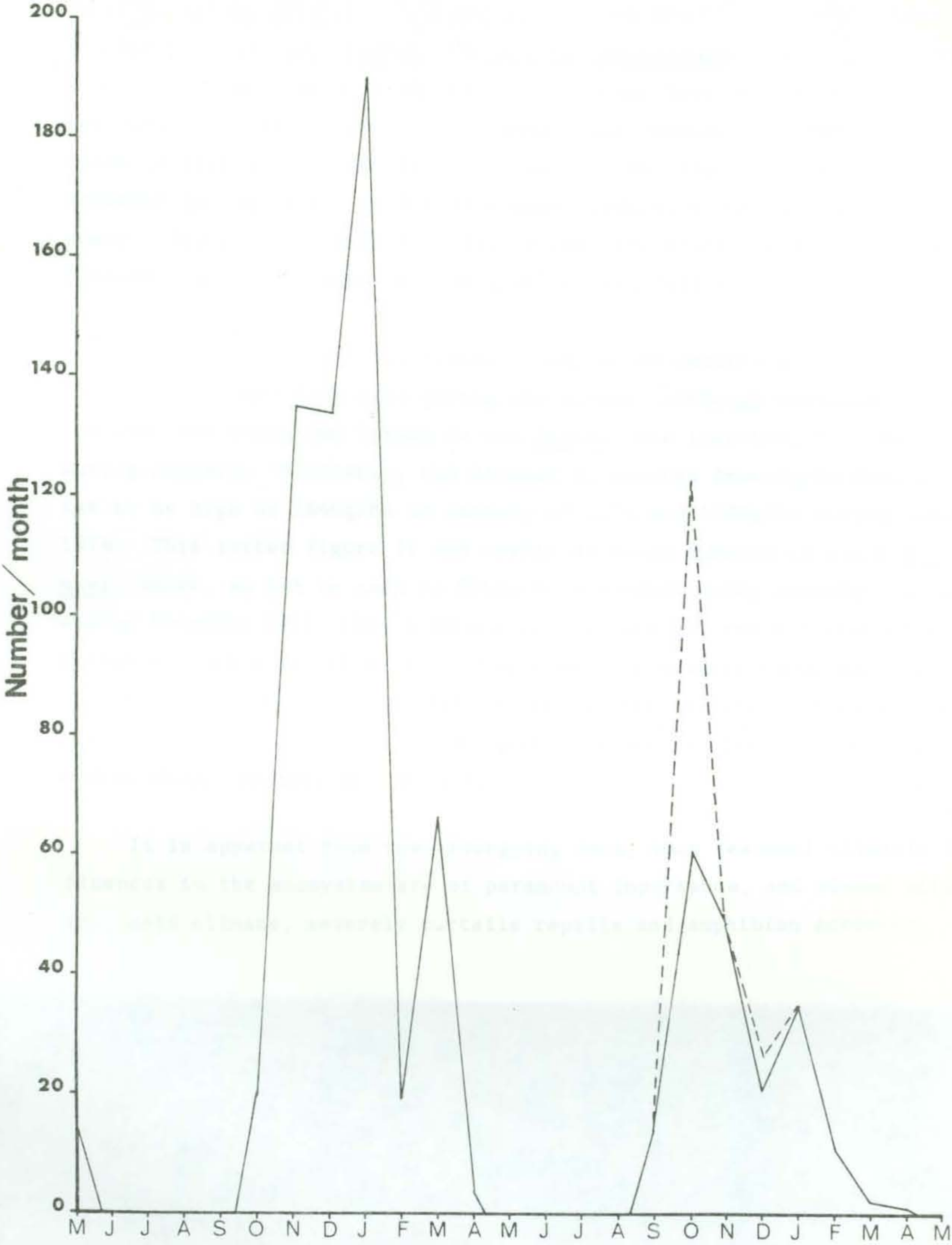


Figure 29. Monthly fluctuations of Kassina senegalensis captured in the Study Area, May 1975 - May 1977. (------------ = extrapolation as census period shortened).

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.

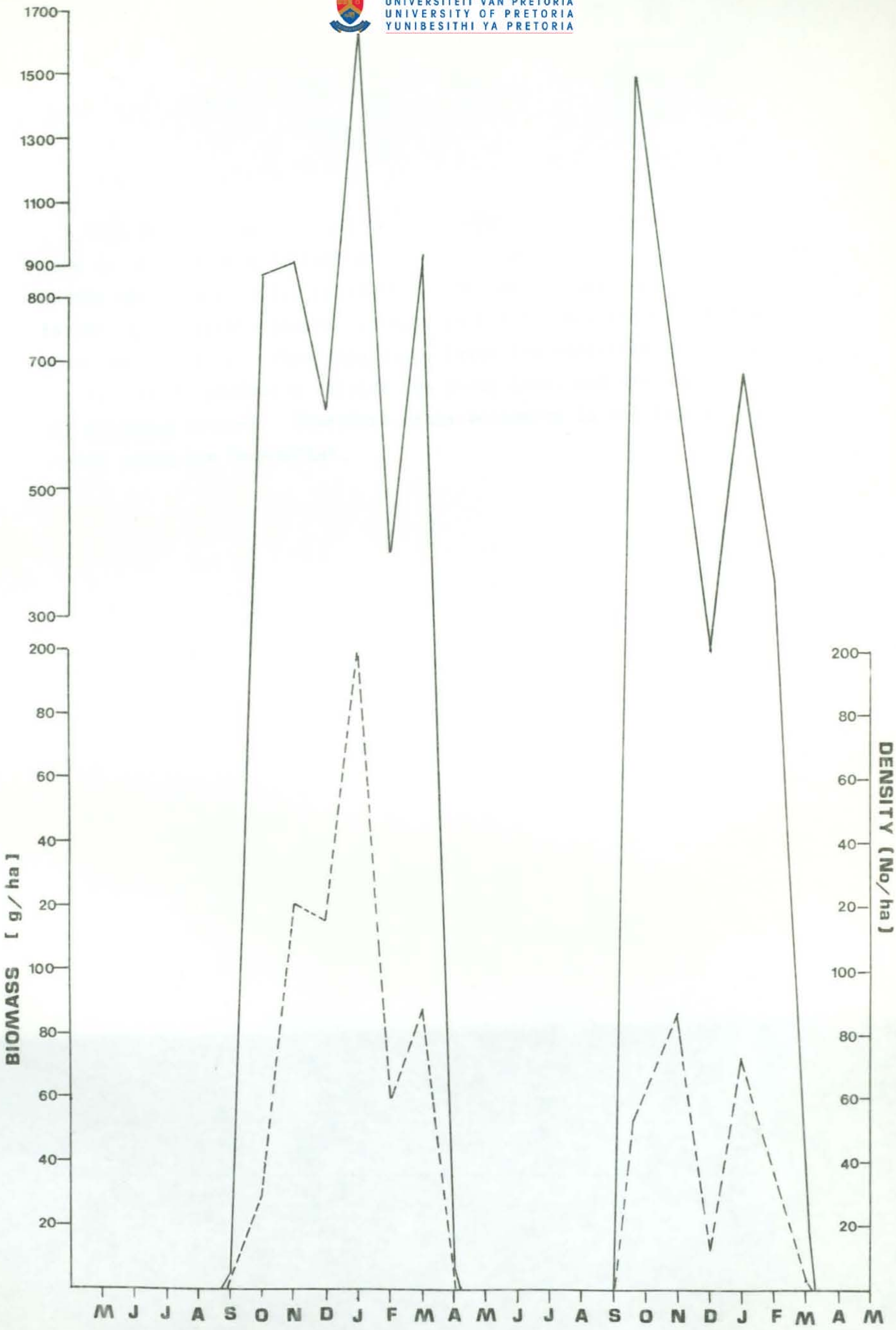


Figure 30. Density and biomass of Amphibians in the *Burkea*

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.

# 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 *Thelotornis capensis*, 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

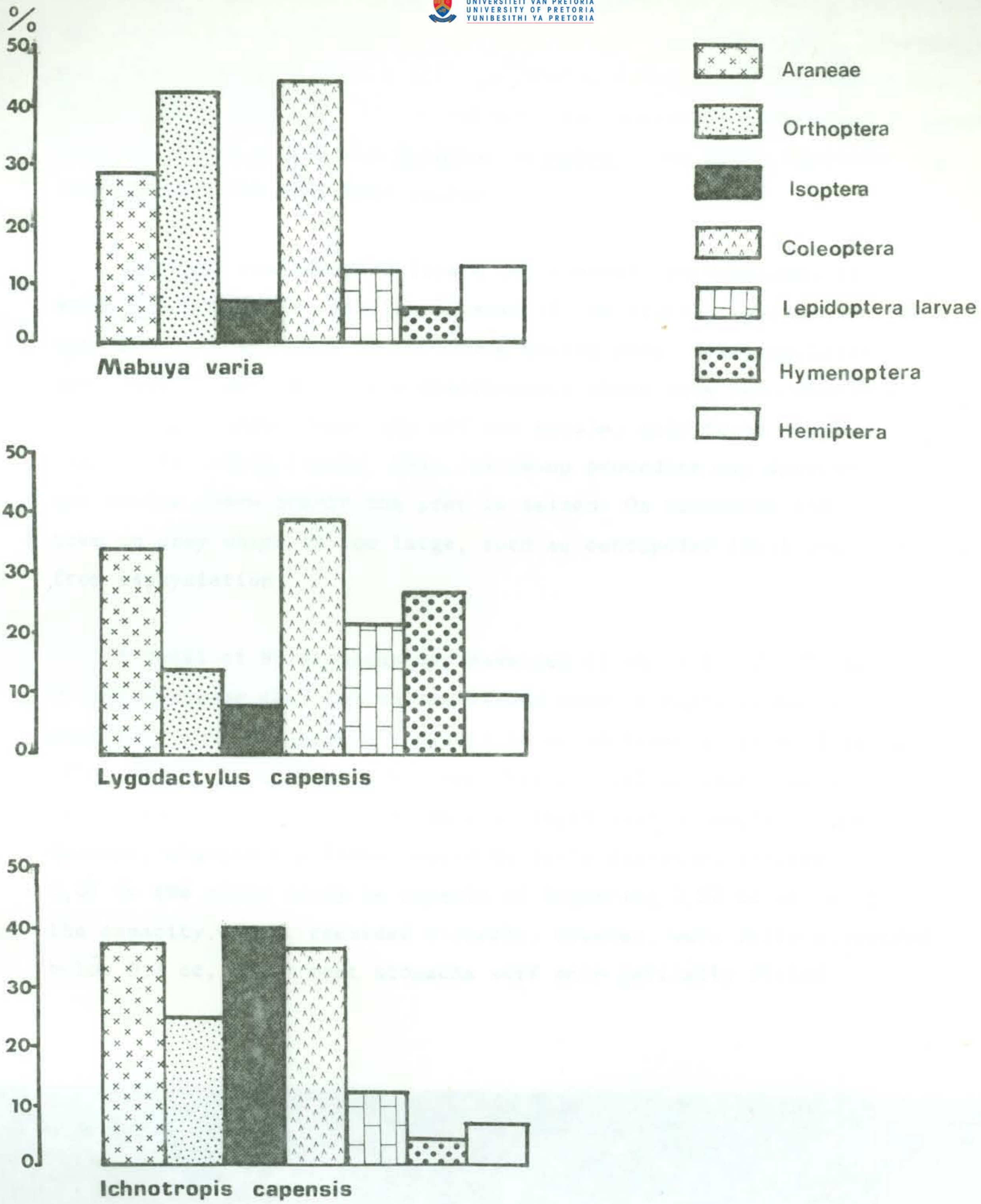


Figure 31. Comparison of main prey of three lizard species in the <u>Burkea africana</u> - <u>Eragrostis pallens</u> Study Area.

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.

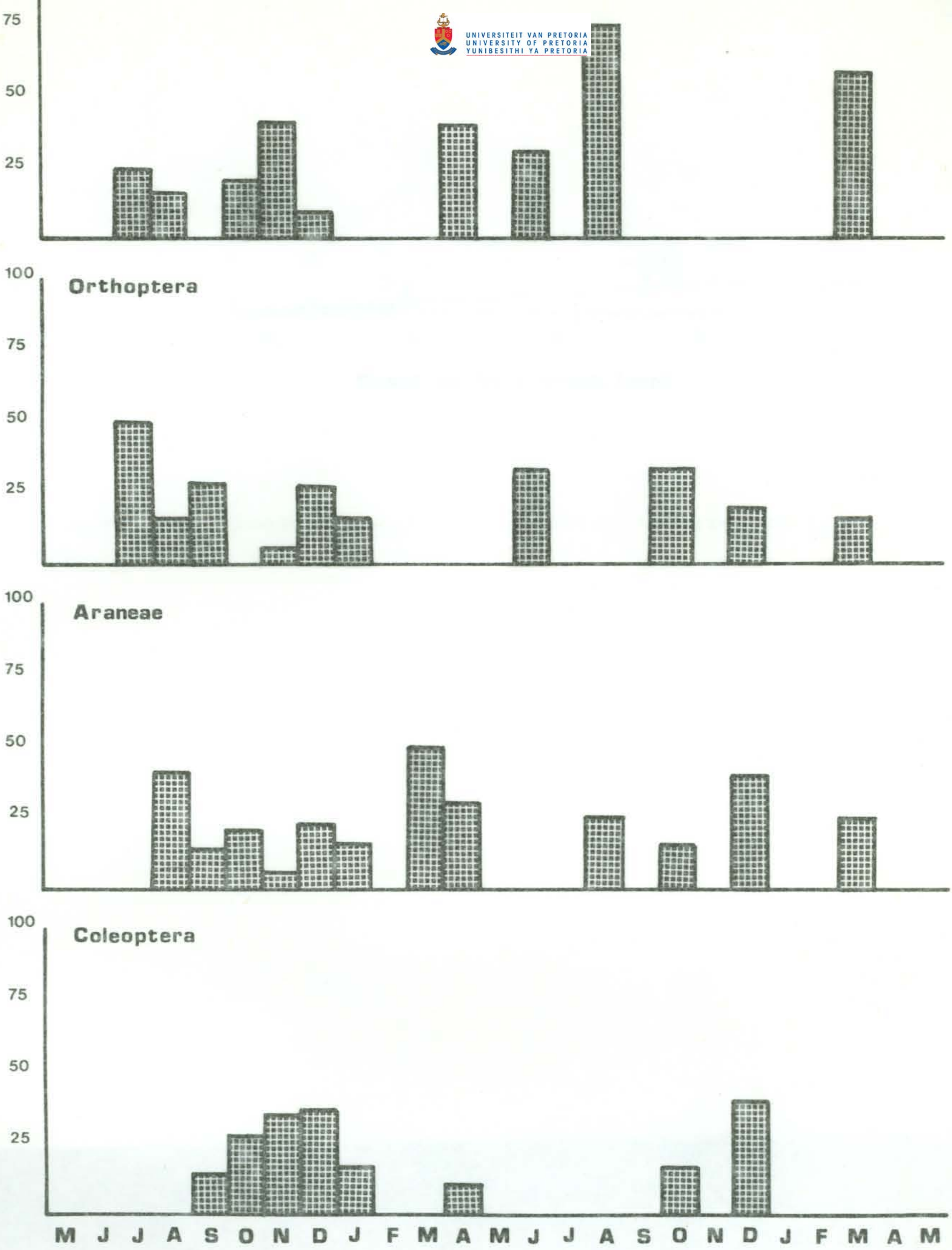


Figure 32. Monthly incidence of main prey orders in the stomachs of Ichnotropis capensis in the Study Area.

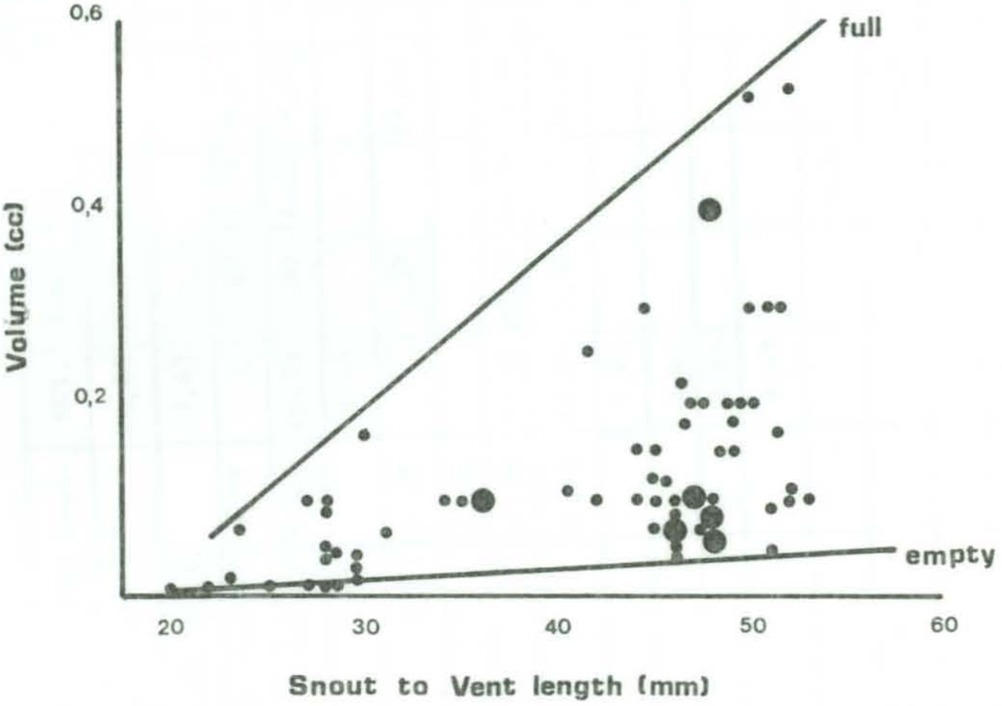


Figure 33. Stomach capacity in relation to size of Ichnotropis capensis in the Study Area.

Table 15. Monthly percentage occurrence of prey in the stomachs of <u>Ichnotropis capensis</u> in the <u>Burkea africana</u> - <u>Egrostis pallens</u> 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.

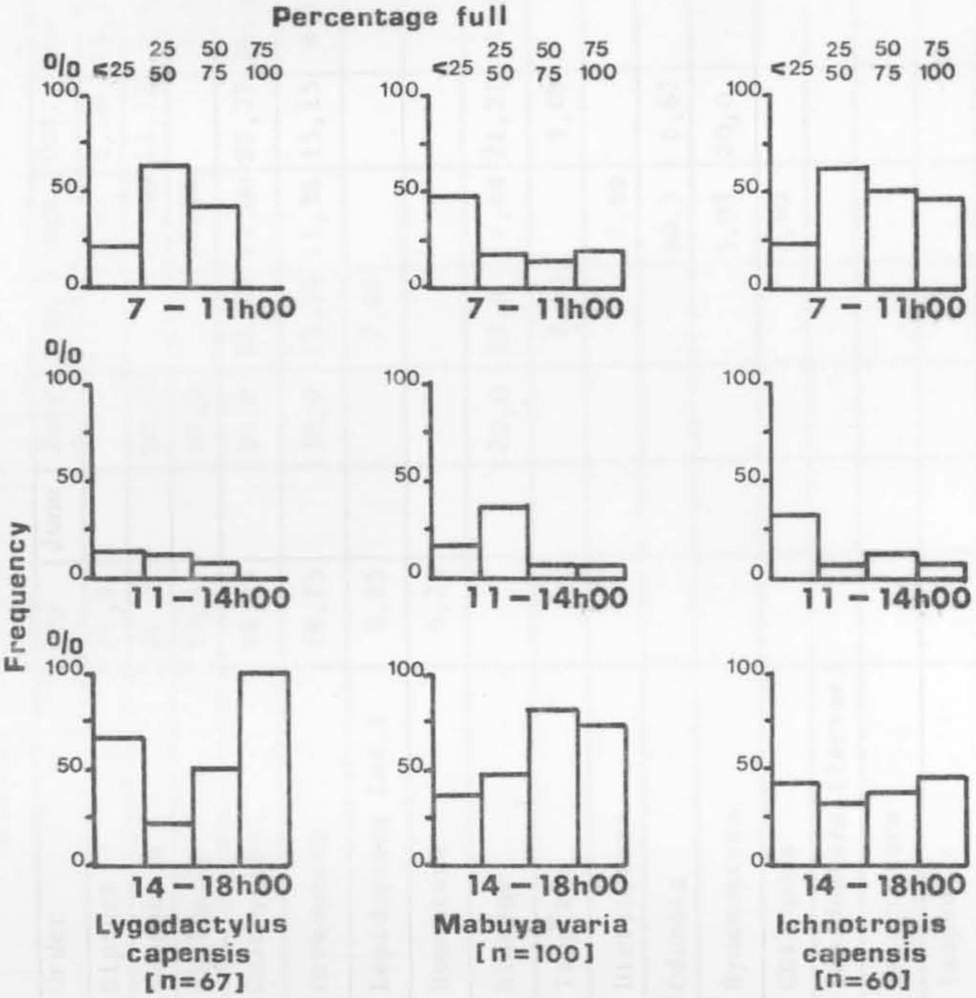


Figure 34. Feeding activity of three savanna lizards in the *Burkea africana* Study Area.

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).

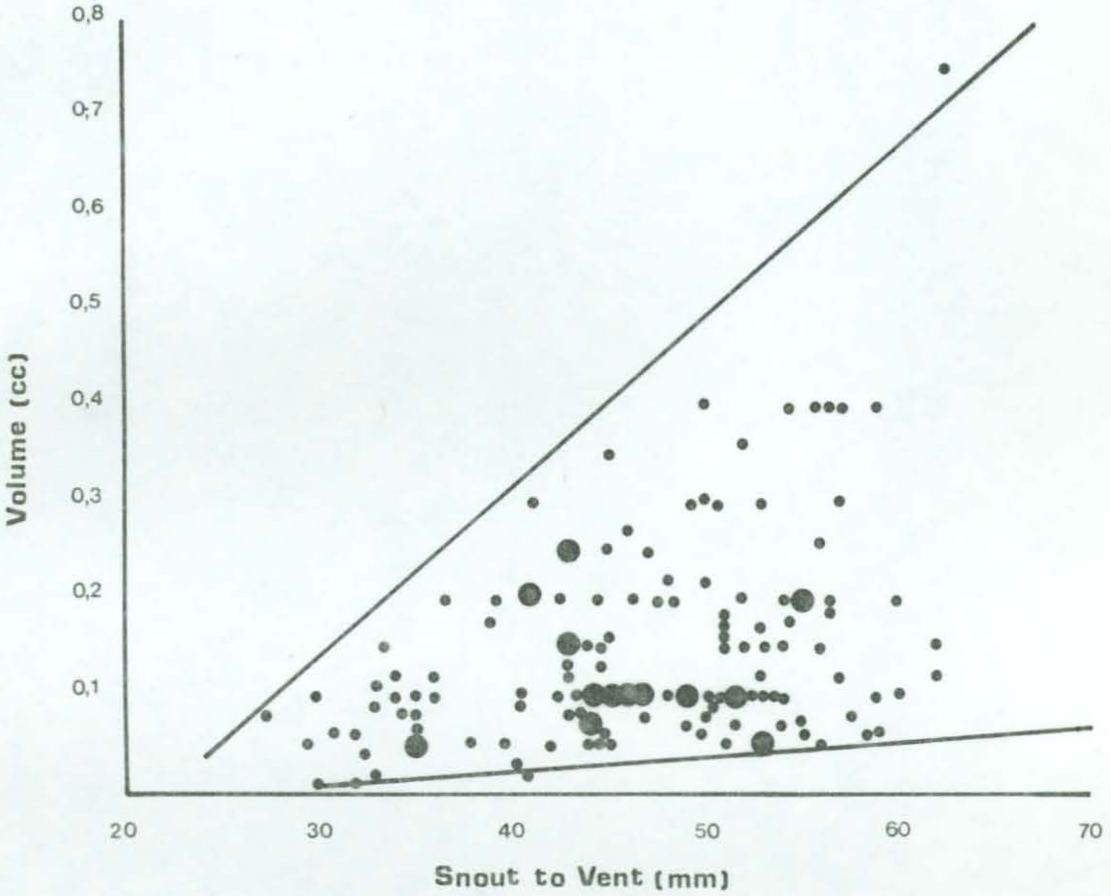


Figure 35. Stomach capacity in relation to size of Mabuya varia in the Study Area.

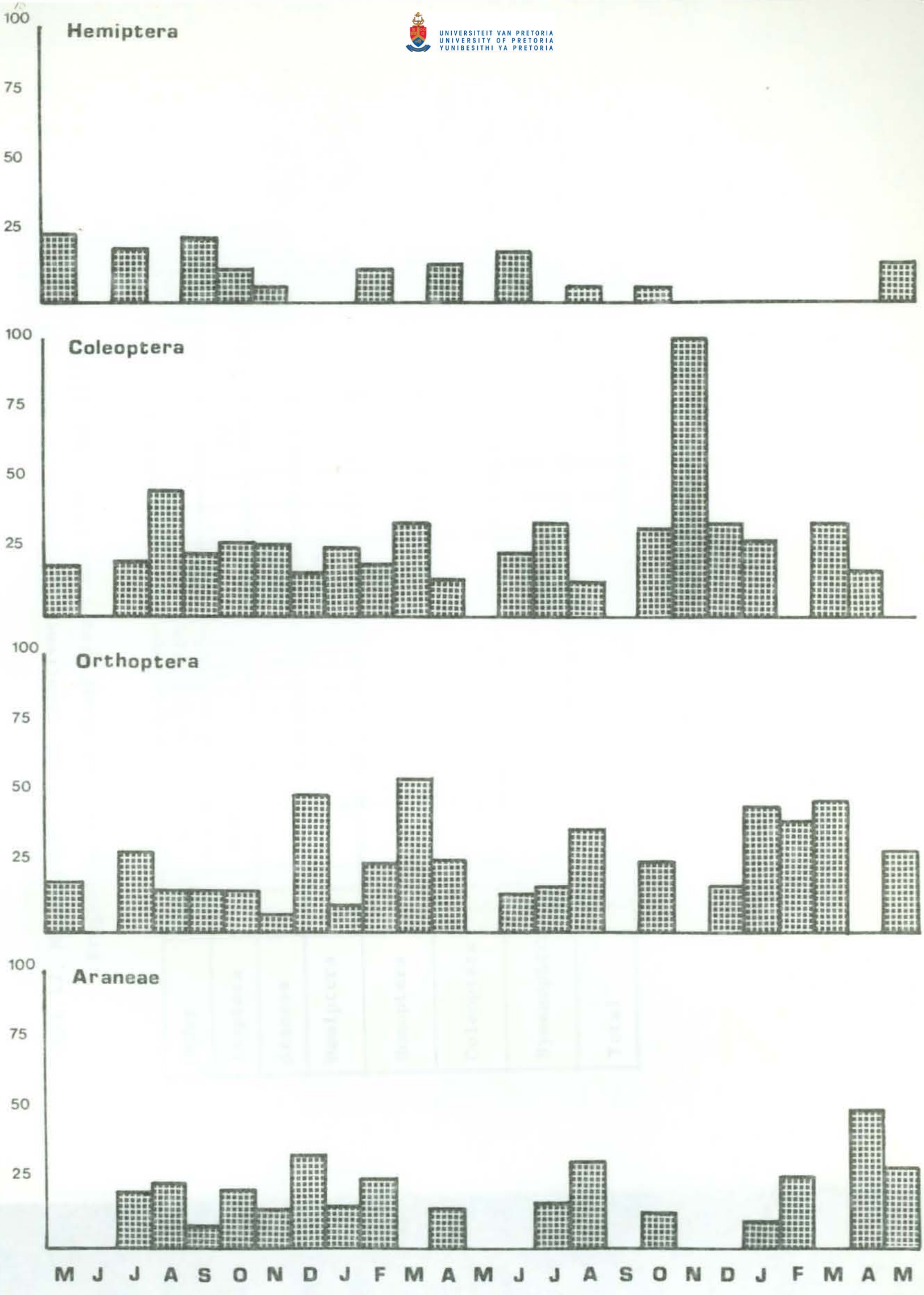


Figure 36. Monthly incidence of main prey orders in the stomachs of *Mabuya varia* in the Study Area.

Table 17. Monthly percentage occurrence of prey in the stomachs of <u>Panaspis</u> <u>wahlbergi</u> in the <u>Burkea</u> <u>africana</u> - 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.

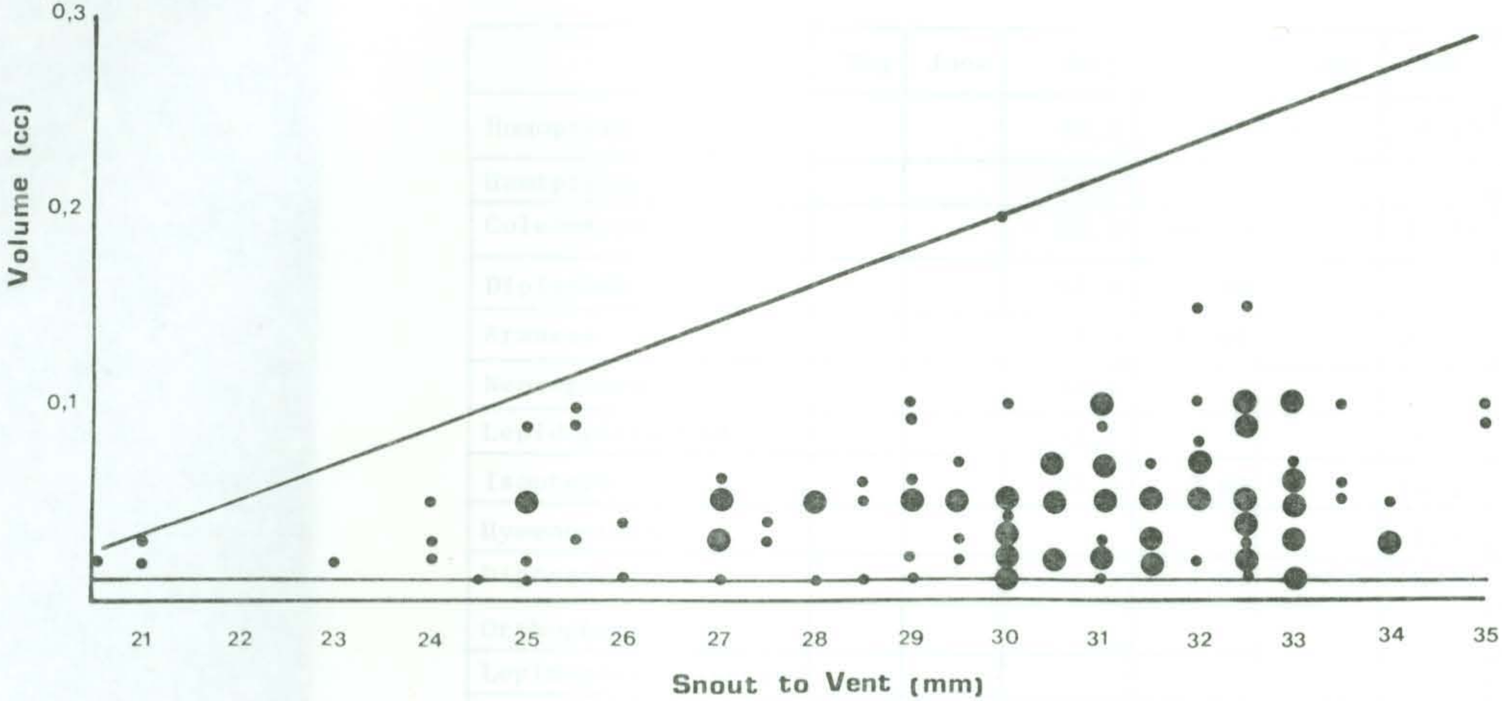


Figure 37. Stomach capacity in relation to size of _Lygodactylus capensis_ in the Study Area.

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<br>Aves, Scorpiones Diplopoda |
| Lygosoma sundevallii | 1 | Isoptera, Hymenoptera (Formicidicae) |

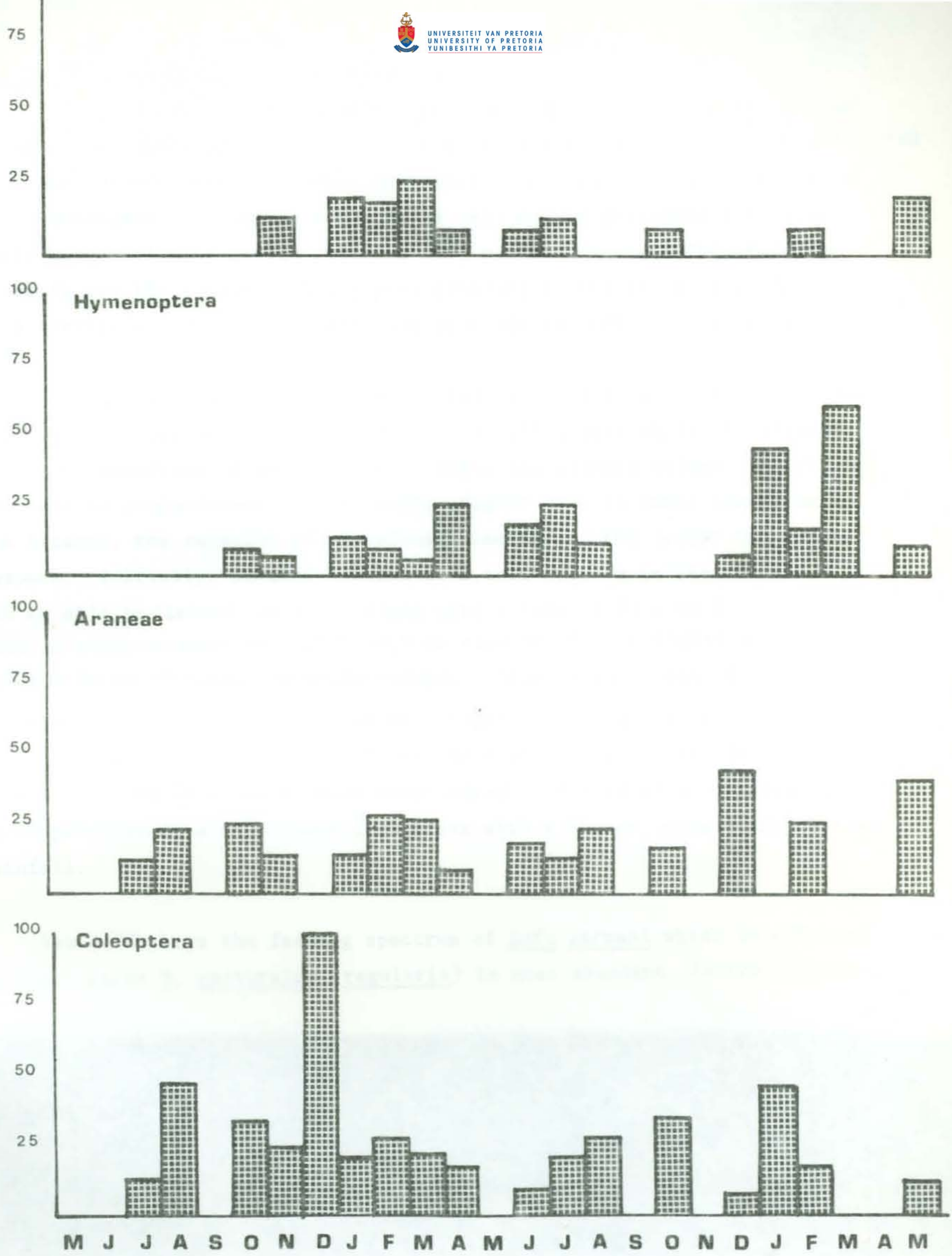


Figure 38. Monthly incidence of main prey orders in the stomachs of Lygodactylus capensis in the Study Area.

## 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

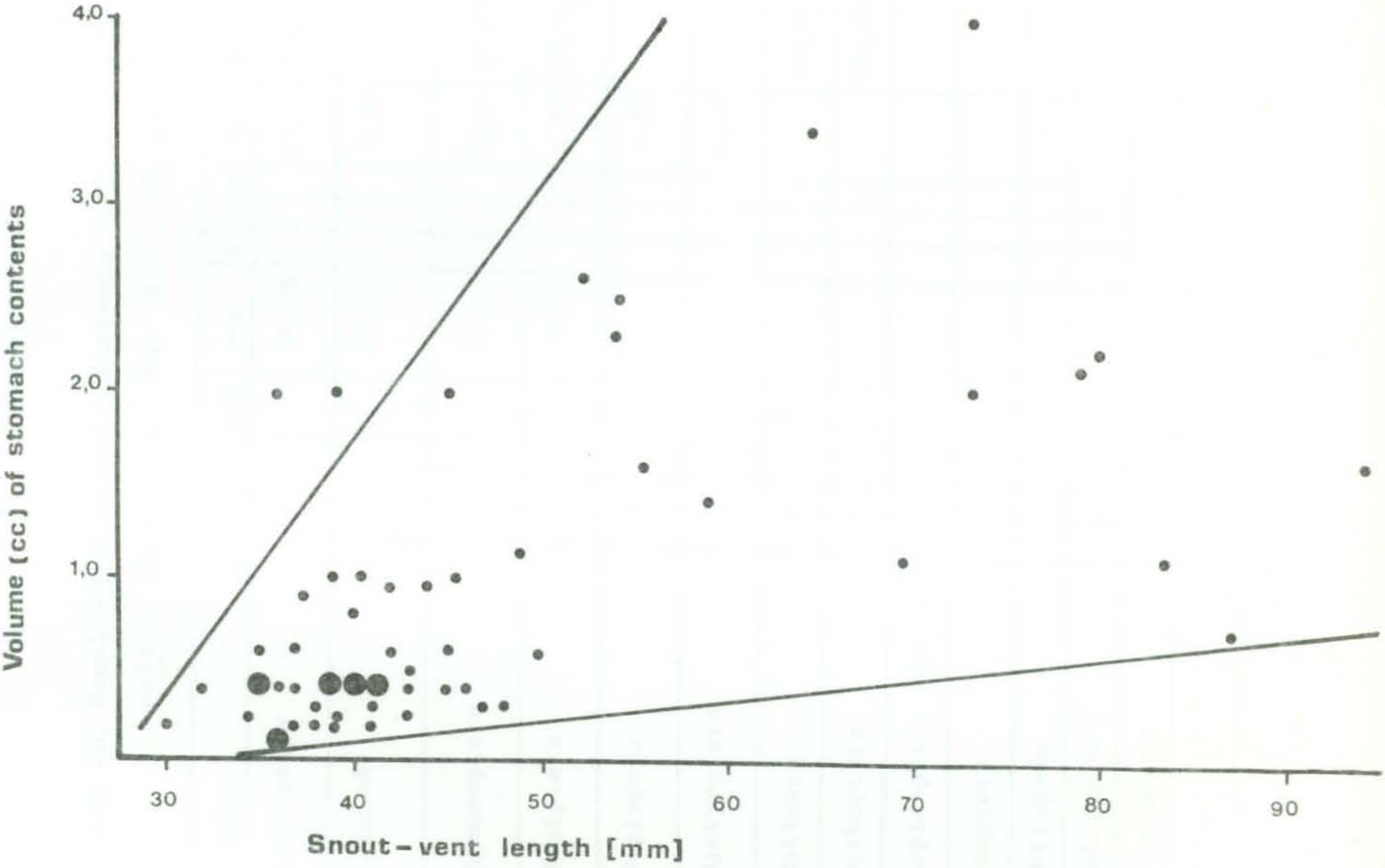


Figure 39. Stomach capacity in relation to size of Bufo garmani in the Study Area.

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.

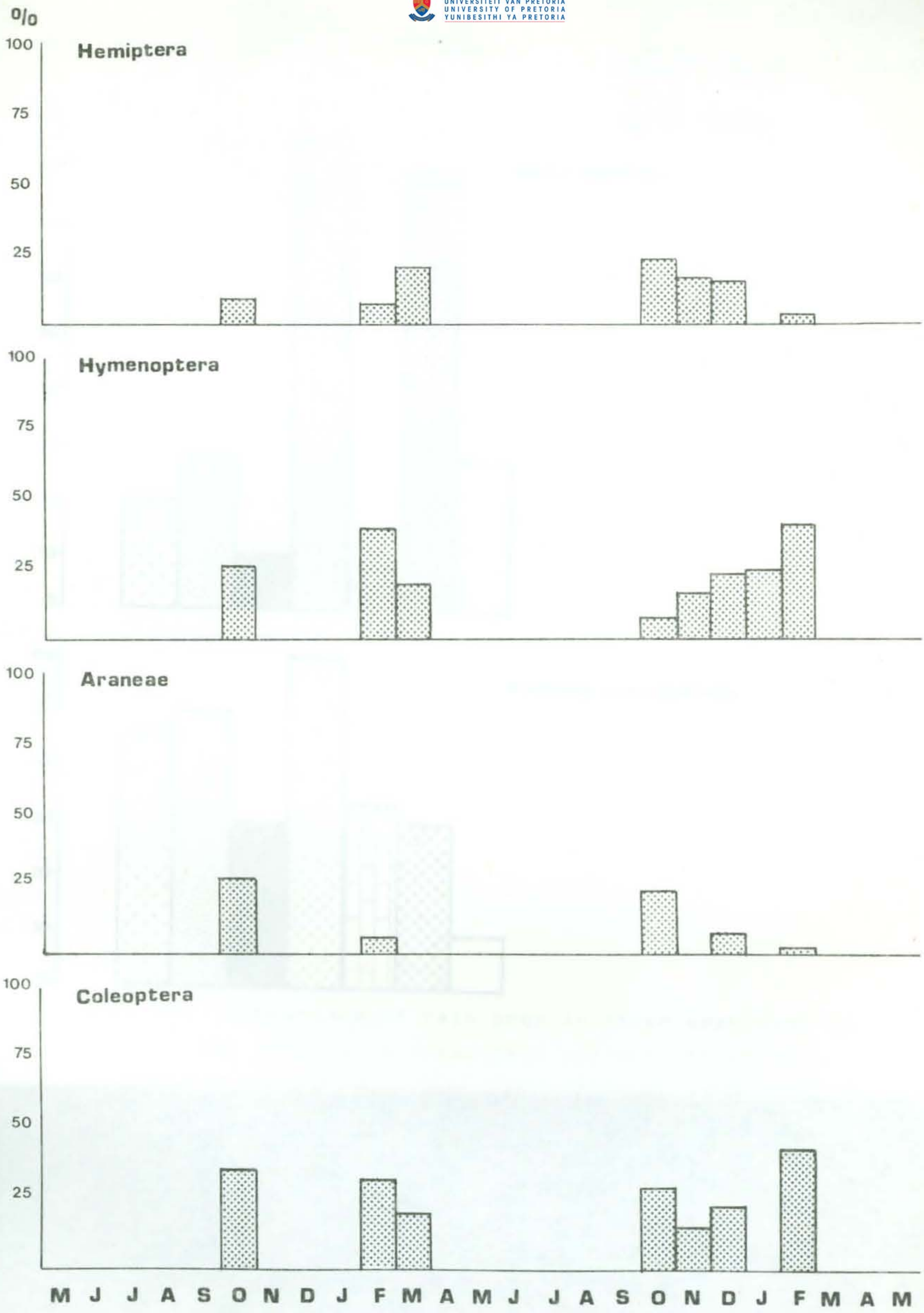


Figure 40. Monthly incidence of main prey orders in the stomachs of Bufo garmani in the Study Area.

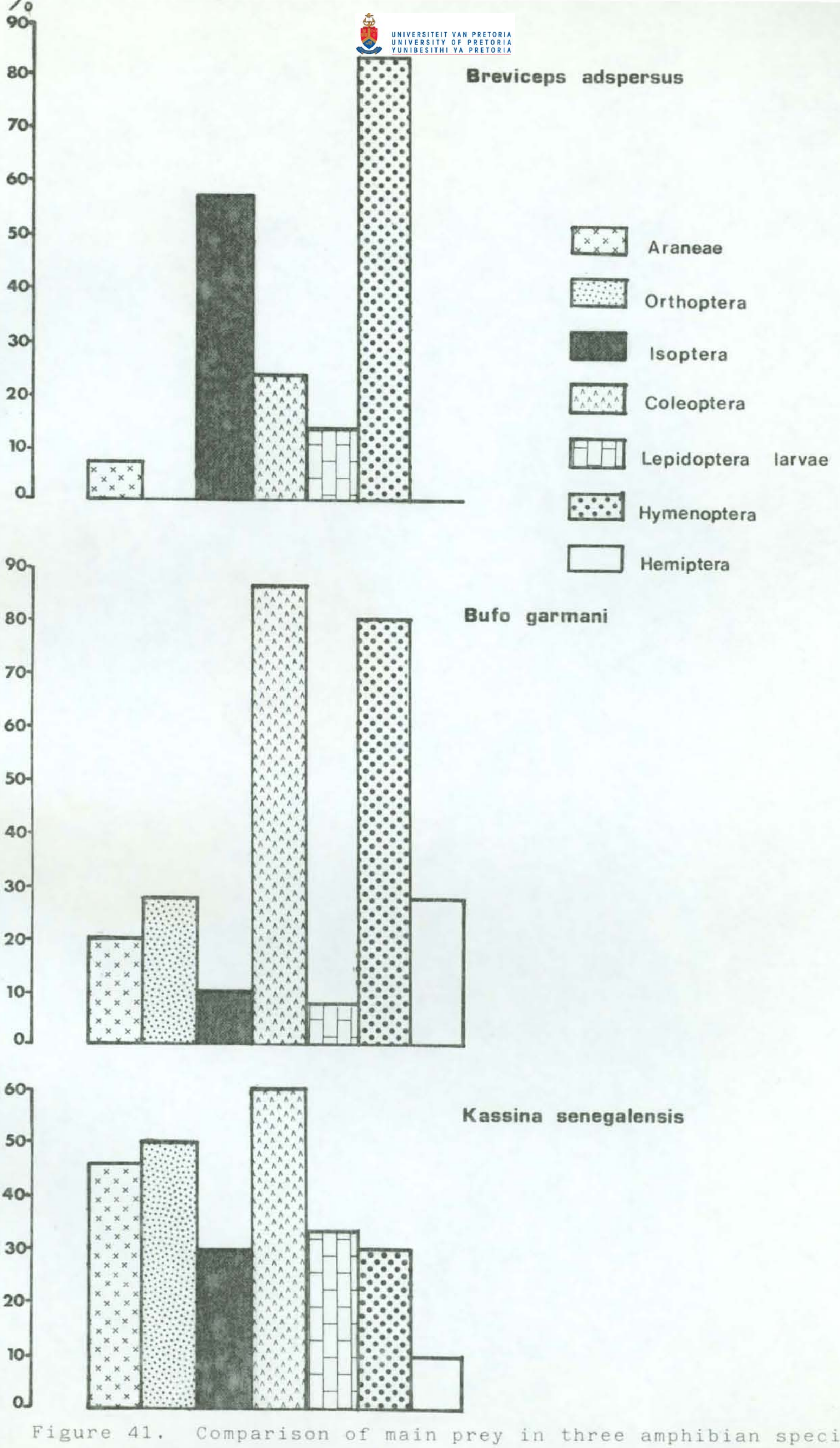


Figure 41. Comparison of main prey in three amphibian species in the Burkea africana - Eragrostis pallens Study Area.

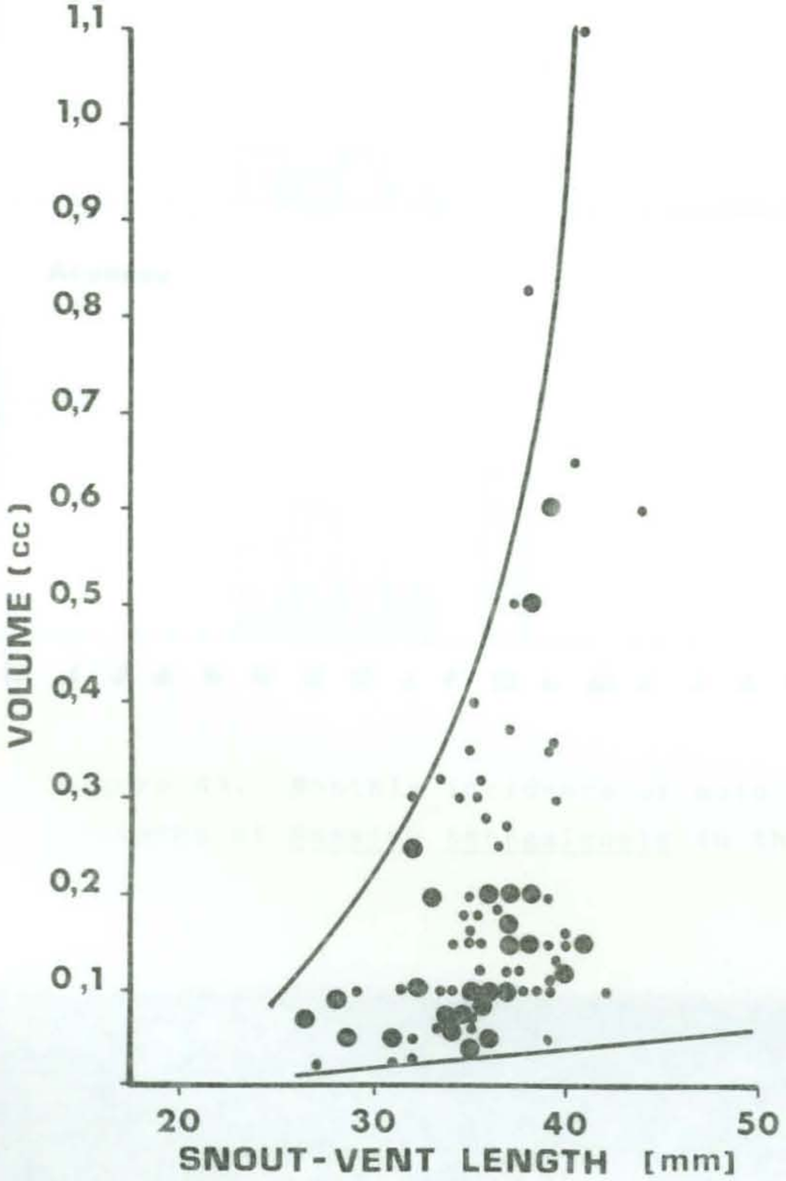


Figure 42. Stomach capacity in relation to size of *Kassina senegalensis* in the Study Area.

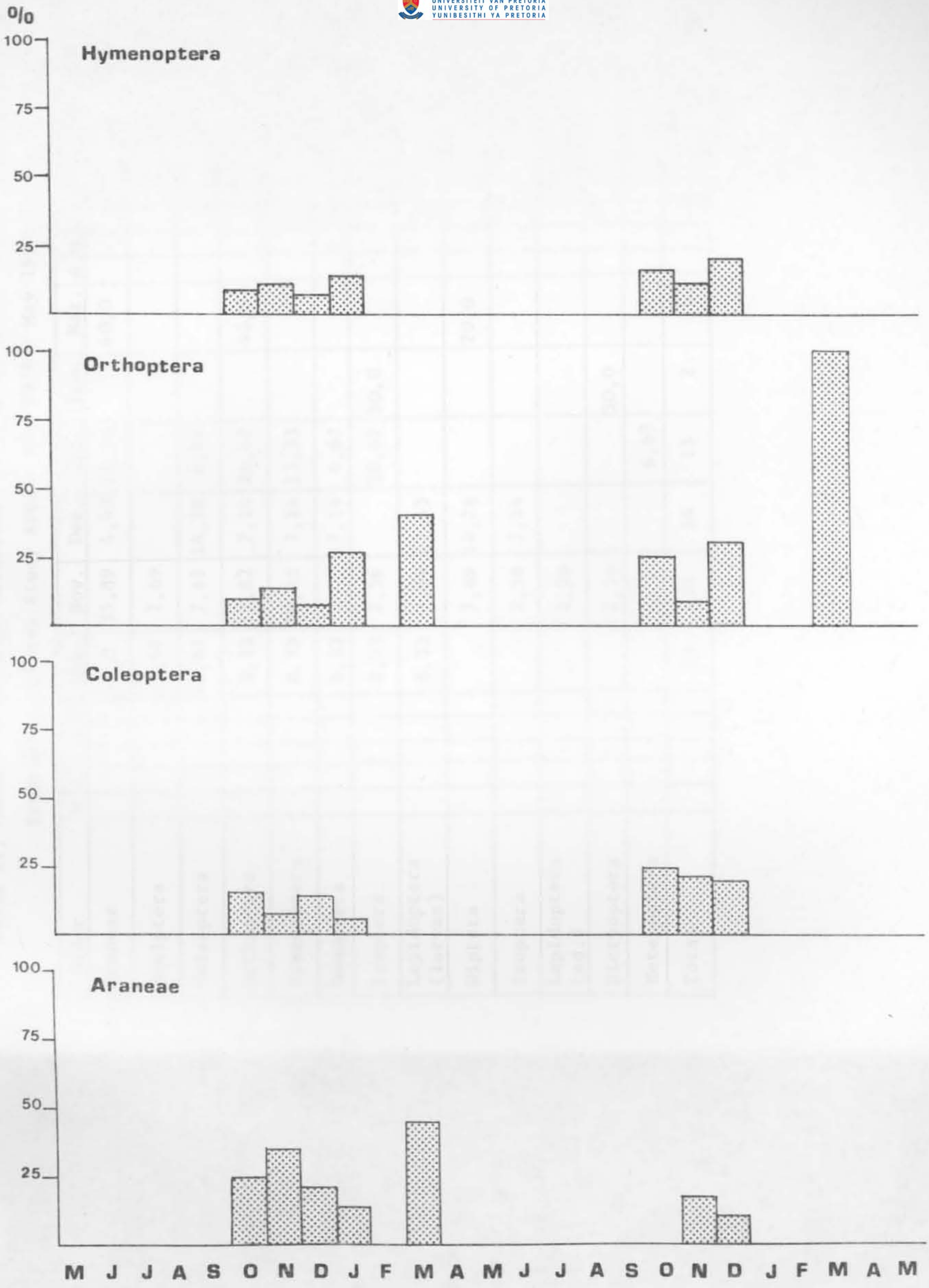


Figure 43. Monthly incidence of main prey orders in the stomachs of Kassina senegalensis in the Study Area.

Table 21. Monthly percentage occurrence of prey in the stomachs of <u>Kassina senegalensis</u> in the <u>Burkea africana - Eragrostis pallens</u> 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 | | | |

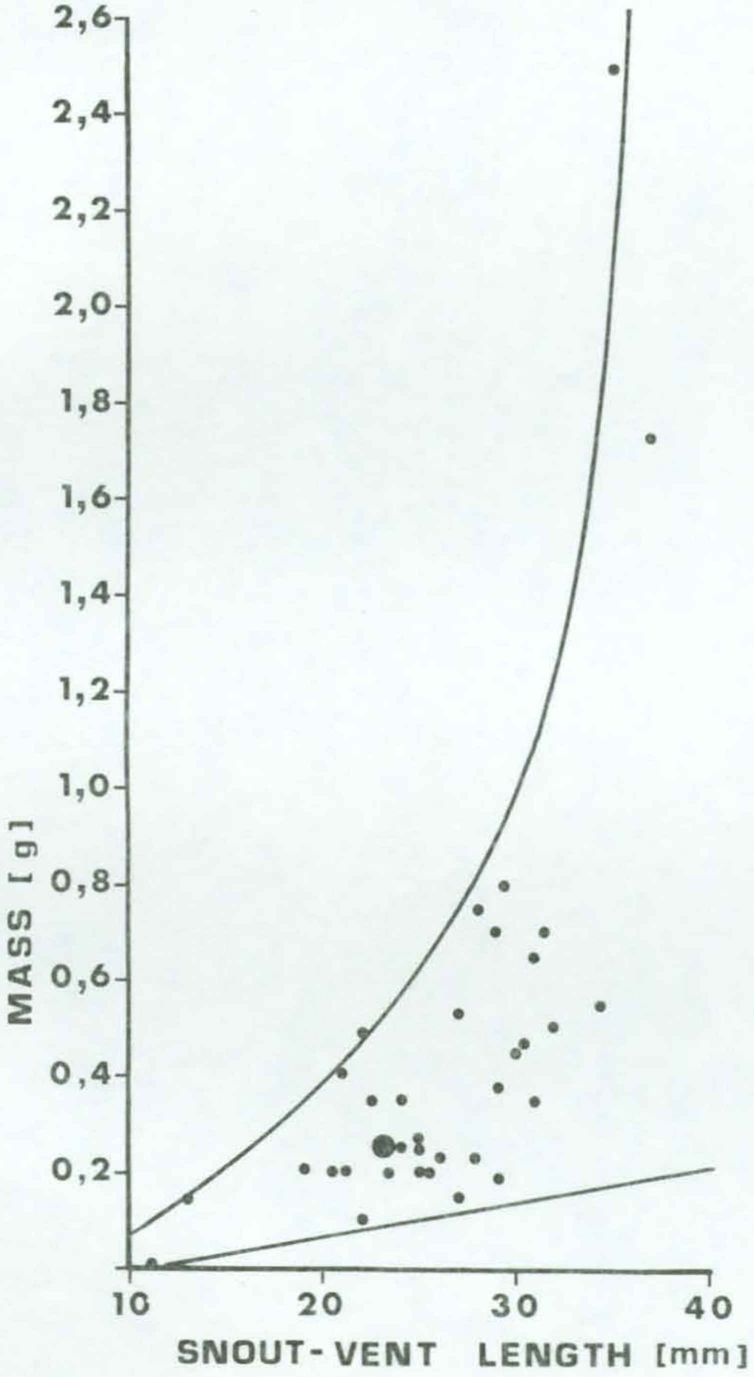


Figure 44. Stomach capacity in relation to size of Breviceps adspersus in the Study Area.

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 Lowveld. 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.

# CHAPTER 6

# ECOLOGY

## REPRODUCTION AND GROWTH

Owing to the pronounced seasonality of the climate, most reproductive strategies of reptiles and amphibians follow suit. Apart from some snakes such as the puff adder (Bitis arietans) and the black mamba (Dendroaspis p. polylepis, most reptiles begin mating after emergence from hibernation, while the amphibians mostly depend on rainfall. At this time of the year, the animals are extremely active and forage widely. Spoor crossings of snakes over the roads surrounding the area are frequently from pairs. The males in particular are very active, which resulted in the capture in most cases of a preponderance of this sex. This feature is not only exhibited by the snakes, but also among the lizards, while the amphibians tend to exhibit the reverse. Although sample size was small in many instances, it is apparent that of all the snake species, only five display parity or approximate parity. Some of them exceed this, but possibly a larger sample may be more objective. A similar situation exists among the lizards where six species approximate parity or exceed it (Table 25). The amphibians mostly exhibit the reverse situation with most species exhibiting a greater abundance of females. Again, in some instances, sample size is very small and, therefore, the figures only serve as an indication. However, the trend is the same in Kassina senegalensis which has an adequate sample size (Table 25). While it is no doubt true that the males of most reptiles and amphibians may be able to mate with more than one female, little appears to be documented on this phenomenon. Taylor (1982) mentions, for instance, that among Bufo garmani, males will mate with several females in succession, if they are available. This can be a fundamental aspect of reproductive strategies.

During September and October, mating and copulation takes place among the reptiles, while in the case of the amphibians, November and December are the main months. Males are easily recognised at this time, either by possessing bright colours, having enlarged hemipenes or by their behaviour. Other less obvious features include a longer tail in males and correspondingly, a longer body in females. (Figure 45). This latter feature is no doubt correlated with the female's function of carrying the young or developing ova internally, whereas the reproductive organs of the male are situated in the base of the tail. There appears to be an apparent linear correlation

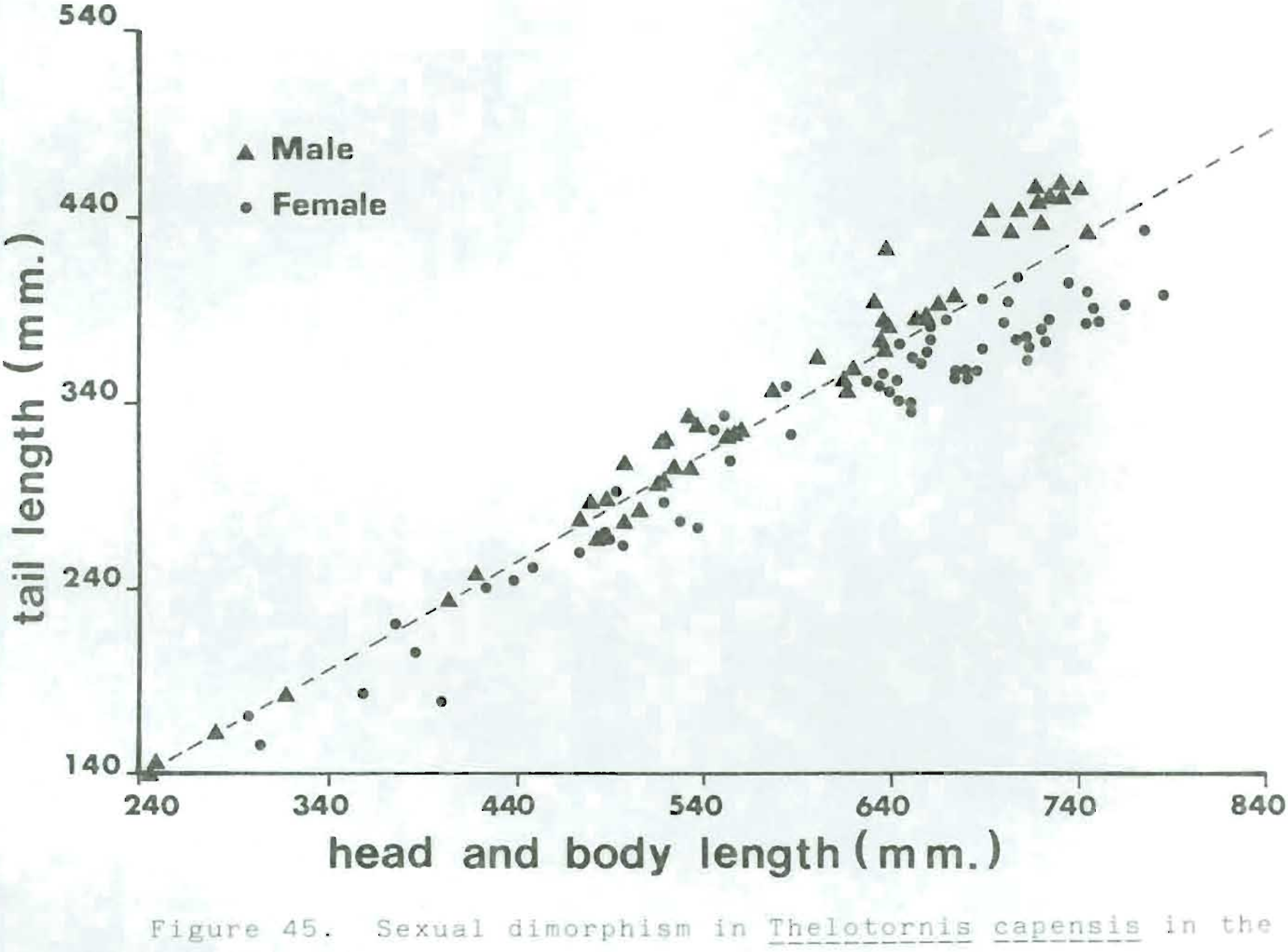


Figure 45. Sexual dimorphism in Thelotornis capensis in the Burkea africana - Eragrostis pallens Study Area.

which is already apparent soon after hatching. Amphibians develop gular discs, pads on the thumbs and the dark colouring in the gular region is emphasized.

The reptiles and amphibians have devised various reproductive strategies to ensure that the species survive, some of which are evident in the relatively dry savanna of the Nylsvley Ecosystem.

Table 25. Mean sex ratios of snakes, lizards and amphibians in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977.

| Species | No. in sample | Sex |  | Ratio |
|---|---|---|---|---|
|  |  | Male | Female | Male : Female |
| Snakes |  |  |  |  |
| Python sebae | 3 | all males |  |  |
| Boaedon fuliginosus | 2 | " |  |  |
| Lycophidion capense | 18 | 7 | 11 | 1:1,57 |
| Mehelya nyassae | 20 | 19 | 1 | 1:0,05 |
| Mehelya capensis | 3 | all males |  |  |
| Philothamnus semivariegatus | 22 | 18 | 4 | 1:0,22 |
| Philothamnus hoplogaster | 1 | male |  |  |
| Prosymna sundevallii | 12 | 10 | 2 | 1:0,20 |
| Dasypeltis scabra | 20 | 15 | 5 | 1:0,33 |
| Telescopus semiannalatus | 4 | 3 | 1 | 1:0,33 |
| Dispholidus typus | 23 | 12 | 11 | 1:0,92 |
| Thelotornis capensis | 205 | 118 | 87 | 1:0,73 |
| Crotaphopeltis hotamboeia | 52 | 34 | 18 | 1:0,53 |
| Psammophylax tritaeniatus | 6 | 4 | 2 | 1:0,50 |
| Psammophis s. brevirostris | 130 | 90 | 40 | 1:0,44 |
| Psammophis jallae | 4 | male |  |  |
| Amblyodipsas polylepis | 1 | male |  |  |
| Xenocalamus bicolor australis | 2 | male |  |  |
| Aparallactus capensis | 23 | 10 | 13 | 1:1,30 |
| Naje haje annulifera | 29 | 27 | 2 | 1:0,07 |
| Naje mossambica | 7 | male |  |  |
| Dendroaspis polylepis | 4 | male |  |  |
| Bitis arietans | 10 | 5 | 5 | 1:1 |

Table 25 (continued)

| Species | Number in sample | Sex Male | Sex Female | Ratio Male:Female |
|---|---|---|---|---|
| Lizards | | | | |
| *Lygodactylus capensis* | 883 | 562 | 321 | 1:0,57 |
| *Pachydactylus capensis* | 4 | 2 | 2 | 1:1 |
| *Pachydactylus bibroni* | 6 | 3 | 3 | 1:1 |
| *Agama atricollis* | 13 | 7 | 6 | 1:0,86 |
| *Chamaeleo dilepis* | 2 | 1 | 1 | 1:1 |
| *Lygosoma sundevallii* | 30 | 19 | 11 | 1:0,58 |
| *Mabuya capensis* | 1 | male | - | - |
| *Mabuya s. punctatissimus* | 1 | male | - | - |
| *Mabuya varia* | 672 | 470 | 202 | 1:0,43 |
| *Panaspis wahlbergi* | 311 | 110 | 201 | 1:1,83 |
| *Ichnotropis capensis* | 1118 | 669 | 449 | 1:0,67 |
| *Ichnotropis squamulosa* | 1 | male | - | - |
| *Nucras intertexta* | 9 | 6 | 3 | 1:0,50 |
| *Gerrhosaurus flavigularis* | 9 | 4 | 5 | 1:1,25 |
| *Varanus e. albigularis* | 21 | 20 | 1 | 1:0,05 |
| Amphibians | | | | |
| *Bufo garmani* | 320 | 131 | 189 | 1:1,44 |
| *Bufo gutturalis* | 30 | 7 | 23 | 1:3,29 |
| *Bufo carens* | 11 | 2 | 9 | 1:4,50 |
| *Breviceps adsperus* | 200 | 117 | 83 | 1:0,71 |
| *Phrynomerus bifasciatus* | 41 | 7 | 34 | 1:4,96 |
| *Tomopterna cryptotis* | 37 | 4 | 33 | 1:8,25 |
| *Phrynobatrachus natalensis* | 14 | 4 | 10 | 1:2,50 |
| *Cacosternum boettgeri* | 13 | 1 | 12 | 1:12,00 |
| *Kassina senegalensis* | 875 | 159 | 717 | 1:4,51 |

## Snakes

Snakes can be classed into two basic categories, oviparous or ovoviviparous. It is understood that viviparity (*sensu stricto*) is very limited among snakes, but the degree of overlap between these categories is of such a nature as to make definition difficult.

At Nylsvley, there are 29 species of snakes of which 20 are relatively common in the Study Area. Of the latter, only one species, the puff adder can be classed as being viviparous, while only the Bibron's blind snake (*Typhlops bibronii*) is ovoviviparous, the remaining 18 species are all oviparous. The advantages of only carrying the eggs to a fully developed size, must outweigh the advantages conferred by being viviparous but having to carry the developing young for possibly a longer period of time. Most oviparous species, therefore, only carry ova for a period of four to six weeks (pers. obs.). Oviparous species are, however, relatively confined with regard to the time of the year when eggs can be laid as opposed to viviparous species which, through the manipulations of the mother, can continue to incubate throughout the year. It is, therefore, generally assumed that viviparity is primarily an adaptation to a cool or cold climate. In the Transvaal, various other factors may also have a bearing, as some species are both viviparous and oviparous in different parts of their range. The climate at Nylsvley, therefore, is such that oviparity has developed and is the standard method of reproduction. Table 26 lists the number and size of eggs or young of the snakes occurring on the Nylsvley Nature Reserve. There are unfortunately several gaps but it is postulated that most of these are species which are oviparous, but on account of their relative rarity, are not well known.

The eggs are laid in a variety of situations, under rocks in rotting vegetation, in holes in the ground and possibly even inside hollow trees. Egg laying, therefore, takes place during November to January or even February. Very few gravid females were seen and egg laying was never observed. It is, therefore, important to find hatchlings, the appearance of which indicate the period of egg laying, as the incubation period for most species is within 60-90 days. Barbault (1971) used this criterion to set out arbitrary age classes, using body mass as an aid. This, however, is too variable and, therefore, it was decided to use snout/vent length to delimit the age classes. Hatchling size was taken from FitzSimons (1962) and mass from Barbault (1971), as well as from personal observations, because measurements taken during the present study did not always conform to those taken by these authors.

Table 26. Number of eggs or young of snake species occurring on the Nylsvley Nature Reserve (after Fitch (1971), FitzSimons (1962), Branch & Patterson (1976), pers obs ).

| Species | No. of eggs/young | Size of eggs | Mean S/V length of hatchlings. |
|---|---|---|---|
| Family: Typhlopidae | | | |
| <u>Typhlops bibronii</u> | 6-12 | 16-20,5 x 10,8-13,5 | 103,9 mm |
| Family : Leptotyphlopidae | | | |
| <u>Leptotyphlops distanti</u> | 2-3 | ? | ? |

Table 26 (continued)

| | | | |
|---|---|---|---|
| Family : Boidae | | | |
| Python sebae | 20-80 | 100,0-110,0 mm | 450-600 |
| Family : Colubridae : Subfamily Colubrinae | | | |
| Boeadon f. fuliginosus | 6-12 | 30,0-40,0 m x 12-24 mm | 235,0 mm |
| Lycophidion capense | 1-8 | 11-20 mm x 8,0-10 mm | 120,0 mm |
| Mehelya capensis | 5-8 | 55,0 x 20,0 mm | ? |
| M. nyassae | 6 | ? | 200-216,0 mm |
| Philothamus semivariegatus | 3-8 | 27-30 x 8,0 mm | 230-260,0 mm |
| P. hoplogaster | 3-8 | 28-34,0 mm x 8-12 mm | 150-200,0 mm |
| Prosymna sundevallii | 3-4 | 28 x 9 mm | 110,0 mm |
| Pseudaspis cana | 30-50 young | - | |
| Subfamily: Dasypeltinae | | | |
| Dasypeltis scabra | 6-14 | 36-38,0 mm x 18-19,5 mm | 115,0-200 mm |
| Subfamily: Boiginae | | | |
| Telescopus s. semiannulatus | 6-14 | 25,0-10,0 mm | ? |
| Crotaphopeltis h. hotamboeia | 3-90 | 21,4 x 13,4 | 118-170,0 mm |
| Dispholidus t. typus | 6-18 | 40,0-50,0 x 16-26 mm | 250,0-300,0 mm |
| Thelotornis c. capensis | 4-10 | 34-43,5 x 14-18 mm | 227-240,0 mm |
| Psammophylax t. tritaeniatus. | 6-14 | 20-25 x 10-12 mm | 130-220,0 mm |
| Psammophis sibilans brevirostis | 4-10 | 28 x 10,0 mm | 192-250 mm |
| P. angolensis | 3-5 | 15-18 x 5-6,0 mm | ? |
| P. jallae | | ? | ? |
| Amblyodipsas polylepis | | ? | ? |
| Xenocalamus bicolor australis | 3-4 | 40-47 x ± 15,0 mm | 181-185,0 mm |
| Subfamily: Aparallactinae | | | |
| Aparallactus c. capensis | 2-4 | 32,0 x 4-5,0 mm | 95-120,0 mm |
| Atractaspis bibroni | 6 | 36,0 x 12,0 mm | ? |
| Family: Elapidae | | | |
| Naja haje annulifera | 8-20 | 50-60 x 30-35,0 mm | 230-340,0 mm |
| N. mossambica | 10-22 | 35 x 20,0 mm | ± 230,0-250,0 mm |
| Dendroaspis p. polylepis | 9-14 | 60-80 x 30-36,0 mm | 370-450,0 mm |
| Family: Viperidae | | | |
| Causis defilippi | 2-6 | 20-25 x 14-16,0 mm | 100,0 mm |
| Bitis a. arietans | 21-56 | - | 150-200,0 mm |

Tables 27-34 show the incidence of hatchlings, juveniles, subadults and adults of the more common snake species in the *Burkea africana* - *Eragrostis pallens* Study Area.

The two commonest species, *Psammophis s. brevirostris* and *Thelotornis capensis* show a broad reproductive season (Tables 27 & 28) indicating that one female may lay several successive clutches of eggs or else there is an extended breeding season. The latter is less feasible, as synchronous matings have been noted for at least one of these two species, namely the vine snake. The fact that a hatchling of this species was found during September, indicates either that a second mating took place in mid-summer, or else that sperm retention, such as has been recorded for the common night adder (*Causus rhombeatus*) Woodward (1933), takes place. The short-snouted sandsnake also appears to have two broods, one during Spring/early summer and the other during mid-summer. Most hatchlings of this species appeared during March, but included the period January to April. One aberrant hatchling in June is indicative of a late brood.

However, the vine snakes appear to be slightly different with mating only observed during September, a phenomenon also reported on by Wilson (1965), in Zambia. Mating in one instance lasted for a minimum of 3 h to a maximum of 30 h, after which they were disturbed The snakes were not observed overnight and, this was the reason for the difference between the minimum and maximum recorded copulatory periods. The snakes lay entwined among the branches of the tree and the male appeared to be relatively passive and may be dragged along by the female as she moves about the branches, the spiny protrusions of the hemipenis serving to anchor the male in the cloaca of the female.

The first hatchlings are recorded in March (Table 28), which coincides well with an ova deposition during late December to early January. Gravid females were only observed during December (Table 28), while Wilson (*loc. cit.*) observed gravid females between September and December, indicating an earlier mating in Zambia. Three of his snakes laid eggs between the 13/xi/59 and 11/xii/59. Clutch sizes are recorded in Table 26, but it is interesting to note that 10 females which Wilson (*loc.cit*) dissected contained 4-6 eggs, while the three which laid, had broods of five each and two observed during the current study had four and seven eggs respectively. Incubation lasts two to three months. Four of the eggs of the three vine snakes under observation by Wilson (*loc.cit.*)hatched on 18/ii/1960 - a

Table 27. Distribution of the three age classes of *Psammophis sibilans brevirostis* in the *Burkea africana* Savanna Study Area : May 1975 - May 1977

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchling 191-250 mm | 1 | 1 | 3 | 1 | | 1 | | | | | | |
| Juvenile 250-380 mm | | 1 | 3 | 5 | 9 | 6 | 5 | 5 | 8 | 7 | 4 | |
| Subad. & Adults > 380 mm | 3 | 6 | 3 | 3 | 3 | 1 | 4 | 9 | 17 | 23 | 8 | (1G)<br>12 |

Table 28. Distribution of the three age classes of *Thelotornis capensis* in the *Burkea africana* Savanna Study Area : May 1975 - May 1977

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchling 227-250 | | ? | 1 | 1 | 1 | | | | 1 | | | |
| Juvenile 250-450 | 1 | | 1 | 2 | 1 | 4 | 1 | 1 | 5 | 2 | 6 | 3 |
| Subad. & Adults >450 mm | 5 | 1 | 10 | 24 | 22 | 28 | 12 | 21 | Mating<br>52<br>period | 10 | 16 | (3G)<br>12 |

Table 29. Distribution of the three age classes of *Dasypeltis scabra* in the *Burkea africana* Savanna Study Area May 1975 - May 1977

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchlings 115-220 mm | | | | | | | | ? | 2 | | | ? |
| Juvenile 200-250 mm | | | | | | | | | | 2 | 2 | 1 |
| Subad. & Adults > 250 mm | 1 | 2 | 2 | | | | | | 2 | 2 | 3 | 4 |

3G = 3 Gravid females
1G = 1 Gravid female.

Table 30. Distribution of the three age classes of <u>Crotaphopeltis hotamboeia</u> in the <u>Burkea africana</u> Savanna Study Area : May 1975 - May 1977.

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchling 118-170 mm | 2 | 2 | 1 | 1 | | | | | | | | |
| Juvenile 170-240 mm | | 2 | 1 | | | | | | 1 | 2 | | |
| Subad. & Adults >240 mm | 2 | 8 | 1 | | 4 | | | | 9 | 7 | 9<br>1M | (1G)<br>6 |

1M = Mating female.

Table 31. Distribution of the three age classes of <u>Naja haje annulifera</u> in the <u>Burkea africana</u> Savanna Study Area : May 1975 - May 1977.

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchling 230-340 mm | ? | Hatchlings | | | | | | | | | | |
| Juvenile 340-600 | | | 1 | 3 | | | | | 2 | 1 | | 3 |
| Subad. & Adults >600 mm | 2 | 2 | 1 | 3 | | | | | 4 | 1<br>3(2G) | | 5 |

1G = Gravid female.

Table 32. Distribution of the three age classes of <u>Lycophidion capense</u> in the <u>Burkea africana</u> Savanna Study Area : May 1975 - May 1977

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchling 120 mm | ? | Hatchlings | | | | | | | | | | |
| Juvenile 120-140 | | | | | | | | | | | | |
| Subad. & Adults >140 mm | | 1 | | 1 | 1 | | 1 | 4 | 5 | 2 | 3(1G) | 2 |

1G = Gravid female

Table 33. Distribution of the three age classes of *Dispholidus typus* in the *Burkea africana* Savanna Study Area : May 1975 - May 1977

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchling 250-300 mm | 1 | 2 | | | | | | | | | | |
| Juvenile 300-450 mm | 1 | 1 | 3 | 1 | 2 | 1 | | | 3 | | | |
| Subad. & Adults 450 mm | 2 | 2 | 1 | | | 1 | | | | 1 | 2 | 3 |

Table 34. Distribution of the three age classes of *Aparallactus capensis* in the *Burkea africana* Savanna Study Area : May 1975 : May 1977.

| | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatchling 120 mm | ? | | | 1 | | | | | | | | |
| Juvenile 120-160 mm | | | | | | | | | | | | |
| Subad. & Adults 160 mm | (1G)<br>3 | 2 | 2 | 1 | 1 | | | 1 | 3 | 3 | 5 | (1G)<br>4 |

. 1G = Gravid female

minimum of 67 and a maximum of 97 days later. A mean between these two extremes is 83 days, which is plausible. The single September hatching discussed previously is somewhat enigmatic, but both theories discussed cannot be discounted, although I favour sperm retention. However, samples are small and, therefore, difficult to interpret. The period of egg deposition, therefore, coincides with the period of most rainfall so that the soil is moist. The egg shells of all the oviparous and ovoviviparous snakes at Nylsvley are porous and dessicate easily. Therefore, the timing of egg-laying must be of great importance for the survival of the species. The fact that most of the snake species at Nylsvley lay small clutches of eggs, is an added insurance against the possibility of drought or flood, which may destroy the clutch. Fewer eggs, but several clutches throughout the rainy season would be the most successful method of the survival of the species under such erratic climate conditions. Late egg-laying would bring additional hazards of dessication and cold and, therefore, eggs deposited during this period are likely to need an incubation period of at least three months.

Most other species exhibit the same trend as that of the short-snouted sand snake and vine snake. Tables 30-34 show that most hatchlings hatch out between January and May. This is also supported by the less abundant species such as the striped skaapsteker, brown house snake, black mamba, Jalla's sandsnake and the bicoloured quill-snout, where hatchings were observed during the same period. The hatchlings mostly emerge at a time when there are also hatchling and juvenile lizards and amphibians about. This is important as it is probable that they would not survive the winter months without first being able to build up some fat reserves. An interesting feature in this connection is that the common egg-eater hatches out during September (Table 29), which also coincides with the period when many of the small bird species breed, thereby also ensuring an adequate food supply. Growth is fairly rapid during the first year but progressively slows down, usually at the age of three years, after which a gradual incline may be maintained. However, some species appear to deviate from this standard pattern. One such species is Psammophis sibilans brevirostris, which appears to have an annual cycle. The percentage frequency of the various size classes during the year can be seen in Figure 46. It is apparent that hatchlings are found mainly from January to April. None or very few adults intrude from the previous year's population. The questionable entity is that found in the 641,0 mm + size class during the month of July, which could belong to the

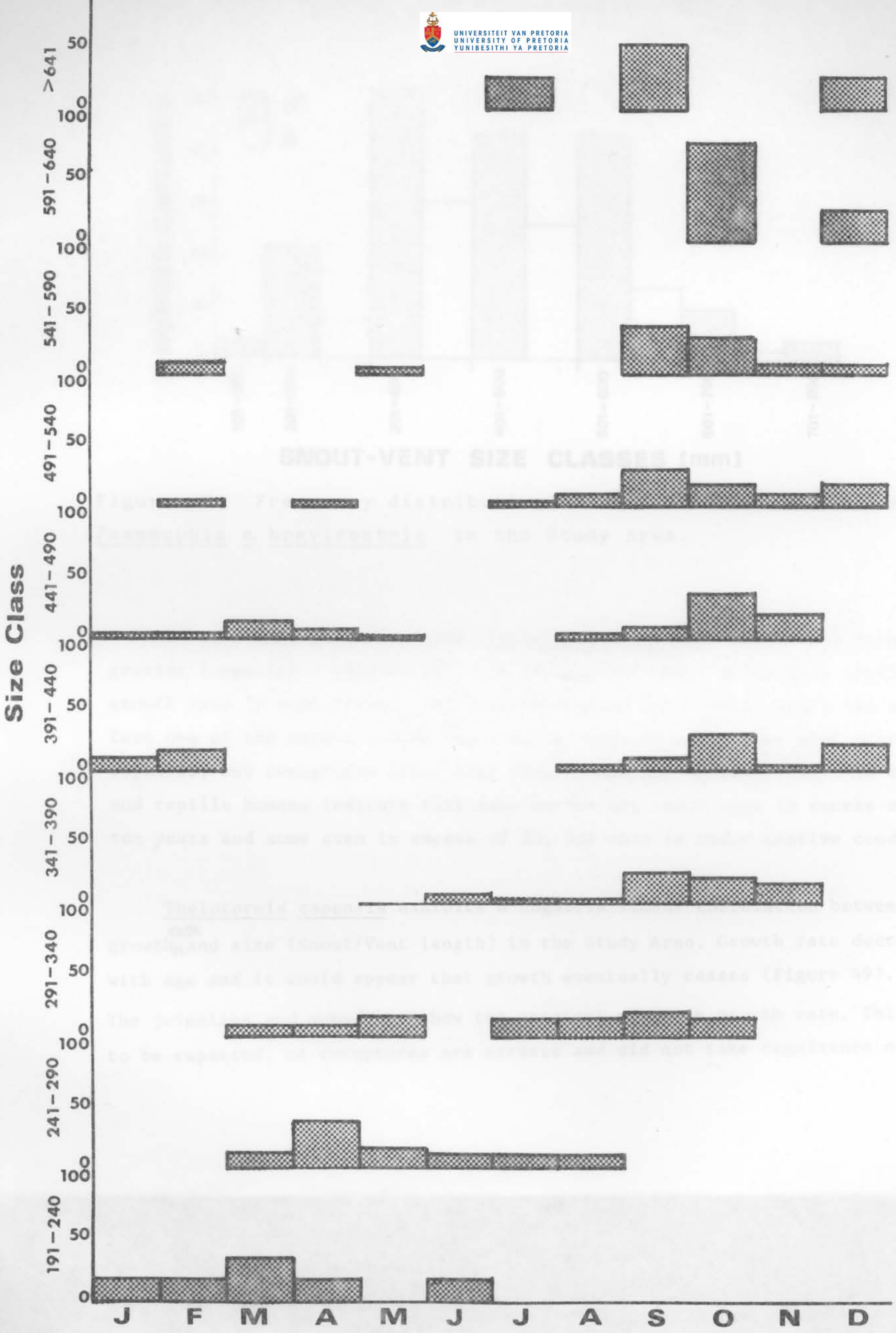


Figure 46. Monthly distribution of size classes of Psammophis s. brevirostris in the Study Area.

previous year's population. There is a noticeable gap in the size classes above 590 mm snout-to-vent length and even that below this size indicate very few individuals. It would, therefore, appear that most individuals die from 12 to 15 months after birth. Rarely do some individuals survive longer to reach the maximum sizes in excess of 591,0 mm S/V length. Figure 47 exhibits the distribution of the short-snouted sandsnake according to the size classes discussed previously, as well as sex.

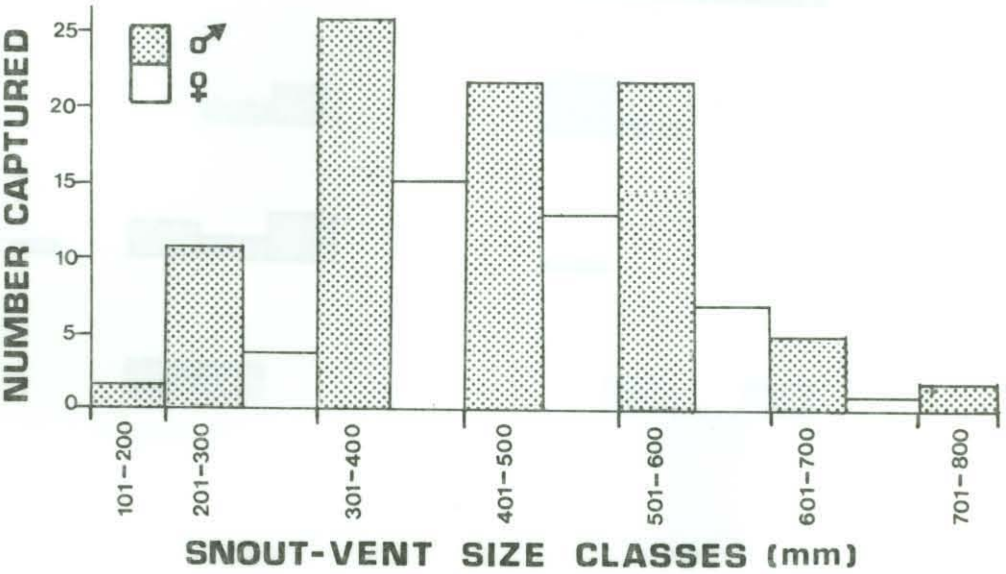


Figure 47. Frequency distribution of size classes and sex of *Psammophis s. brevirostris* in the Study Area.

In contrast, the vine snake (*Thelotornis capensis*) exhibits a trend of greater longevity (Figure 48). It is apparent that, although a similar growth rate is experienced, individuals survive for several years and in fact one of the marked snakes which was already of adult size when initially captured, was recaptured after four years. Records of longevity in zoos and reptile houses indicate that many snakes may reach ages in excess of ten years and some even in excess of 20, but this is under captive conditions.

*Thelotornis capensis* exhibits a negative linear correlation between growth rate and size (Snout/Vent length) in the Study Area. Growth rate decreases with age and it would appear that growth eventually ceases (Figure 49). The juveniles and subadults show the greatest range in growth rate. This is to be expected, as recaptures are erratic and did not take cognisance of

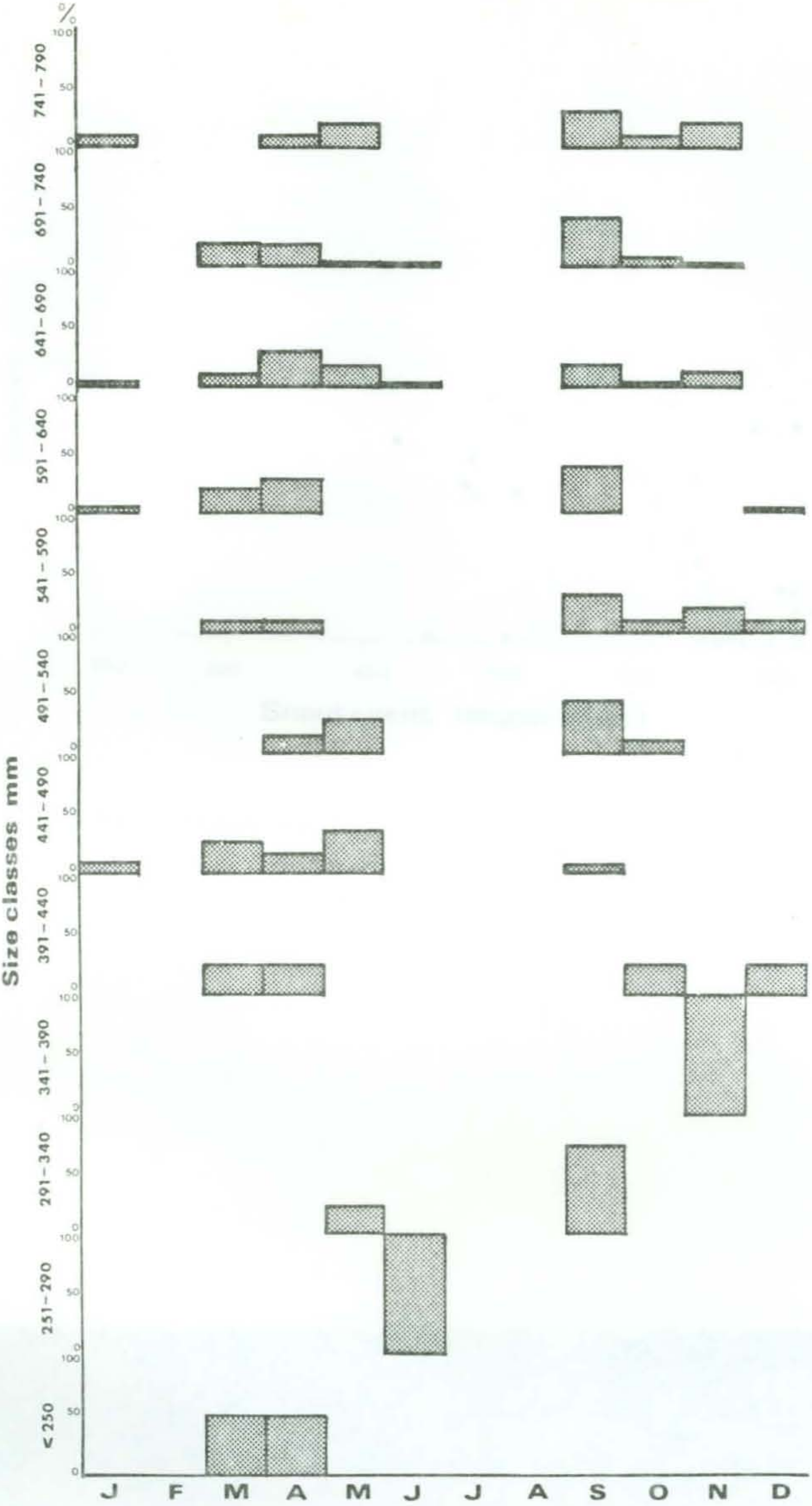


Figure 48. Monthly distribution of size classes of Thelotornis capensis in the Study Area.

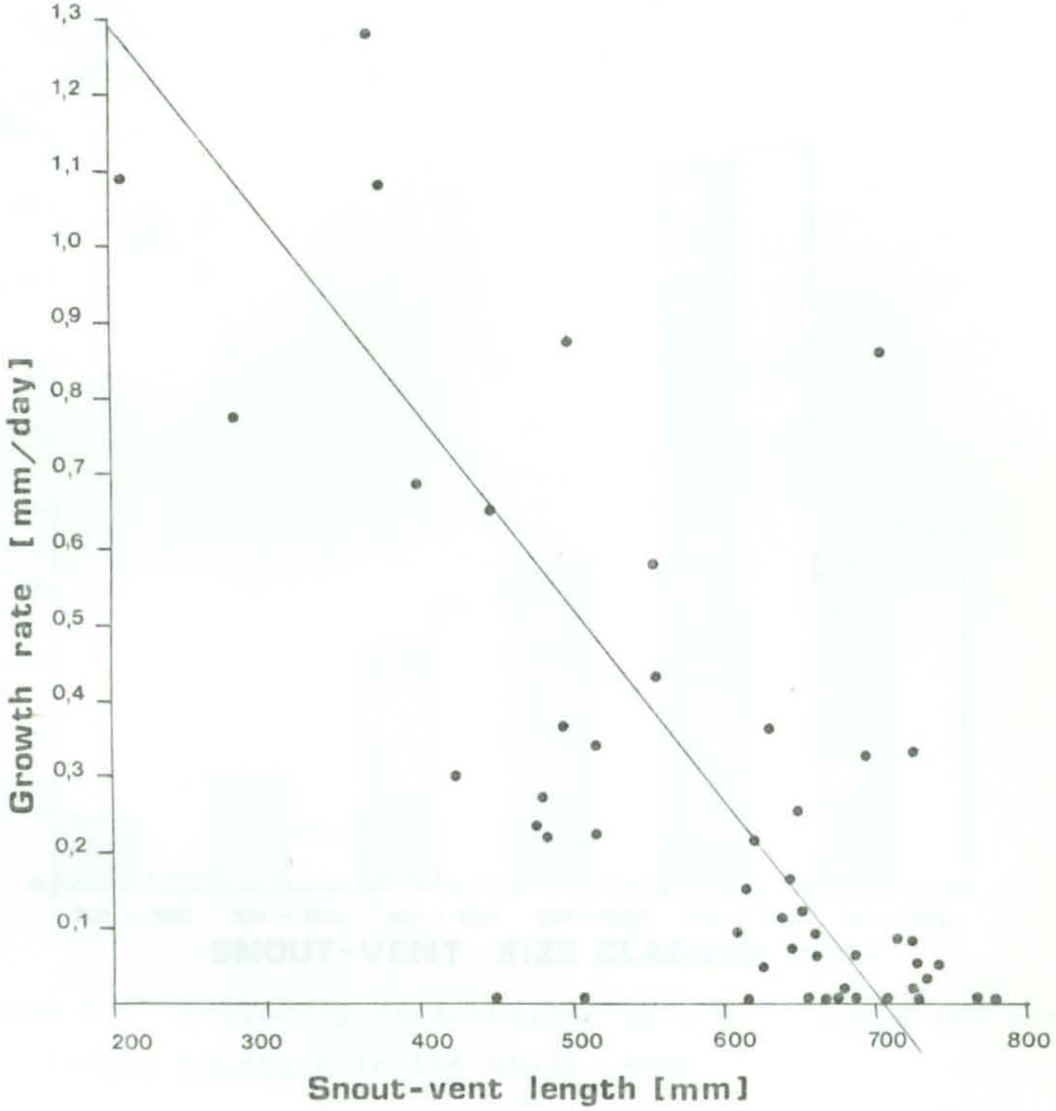


Figure 49. Negative linear correlation between size and growth rate in Thelotornis capensis in the Study Area.

the seasons. If a snake was marked prior to winter and was recaptured some four months later, it will have grown less than were it captured and marked after winter and then recaptured four months later. One snake, No. 116, grew from a total length of 580,0 mm on the 23/10/75 to 959,0 mm on 1/5/77, at a rate of 0,68 mm/day. It was recaptured again on the 11/5/79, during which period it increased at a rate of 0,19 mm/day or at slightly less than a third of its previous rate. Overall it therefore achieved a mean growth rate of 0,54 mm over a period of 1 296 days to reach a size of 1 103,0 mm. This is considerably slower than that recorded for the black mamba under artificial conditions. Growth rate is influenced by the amount of food ingested, as well as temperature and, possibly, humidity. Sweeney (1961) observed under captive conditions that the vine snake required to feed on average about every fifth day, but they require a very low energy budget.

Figure 50 illustrates the distribution and frequency of each size class. A skewed distribution pattern is apparent. Most animals appear to fall into the large adult class, and size tapers rapidly off thereafter.

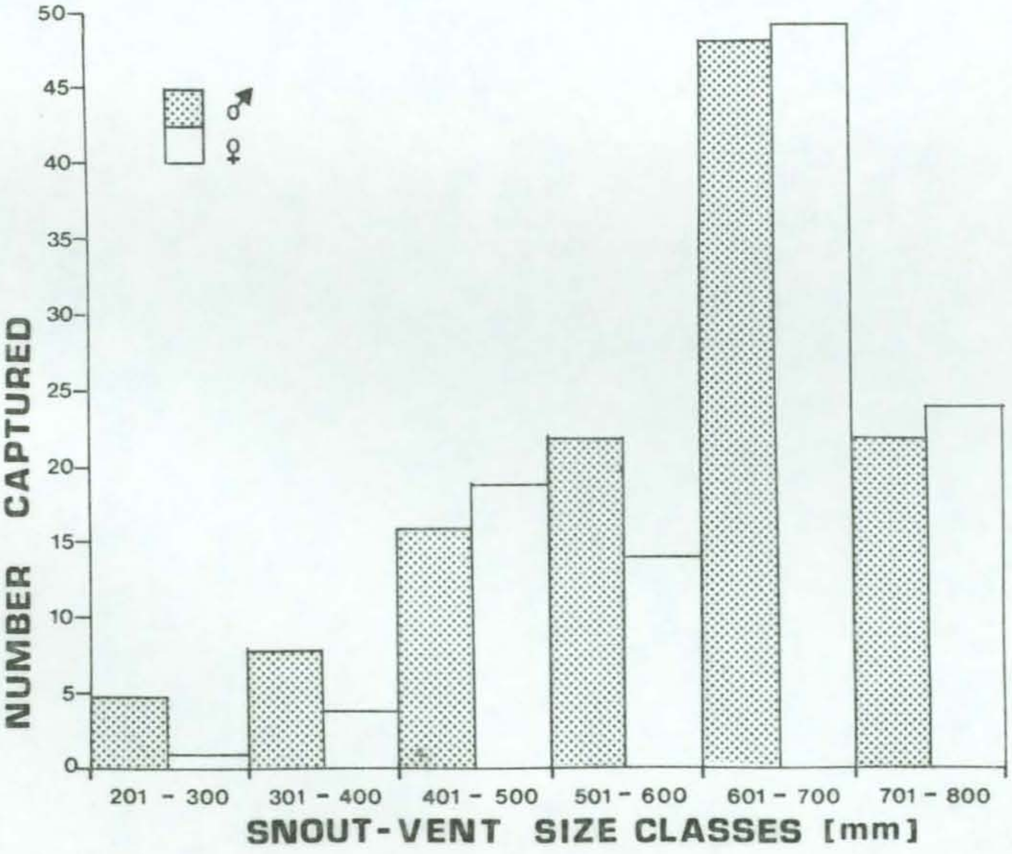


Figure 50. Frequency distribution of size classes and sex of Thelotornis capensis in the Study Area.

It is apparent that the populution is mostly adult with low recruitment taking place. Mention has been made previously of the relative longevity of this species. Mortality appears low, only two vine snakes were seen dead in the Study Area, both having been killed by a slender mongoose (Herpestes sanguineus) and left hanging in the trees. A third vine snake had a portion of its tail chewed off, possibly also by a mongoose.

A juvenile black mamba (Dendroaspis p. polylepis) captured on Nylsvley with a snout-to-vent length of 450,0 mm, reached 1 500,0 mm within a year, and may even reach 2 100,0 mm (H. Erasmus pers. comm.) However, this is only achieved under artificial conditions as the animal cannot move about and is fed regularly, thereby expending energy solely on growth. Under natural conditions, this growth rate may be far less. Measurement based on recapture data have been summarized in Table 35.

Bauerle (1972), studied four snake species in the Grassland Biome. The prairie garter snakes (Thamnophis radix)achieved a growth rate of ,018 mm/day during the two years of observation. Growing days were considered to be restricted to the period May to September. Maximum growth rate was achieved by a female which grew 296 mm in 52 growing days.

The prairie rattlesnake (Crotalus viridis) achieved a growth rate of 0,028 mm/day. It would appear, therefore, that these temperate climate snakes do not grow at the rate of the snakes at Nylsvley, which can be considered as subtropic. It is also probable that during the cold winters at Nylsvley, very little, if any, growth takes place, in which case the growth rate during the eight active months of the year would be even more pronounced.

Four captive puff adders (Bitis arietans) two males and two females, achieved a mean growth rate of 0,516 mm/day over a period of 32 months, with a range of 0,395 to 0,655 mm/day. This compares favourably with that of the vine snake under natural conditions. Their mean daily food intake amounted to 2,807 g with a range of 2,475 to 3,197 g/day. Therefore, for every 100 g of food consumed, the snakes grew 16,13 mm. Both males ate marginally more than the females, but one of them remained stunted after an auspicious beginning. The one male grew longer in total length than the females, both of which grew longer and larger than the stunted male. Most of the food offered to the puff adders were white mice (Mus musculus) and rats

(Rattus norvegicus). Bauerle (loc.cit.) found that 32% of the live weight of these mice was dry weight. Therefore, for every 100 g of live weight, the snakes consumed 32 g dry weight. Odum (1971) lists small vertebrates as yielding on average 15,08 x $10^3$ J/g dry weight. Therefore, for every 100 g of rodent consumed, a potential amount of 750,85 x $10^3$ J of energy was consumed. Unfortunately, it was not possible to collect and analyse the faeces of the puff adders for energy loss, but using the data from Bauerle (loc. cit.) on the prairie rattlesnakes, which are remarkably similar in habit and disposition, it was determined that 4,98 g of waste was produced, which when measured by bomb calorimetry, contained 15,13 x $10^3$ J/g. Therefore, of the original 750,85 x $10^3$ J ingested, 75,33 x $10^3$ J was lost in the faeces. This shows that about 90% of the available energy was assimilated by the puff adders for use in reproduction, respiration, growth and storage to last the snakes over the cold dry winter.

From Table 35, it is apparent that the growth rate of most snakes in the Ecosystem Study Area is comparable to that of the vine snake. Problems were experienced in those instances where little or no growth had taken place, as it is difficult to measure the live animal. To this problem, errors in measurement can be attributed, as the snake stretches and flexes, thereby making it necessary to allow the animal to flex and relax for a brief period of time. Measurements taken were usually during the relaxed phase, but care was taken not to stretch the snake over much, as this could cause injury to the fragile vertebrae. Measurements of loss or gain in weight were also taken, but this figure is meaningless over long intervals of time, as it is felt that fluctuations in mass are greater over the relative short term. However, these are included in the Table. The mean growth rate of Psammophis s. brevirostris is 0,35 mm/day, which is virtually the same as that for the vine snake (0,32 mm/day), in spite of the different habits of the two snakes, the former being essentially a 'hunter', as opposed to the 'percher' or 'wait and see' method of the latter. The difference no doubt lies in the fact that being a smaller snake (Table 4), it matures earlier as opposed to the longer life span of the latter. It is probable that Psammophis s. brevirostris becomes sexually mature at one year of age, while the vine snake, similar to the puff adder, only reached this stage at three years of age (pers. obs.). It is a curious phenomenon that these active reptiles have a short life cycle. Several lizard species also share this characteristic and are essentially similar in foraging habits, whereas those species which adopt a 'wait and see' foraging strategy appear to be longer lived.

Table 35. Growth of individual snakes of 10 species recaptured during the period May 1975 to May 1977, in the *Burkea africana* - *Eragrostis pallens* Study Area

| Snake number | Sex | Growing time (days) | Weight change (g) | Length change (mm) | Growth rate (mm/d) |
|---|---|---|---|---|---|
| *Psammophis sibilans brevirostris* | | | | | |
| 20 | M | 190 | -19,35 | 0 | 0 |
| 35 | F | 411 | 19,60 | 201 | 0,50 |
| 39 | F | 33 | 0,85 | 5 | 0,15 |
| 41 | M | 30 | 2,80 | 15 | 0,50 |
| 70 | M | 75 | 2,50 | 0 | 0 |
| 72 | M | 32 | -18,50 | 10 | 0,31 |
| 95 | M | 21 | - 3,05 | 11 | 0,52 |
| 110 | M | 28 | 4,50 | 16 | 0,57 |
| 173 | M | 208 | 2,85 | 25 | 0,12 |
| 222 | M | 241 | 11,65 | 74 | 0,31 |
| 224 | M | 29 | - 0,90 | 9 | 0,31 |
| 281 | M | 25 | - 0,15 | 2 | 0,08 |
| 286 | F | 294 | 22,60 | 220 | 0,75 |
| 381 | F | 25 | - 0,05 | 12 | 0,48 |
| *Philothamus s. semivariegatus* | | | | | |
| 186 | F | 47 | 3,4 | 15 | 0,32 |
| *Telescopus s. semiannulatus* | | | | | |
| 44 | M | 33 | - 0,85 | 0 | 0 |
| 44 | M | 47 | -1,85 | 5 | 0,10 |
| *Dasypeltis s. scabra* | | | | | |
| 148 | M | 22 | 3,10 | 8 | 0,36 |
| 172 | F | 347 | 3,25 | 87 | 0,25 |
| *Naja mossambica* | | | | | |
| 21 | M | 164 | ? | 76 | 0,46 |
| 73 | M | 152 | 140,0 | 20 | 0,13 |
| *Aparallactus c. capensis* | | | | | |
| 152 | F | 14 | 0,70 | 0 | 0 |
| *Lycophidion capense* | | | | | |
| 77 | F | 151 | -10,50 | 12 | 0,08 |
| 77 | F | 192 | - 0,50 | 0 | 0 |

Table 35 (continued)

| Snake number | Sex | Growing time (days) | Weight change (g) | Length change (mm) | Growth rate (mm/d) |
|---|---|---|---|---|---|
| *Naja haje annulifera* | | | | | |
| 15 | M | 132 | 27,20 | 0 | 0 |
| 15 | M | 356 | -265,00 | 32 | 0,09 |
| 66 | M | 78 | 32,50 | 184 | 2,36 |
| 153 | M | 14 | -17,20 | 0 | 0 |
| 194 | M | 275 | -50,00 | 4 | 0,01 |
| 389 | M | 89 | 64,50 | 1 | 0,01 |
| *Dispholidus t. typus* | | | | | |
| 160 | M | 363 | 120,00 | 19 | 0,05 |
| *Crotaphopeltis h. hotamboeia* | | | | | |
| 53 | M | 38 | 3,65 | 30 | 0,79 |
| 78 | M | 31 | 2,10 | 0 | 0 |
| 226 | M | 220 | 1,80 | 11 | 0,05 |

Further reference to this will be made when discussing the various species.

The ratio of hatchlings to juveniles to subadults and adults is inversely proportional to that normally assumed to be the ideal where there are a large number of juveniles, decreasing pyramidally to a very few old age individuals. While it is not possible to determine the full age structure of populations of the captured snakes, it is nevertheless clear that a relatively small number of hatchlings are found at the apex of the triangle with a broad base of subadults and adults. This would indicate a declining population, although Odum (1971) mentions that a population may pass through changes in age structure without changing in size. It is, of course, assumed that all age classes have an equal catchability rating. One possible reason for this age distribution is that many of the smaller snake species may in actual fact be short-lived and reach adult size within one year, thereby overshadowing the other longer lived species while simultaneously having a high hatchling and juvenile mortality. All snake species captured in the Ecosystem Study Area show a preponderance of subadults and adults. For most species no hatchlings were captured, indicating very little breeding success. Figure 51 shows the relationship of hatchlings to juveniles to subadults and adults, both as a pyramid and as a cumulative percentage. Barbault (1971) exhibits a similar phenomenon, although a more even distribution of the three age classes is apparent with hatchlings and juveniles, forming more than 50% of the total. However, his data are based on the six principal species, whereas the data recorded during this study relate to all the species irrespective of abundance.

### Lizards

With the exception of two species, all the lizard species on Nylsvley are oviparous, and all markedly seasonal in their reproductive pattern. Some of the larger lizards, such as the veld monitor (Varanus exanthematicus albigularis) may be found mating during July/August, as well as September, whereas most other species only initiate mating after their emergence from hibernation in the latter half of September, and most activity takes place during October/November, but can extend into December. The arboreal Cape dwarf gecko (Lygodactylus capensis) however, does not have a set mating season and reproduction takes place throughout the year, with a possible increase in activity during the winter months.

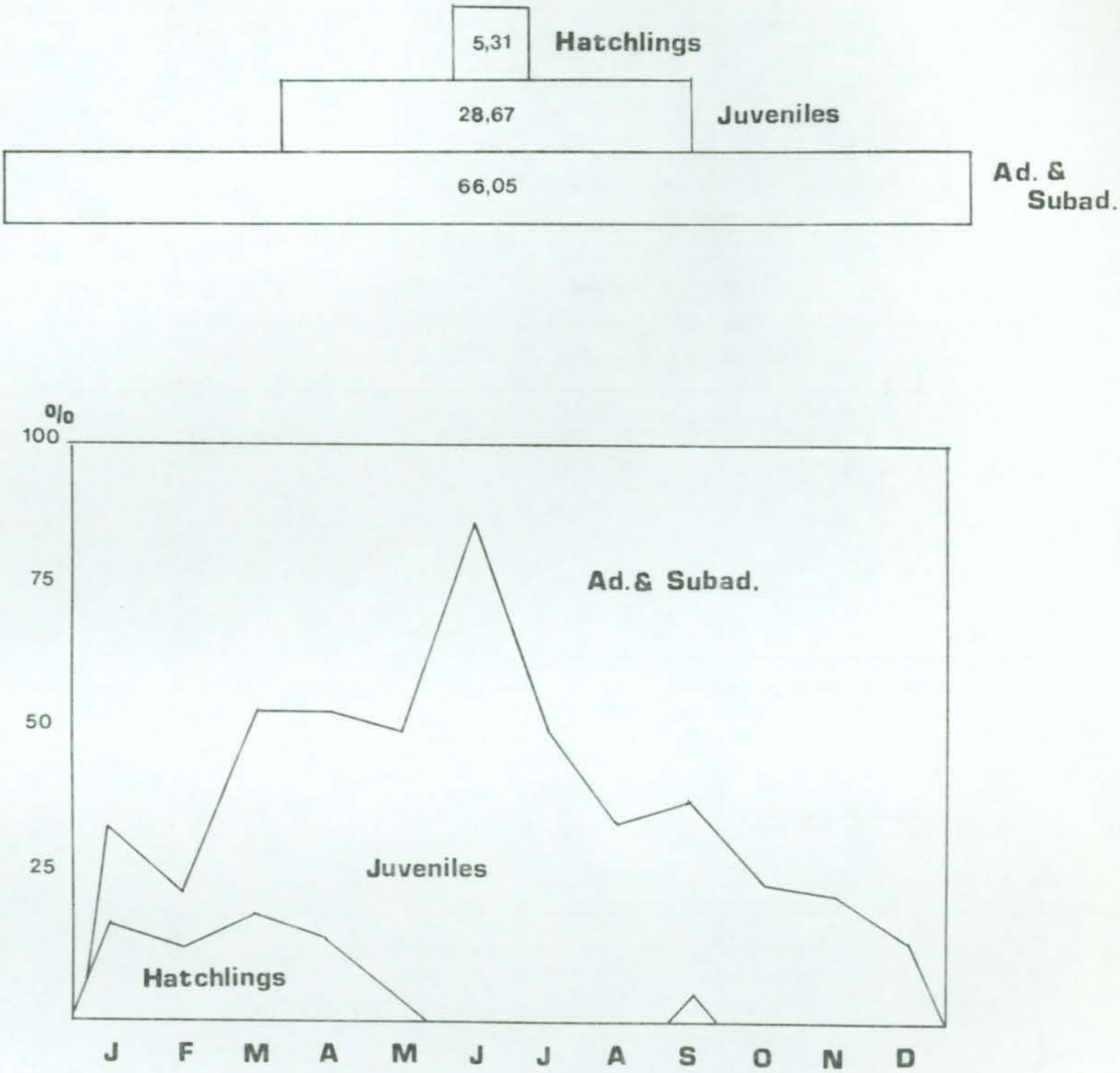


Figure 51. Relationship of three arbitrary age classes of snakes capture in the *Burkea africana - Eragrostis pallens* Study Area, May 1975 to May 1977.

Mating is generally stereotyped, with the male initiating the advance by following a female and flicking his tongue at her. This is followed by a neck bite, where the male retains hold of the female while twisting his body so that one leg is under the female and the other is over her back. Their cloacas then come into contact and a hemipenis is inserted (Figure 49). This is typical of Ichnotropis capensis, the Cape rough-scaled lizard, although at times the male may rush at the female with such force as to bowl them both over. Mating lasts up to 96 min. Once mating is completed the animals part, although on one occasion the male was actually seen to threaten the female with an open mouth in order to make her move away, so that copulation could be broken off. Females that have mated and have laid eggs or for some reason are not ready to be mated, were seen to perform avoidance behaviour by raising the body on stilt-like legs, at the same time arching the back, while the body is laterally flattened and the head points to the ground. On occasions the head points away from the aggressor. As mentioned previously, at times the male would rush at the female from distances of 60-90 cm and bite her on the neck or even the tail, whereupon she may be flung onto her side or even her back, where she then lies completely passive until the male loses interest and both move off. No aggression was observed between males with one exception, when two copulating lizards were disturbed by another male. The copulating male just threatened the intruder with an open mouth, who then moved off. No aggression was observed between the females.

Incidence of mating appeared to vary from year to year and seems dependent on the appropriate environmental conditions. During 1975, copulations were witnessed during October through to December, whereas during 1976, mating first started in November and continued to include January 1977. During 1977, mating was seen in December, following an abnormally dry period. This position appears also to be reflected by the gravid females which contained eggs in the oviducts ranging October,November, December during 1975, then only from November to December and during 1977, December appeared to be the month with the most oviducal eggs present.

The deposition of the ova took place mostly during November/December. The female would actively dig an inclining hole ($30-40^{\circ}$) to a depth of 10 to 20 cm. Digging was done with the fore-feet, using alternately left and right fore-feet with an occasional pause to scoop the accumulated material

Figure 52. Mating Ichnotropis capensis in the Study Area.

away from the entrance of the burrow. Once satisfied that the hole is deep enough, she reverses into the hole until she has all but disappeared. Egg-laying is of short duration (approximately five to 10 min). She then emerges and re-enters the hole, pushing loose soil onto the eggs and, with her snout, tamps it down. She then again emerges and with rapid raking movements of her forefeet, scrapes the soil back towards the hole, stops and shovels the soil backwards with her hindfeet, and then turns around and pushes soil down the hole and tamps it down again with her snout. This process is repeated until the hole has been completely closed. She then moves off and starts foraging. On occasions she may return and do some additional displacement digging, ineffectually scratching here and there, but apparently aimlessly. The hole has been well camouflaged. From 3-9 eggs are laid ($\bar{x}$ = 5,94 n = 19) and have an average mass of 0,15 g (range 0,100 - 0,156 g) which incubate for between 56-77 days. The juveniles, therefore, emerge during January and February, but a few may even emerge in March and even as late as May (Figure 53). Up to two clutches of eggs may be laid by the female, prior to her death. Mass at birth is 0,15 g and they measure 19,0-21,0 mm S/V and growth is rapid (Figure 54), with the animals reaching sexual maturity at a mass of 2,2 g, with a snout/vent length of 45,0 mm at the age of seven months. This is also exhibited among the females by the incidence of ovulation at this stage.

However, developing ova are first observed in lizards with S/V length of 48,0 mm. Figure 55 exhibits the incidence of gravidity according to the size class. It is apparent that female lizards between 52,0 and 57,0 mm have the highest frequency and that the spread follows a poisson distribution. This is, therefore, an indication of fecundity. This feature is also common to most of the other species, which will be discussed later.

Figure 56 exhibits the distribution of the rough-scaled lizards captured according to the size classes illustrated previously (Figure 53). An apparent occurrence is that the first three size class groupings exhibit parity or almost so, whereas later there is a preponderance of males, as has already been discussed. It is not clear why there should be such a difference, particularly in the 46-50 mm size class, which would indicate an age of 8,5 to 10,25 months or during the peak of reproductive activity.

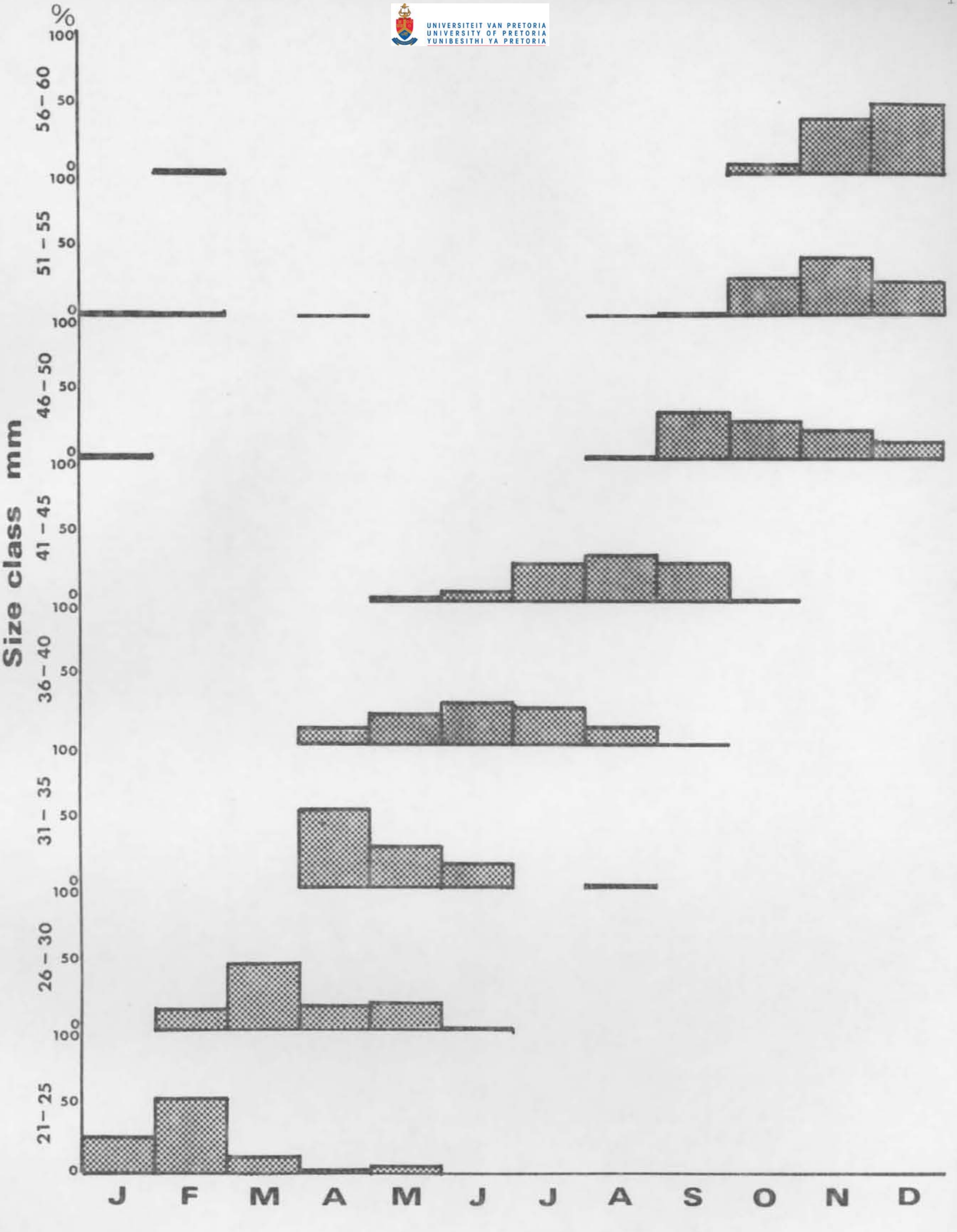


Figure 53. Monthly distribution of size classes of _Ichnotropis capensis_ in the Study Area.

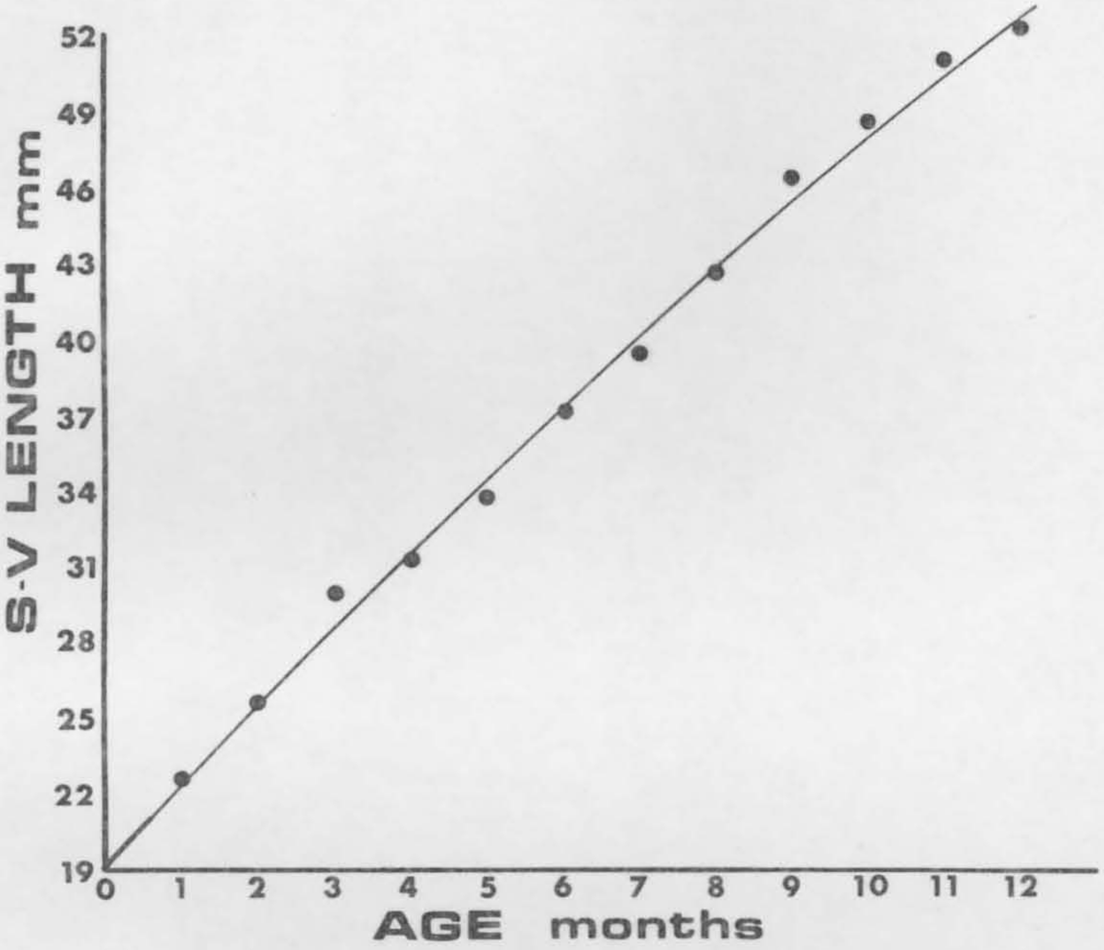


Figure 54. Mean growth rate of *Ichnotropis capensis* in the Study Area.

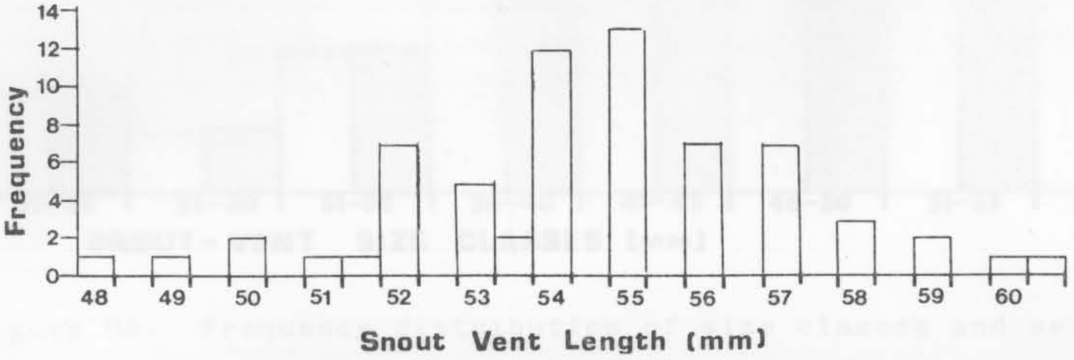


Figure 55. Size class frequency distribution of gravid Ichnotropis capensis in the Study Area.

At this time too, nuptial colours are becoming apparent, which reach their greatest intensity during September/October. Chromatic sexual dimorphism is at this stage apparent and the males in particular are now brightly coloured. Similar to that of the snakes, these lizards also show sex differentiation in size, with the females having longer bodies and shorter tails than the males. In addition, the scales just anterior to the vent are small in females and large in males, a feature which is present in hatchlings and, therefore, permits the sexing of these lizards while still very young, a feature not possible with the other species of lizards or snakes.

No doubt predation pressure is the heaviest at this time and would appear to be selective. This trend is reversed in the ultimate size class that is 56-60 mm S/V length, but only serves to indicate that the females grow larger than the males and possible exhibit a greater longevity.

Male and female Cape rough-scaled lizards also show a differential growth rate with females achieving a greater snout/vent length due to her function of carrying the eggs (Figure 57).

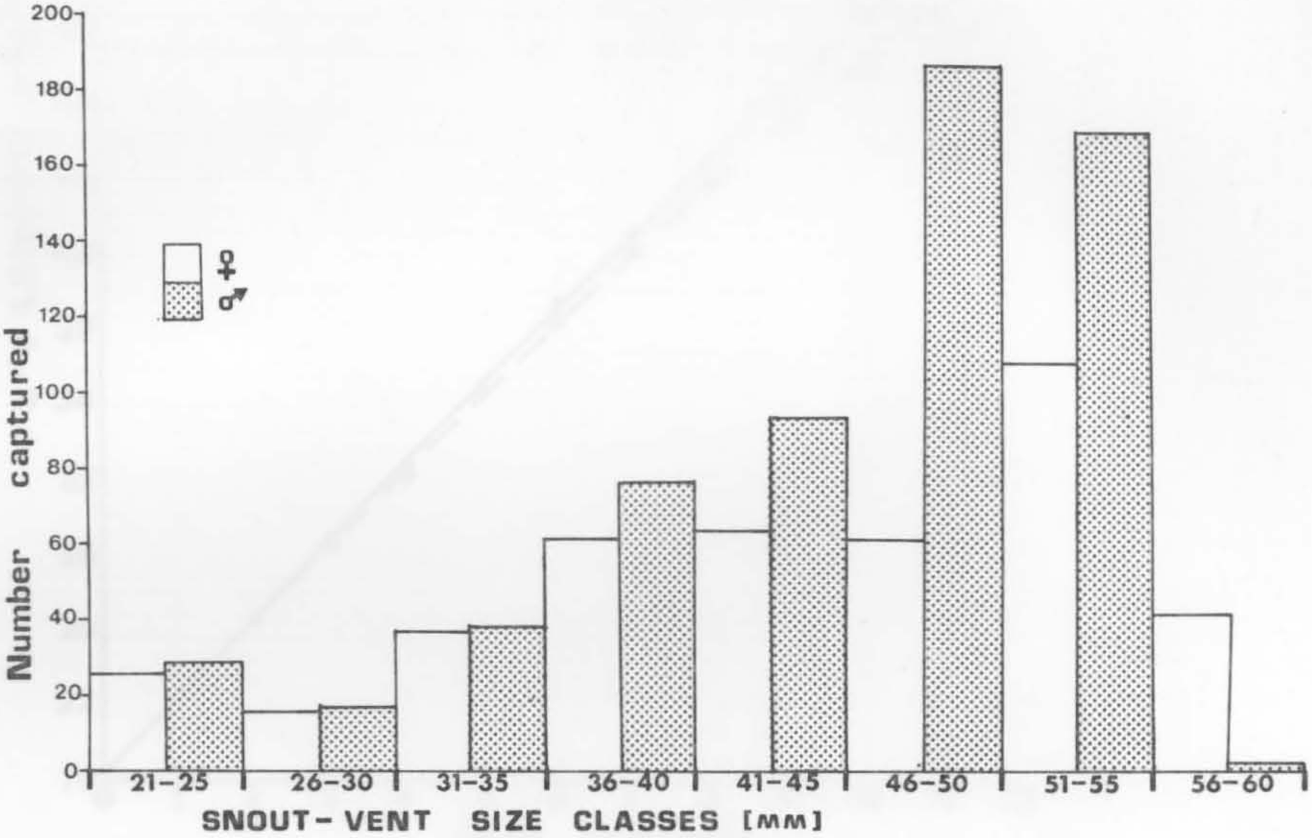


Figure 56. Frequency distribution of size classes and sex of *Ichnotropis capensis* in the Study Area.

From recapture data it can be seen that the growth rate is variable (Figure 58), but a mean of 0,08 mm/day for males (n =19) and 0,11 mm/day for females(n =18) was maintained. Growth appeared to be more rapid prior to and after winter, but owing to an insufficiency of recaptures, little more can be said. The mean growth rate curve (Figure 54) is of importance when comparing the other less active lizard species. It is seen that it encompasses and maintains a steep slope throughout the life span of these lizards. Broadley (1967), first documented the short life cycle of these lizards. It is even more remarkable when one sees that the growth curve of the female is mostly responsible for the steep incline. It is perhaps their active foraging habit which is responsible for the rapid rise and short life cycle. Most individuals appear to be dead by December, although

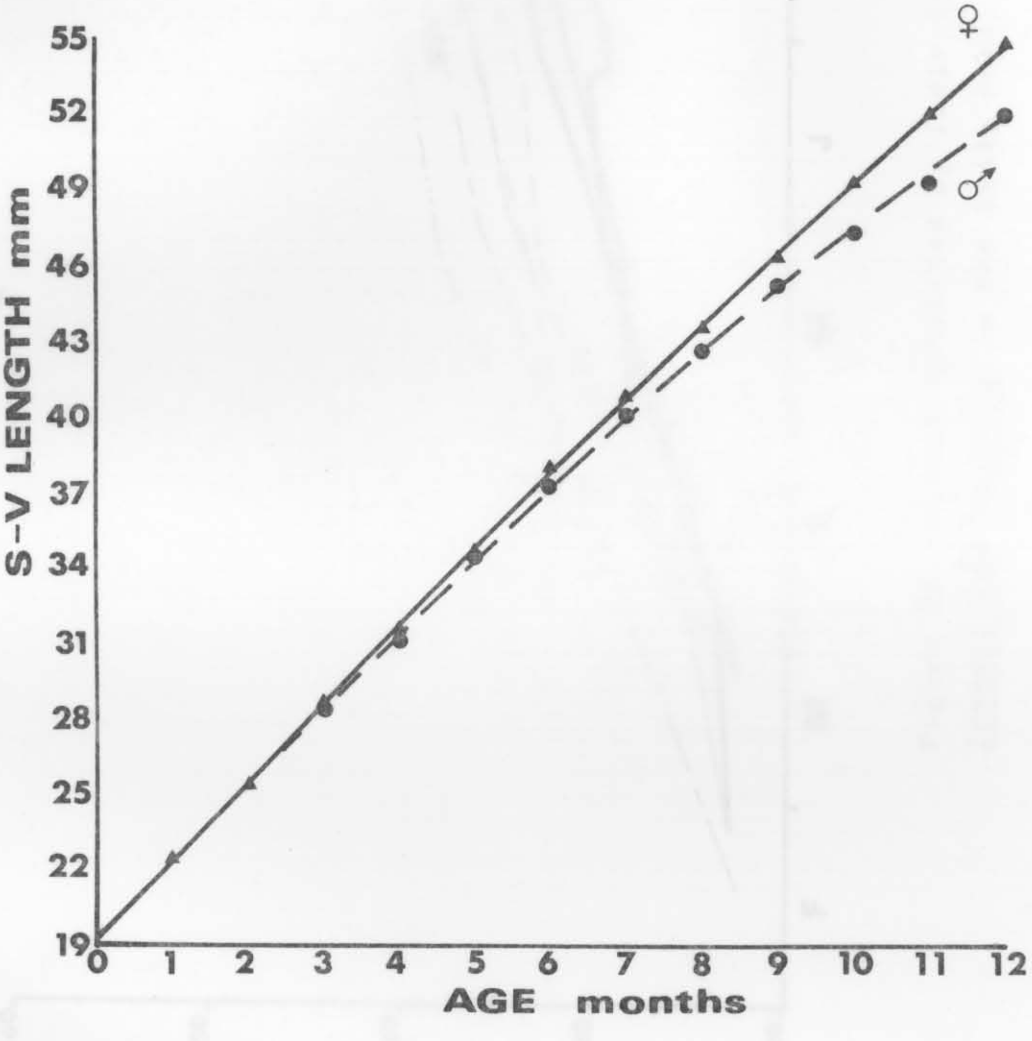


Figure 57. Differential mean growth of male and female *Ichnotropis capensis* in the Study Area.

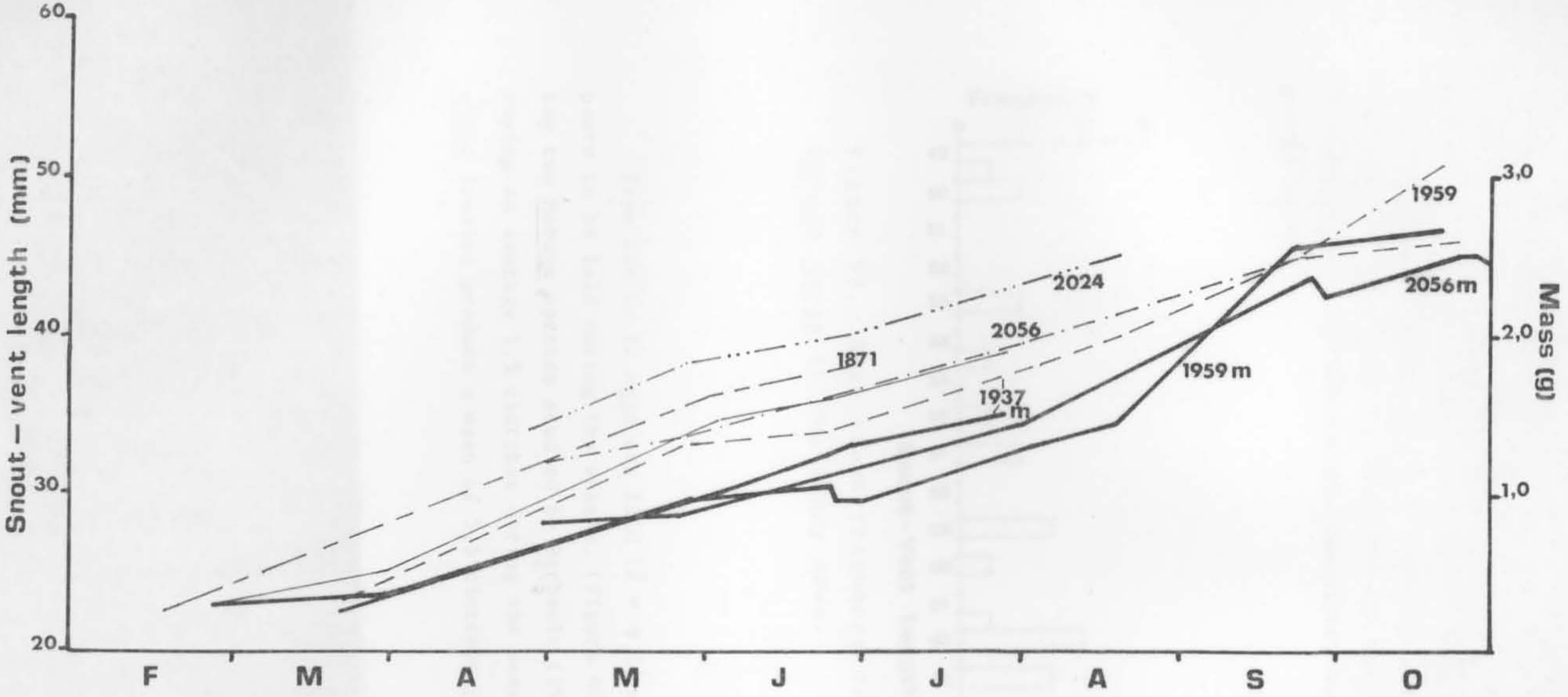


Figure 58. Growth exhibited by individual recaptured <u>Ichnotropis capensis</u> in the Study Area.

a few continue to be seen and captured up to May, at which time they may be 15 to 16 months old. The majority, as we have seen, die off at the age of 10 to 11 months. A curious feature is that they can be kept artificially in an enclosure for as long as 20 to 24 months before dying.

Mabuya varia (variable skink) on the other hand, appears to breed earlier than Ichnotropis capensis with young already appearing during December and extending into January, which is the peak month. The females are ready for ova deposition during October/November. At this time the female, apart from being distended with ova, develops a bloom to her scales, appearing irridescent and easily distinguishable from the duller and usually smaller male. During October 1975, three of 14 females (21%) were visibly gravid, while during November 1975, 12 out of 14 (85%) females were visibly gravid and during December one of four (25%) was visibly gravid. Figure 59 shows the distribution of gravid females plotted against S/V length. Again, a relatively even distribution is apparent, although somewhat skewed to the right on account of the fact that the smaller S/V length records were of lizards dissected and record therefore, developing ova and not visibly gravid as yet.

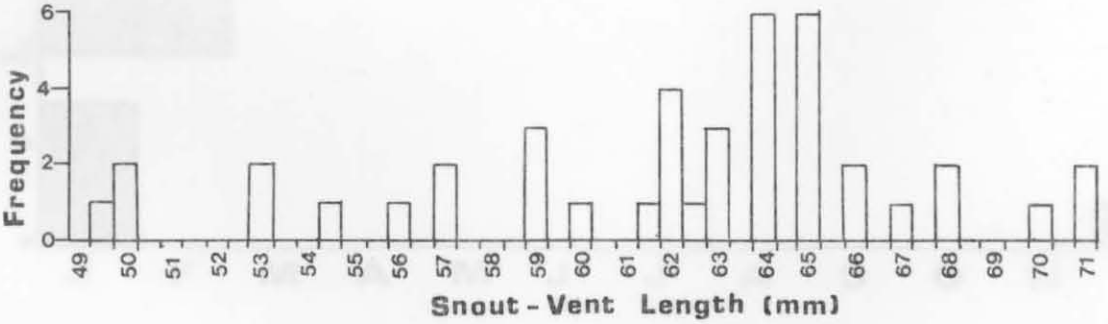


Figure 59. Size class frequency distribution of gravid Mabuya varia in the Study Area.

From six to 12 eggs are laid ($\bar{x}$ = 9,11 n = 9) and only one clutch appears to be laid during the season. (Figure 60). This is in contrast to the two Mabuya species studied by Barbault (1973, 1976a). Mabuya buettneri laying an average 1,5 clutches during the season, whereas Mabuya maculilabris females produce a mean of 5,5 clutches per year.

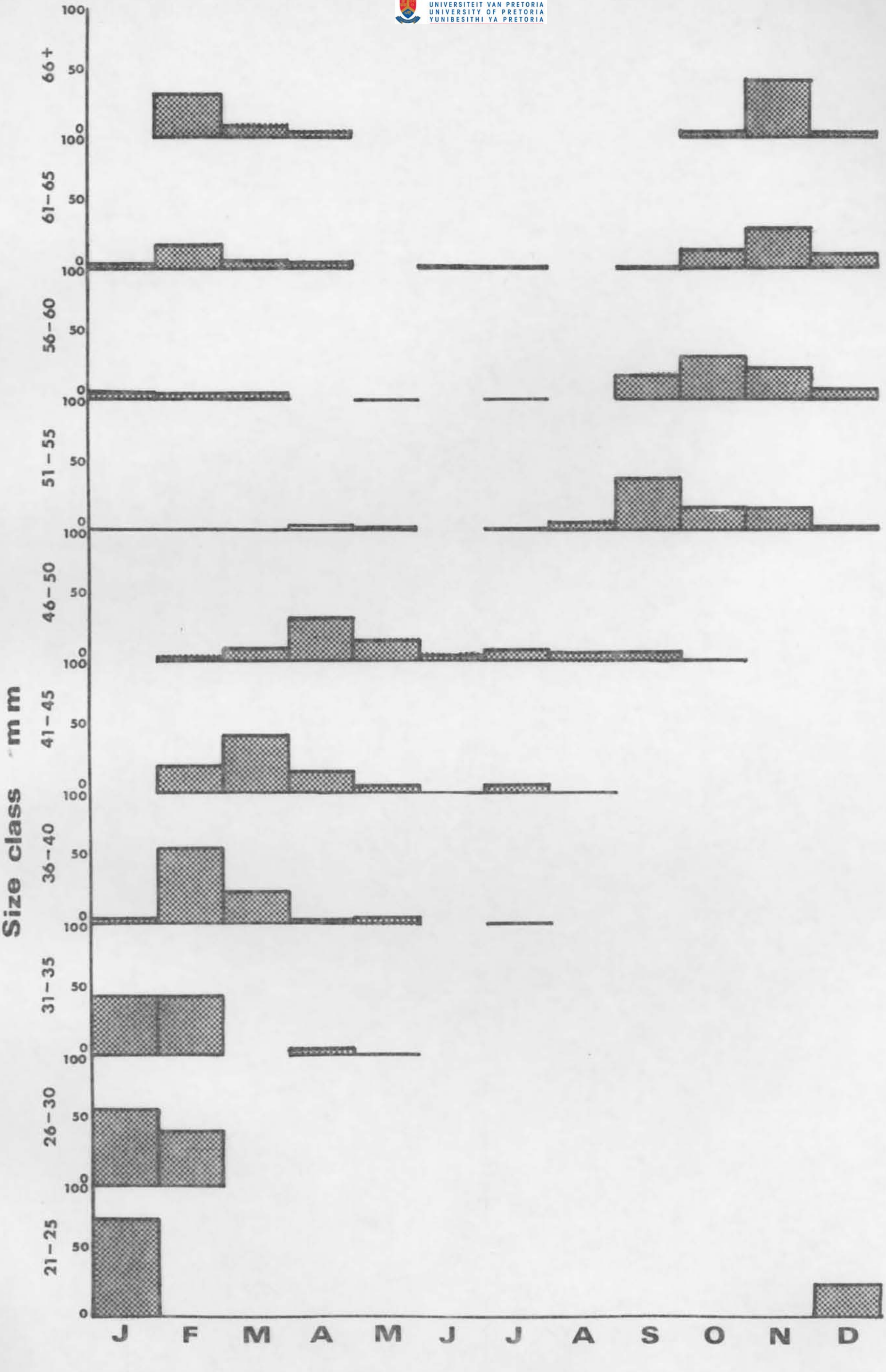


Figure 60. Monthly distribution of size classes of *Mabuya varia* in the Study Area.

Mabuya buettneri appears to closely resemble M. varia and lays its eggs during November and December, whereas M. maculilabris lays throughout the year with a peak from November to February.

M. buettneri apparently has a prolonged incubation period of four months which is exceptionally long for skinks. Mabuya varia has a two-month incubation period. Hatching success appears to be good as during the 10-day period during January 1976, 18 of 26 (69%) skinks captured were hatchlings and juveniles. Growth is rapid during the first two months, from a hatchling size of 22,0 mm S/V length to 35,5 mm (Figure 61), after which it begins to slow down. Again, a differential growth rate is apparent with the female achieving a greater size than the male (Figure 62).

Barbault (1976a)found that there was a differential mortality between the sexes and this appears also to be the case with Mabuya varia with some females and males reaching at most 23 months of age. Some females, therefore, survive two reproductive seasons, which may account for their success. The growth rate from recaptures indicate that both males and females grow at a mean rate of 0,12 mm/day, but this ranges from 0,3 mm/day to 0,01 mm/day, depending on the age and size of the animal (Figure 63). It is apparent from Figure 63 that the growth rate is depressed during the winter months but increases once summer and, therefore, warmer temperatures appear. Sexual maturity is reached by September when the males are seen with swollen hemipenes, while the females, if gravid, take on a bloom as mentioned previously. The lizards now have a mean S/V length of 53,79 mm and a mean mass of 3,36 (n = 111) at the age of eight months. However, some females are already sexually mature earlier at a S/V length of 49,5 mm (Figure 59) as at this stage the ova are already swelling in the ovary but have not migrated down the oviduct yet. Growth, however, continues gradually until the animals die off.

Figure 64 shows the distribution of the various size classes mentioned previously (Figure 60). From this it is apparent that there is an abnormal preponderance of males, particularly in the 51-55 mm and 56-60 mm size classes, which are attained at ages ranging from 8,25 and 9,25 to 13 months or more for females and males respectively. Thereafter, there is a preponderance of females which attain the largest sizes. The abnormally high abundance of males within the two size classes discussed previously is very difficult to explain except that it also occurs during the mating season and, therefore, at a time of greatest activity. This may induce the males

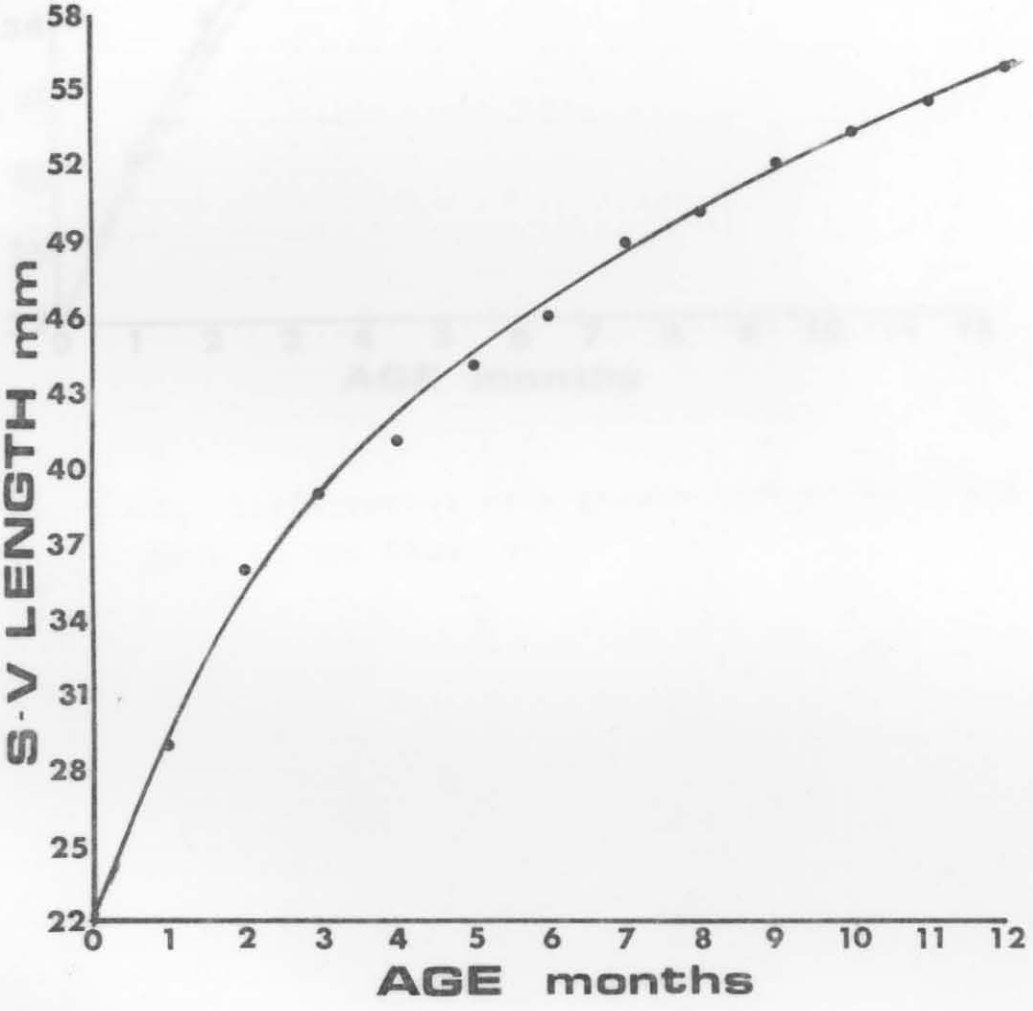


Figure 61. Mean growth rate of Mabuya varia in the Study Area.

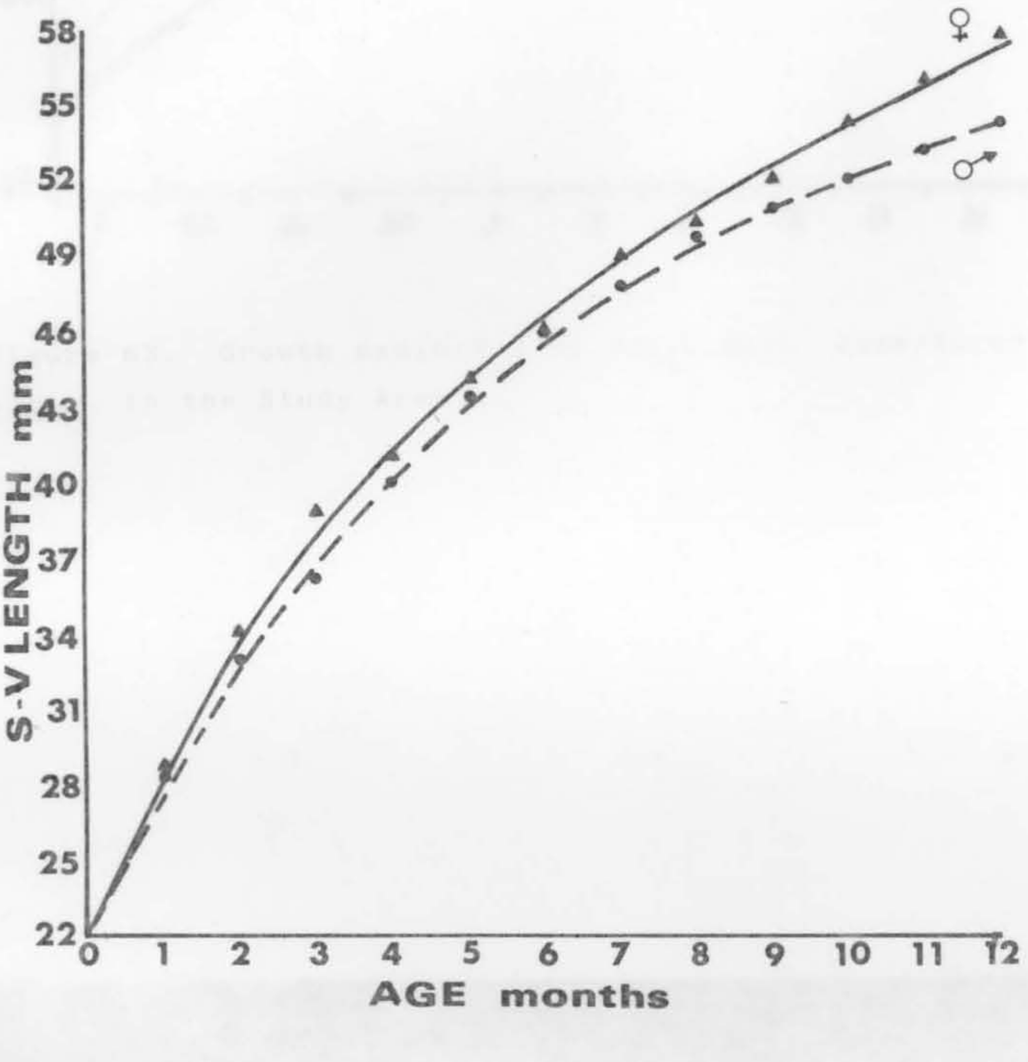


Figure 62. Differential mean growth rate of male and female *Mabuya varia* in the Study Area.

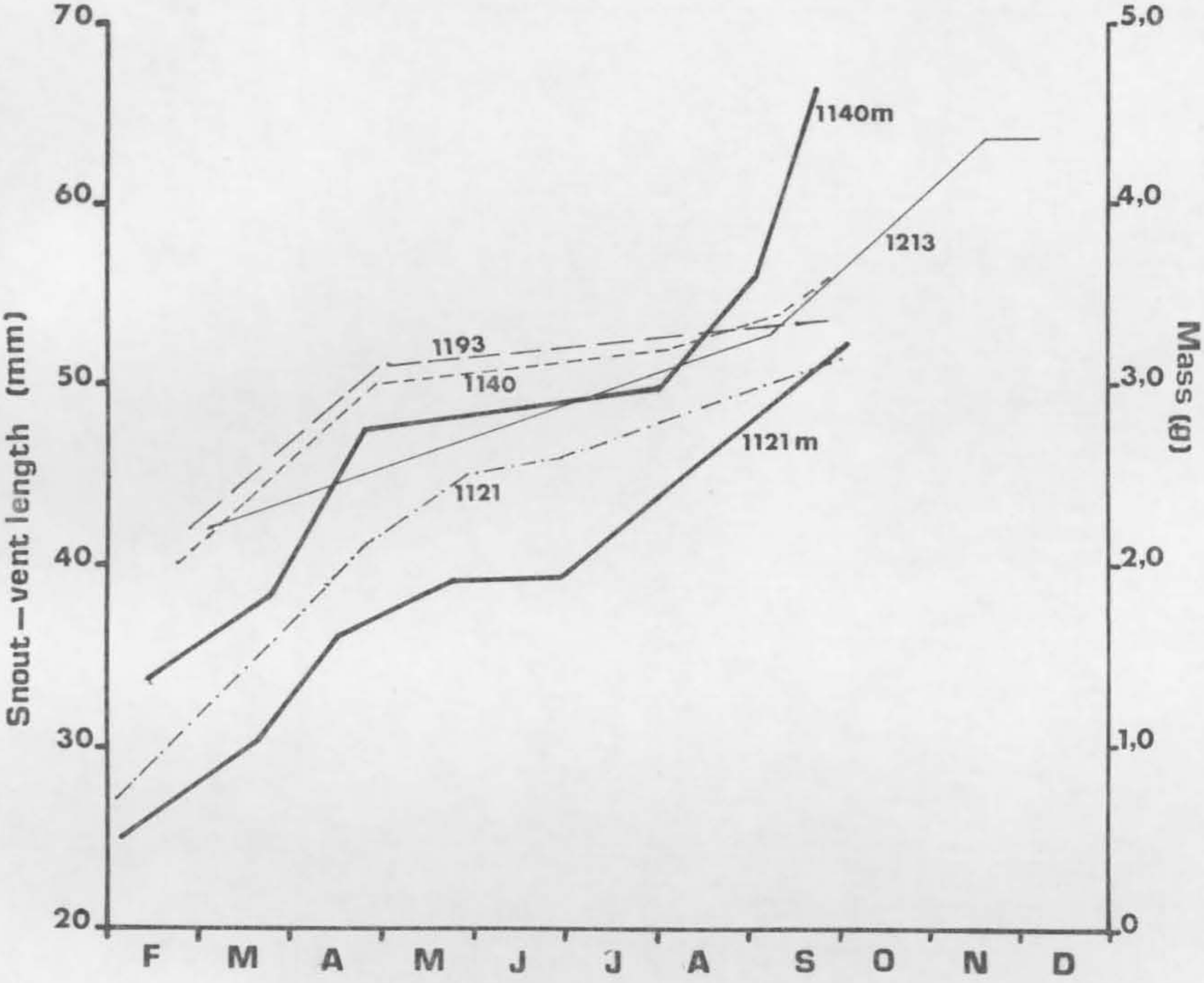


Figure 63. Growth exhibited by individual recaptured *Mabuya varia* in the Study Area.

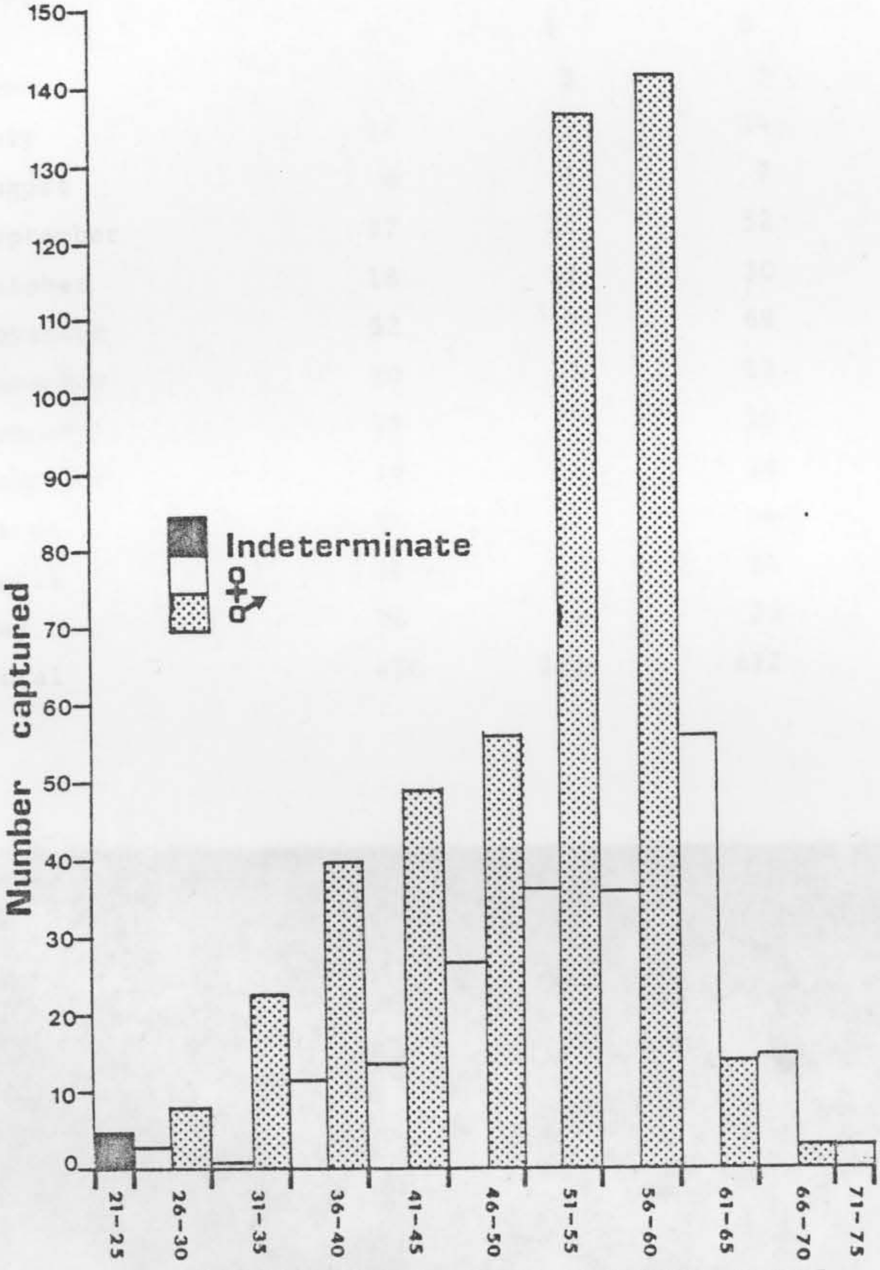


Figure 64. Frequency distribution of size classes and sex of *Mabuya varia* in the Study Area.

to forage further afield, particularly when the females occur at a ratio of nearly one to four. Greater search effort would be necessary in order to find a female which may, therefore, account for this great discrepancy.

As mentioned previously, there appears to be a differential die-off, males dying earlier than females. The sex ratio from the mark-recapture study can be seen in Table 36.

Table 36. Sex ratios of <u>Mabuya varia</u> during the period May 1975 to May 1977 in the <u>Burkea africana</u> - <u>Eragrostis pallens</u> Study Area.

| Month | Male | Female | Total | Ratio Male : Female |
|---|---|---|---|---|
| May | 1 | 4 | 5 | 1:4 |
| June | 1 | 3 | 4 | 1:3 |
| July | 5 | 2 | 4 | 1:0,40 |
| August | 12 | 1 | 13 | 1:0,80 |
| September | 43 | 16 | 59 | 1:0,37 |
| October | 59 | 14 | 73 | 1:0,24 |
| November | 22 | 14 | 36 | 1:0,64 |
| December | 13 | 4 | 17 | 1:0,31 |
| January | 15 | 1 | 16 | 1:0,67 |
| February | 36 | 18 | 54 | 1:0,50 |
| March | 10 | 8 | 18 | 1:0,80 |
| April | 26 | 8 | 34 | 1:0,31 |
| May | 4 | 1 | 5 | 1:0,25 |
| June | 2 | 3 | 5 | 1:1,50 |
| July | 11 | 3 | 14 | 1:0,27 |
| August | 6 | 1 | 7 | 1:0,17 |
| September | 27 | 25 | 52 | 1:0,93 |
| October | 18 | 12 | 30 | 1:0,67 |
| November | 52 | 17 | 69 | 1:0,33 |
| December | 10 | 3 | 13 | 1:0,30 |
| January | 13 | 7 | 20 | 1:0,54 |
| February | 26 | 10 | 36 | 1:0,38 |
| March | 26 | 18 | 44 | 1:0,69 |
| April | 16 | 5 | 21 | 1:0,31 |
| May | 16 | 4 | 20 | 1:0,25 |
| Total | 470 | 202 | 672 | 1:0,43 |

Table 36 (continued)

| | | | | |
|---|---|---|---|---|
| $\bar{x}$ | 18,8 | 8,08 | 26,88 | 1:0,43 |
| 1975 | 156,0 | 58,0 | | 1:0,37 |
| 1976 | 217,0 | 100,0 | | 1:0,46 |
| 1977 | 97,0 | 44,0 | | 1:0,45 |

It is interesting to note the continual preponderance of males throughout the duration of the study with few exceptions. However, a more detailed breakdown after the reproductive season, i.e. from January of the following year at the age of 12 months of the current generation revealed that there is a reversal of this trend and adult females are more frequently captured than males (Table 37). Statistically it is not significant, based on the data, but there is a trend.

Table 37. Differential mortality among male and female *Mabuya varia* in the *Burkea africana* - *Eragrostis pallens* savanna over the period when the lizards are in their second year of life.

| Month | Males captured | Females captured | Total | % Male:Female |
|---|---|---|---|---|
| J | 10 | 6 | 16 | 62,50:37,50 |
| F | 12 | 19 | 31 | 38,71:61,29 |
| M | 6 | 11 | 17 | 35,29:64,71 |
| A | 1 | 5 | 6 | 16,67:83,33 |
| M | 0 | 2 | 2 | 0:100,00 |
| J | 0 | 0 | 0 | 0:0 |
| J | 1 | 0 | 1 | 100,00:0 |
| A | 0 | 0 | 0 | 0:0 |
| S | 1 | 1 | 2 | 50,00:50,00 |
| O | 4 | 2 | 6 | 67,00:33,00 |
| N | 3 | 4 | 7 | 42,86:57,14 |
| Total | 38 | 50 | 88 | 43,18:56,82 |

This tendency leads one to the conclusion that the males are dying earlier than females, the former mostly reaching 15 to 16 months of age as opposed to 16 to 17 months in the latter. Although both sexes may survive as long as 23 months, it can be seen that there are a greater percentage of females surviving on average than males.

Panaspis wahlbergi showed a similar reproductive cycle to that of Mabuya varia although being a much smaller lizard. They exhibit a marked chromatic sexual dimorphism with the males attaining a pinkish-orange ventrum from tip of chin to tip of tail, in the breeding season. During the remainder of the year, this colour fades or is not present at all but as the summer approaches, the ventrum gradually changes its hue until September when they are in full bloom. Although not always consistant, the males tend to have a broken dark-brown vertebral line extending from the nape to the base of the tail. Females tend to be uniform brown above. Table 38 shows the sex ratio of the snake-eyed skink over the period of one year.

Table 38. Sex ratios of Panaspis wahlbergi in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977.

| Month | Male | Female | Total | Ratio |
|---|---|---|---|---|
| May | 0 | 9 | 9 | 0:9,00 |
| June | 1 | 0 | 1 | 1:0,00 |
| July | 5 | 9 | 14 | 1:1,30 |
| August | 1 | 4 | 5 | 1:4,00 |
| September | 32 | 21 | 53 | 1:0,66 |
| October | 14 | 5 | 19 | 1:0,36 |
| November | 28 | 17 | 45 | 1:0,61 |
| December | 18 | 9 | 27 | 1:0,50 |
| January | 5 | 4 | 9 | 1:0,80 |
| February | 3 | 6 | 9 | 1:2,00 |
| March | 0 | 7 | 7 | 0:7,00 |
| April | 3 | 10 | 13 | 1:3,33 |
| Total | 110 | 201 | 311 | 1:1,83 |
| $\bar{x}$ | 9,2 | 16,75 | 25,92 | |

From a sample of 75 skinks trapped during 1977, there were 1,42 females per male. It is, unfortunately, difficult to sex these lizards at hatchling size, so it is not possible to determine their ratio at birth. Mating takes place during early summer, i.e. from August to October. Table 39 shows the distribution of gravid females during the year. This means that ova deposition is distinctly seasonal with a pronounced peak during November, indicating a certain degree of synchronization.

Table 39. Seasonal variation in the rate of gravidity of *Panaspis wahlbergi* at Nylsvley : May 1975 - December 1977.

| | Jan. | Feb. | Mar. | Apr. | May | June |
|---|---|---|---|---|---|---|
| ♀ gravid | 1 | 0 | 0 | 0 | 0 | 0 |
| ♀ adults (non-gravid) | 5 | 3 | 1 | 3 | 1 | 0 |
| % gravidity | 16,67 | 0 | 0 | 0 | 0 | 0 |

| | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|
| ♀ gravid | 0 | 0 | 0 | 2 | 13 | 7 |
| ♀ adults (non-gravid) | 5 | 3 | 20 | 15 | 25 | 17 |
| % gravidity | 0 | 0 | 0 | 11,76 | 34,21 | 29,17 |

This is in contrast to *Panaspis nimbaensis*, which on the Ivory Coast at Lamto breeds throughout the year with the exception of two months, November and December, i.e. mid-winter, Barbault (1974a). This again illustrates what effect seasonality of climate has on reptile populations. The females normally lay 3-6 eggs (7,0 x 4,4 mm) with a mean of 4,43 (n = 7). This is in effect double that of *P. nimbaensis* ($\bar{x}$ = 2,51), Barbault (*loc. cit.*) and illustrates the strategy of a seasonal lizard, because *P. nimbaensis* with its small clutch of eggs produces a mean of 5,0 clutches per year, whereas *P. wahlbergi* probably produces one and at the very most two clutches per season which is, therefore, from approximately half to almost equal that of the tropical lizard. Barbault (1974) recorded a mean incubation period of 41,8 days (range 36-50) which appears to be similar to that recorded at Nylsvley for *P. wahlbergi*. Hatchlings were only recorded during January, February and March (Figure 65), whereas gravid females with oviducal eggs were recorded during the preceding three months. However, this may vary from year to year as hatchlings and gravid females were found in January 1977. The hatchlings vary from 15,0 to 16,0 mm ($\bar{x}$ = 15,33 mm, n = 7) from snout to vent, with a mass of 0,1 g.

The distribution of the various size classes over the period is illustrated in Figure 65. It is again apparent that the species is short-lived. Very few individuals reach a ripe old age and size as can be seen from the gap between the larger size classes during January and November/December. Obviously most individuals die off or suffer predation.

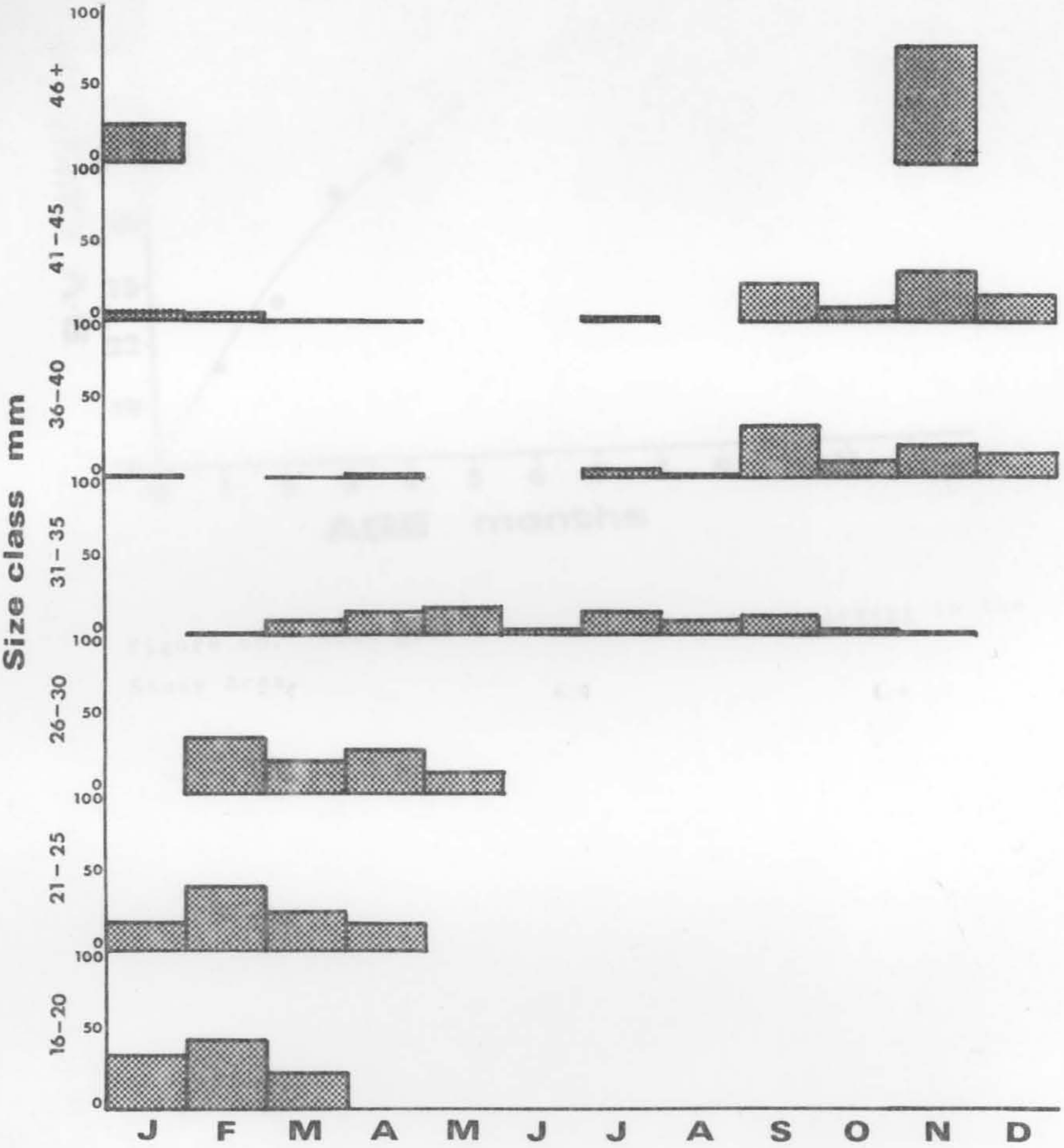


Figure 65. Monthly distribution of size classes of *Panaspis wahlbergi* in the Study Area.

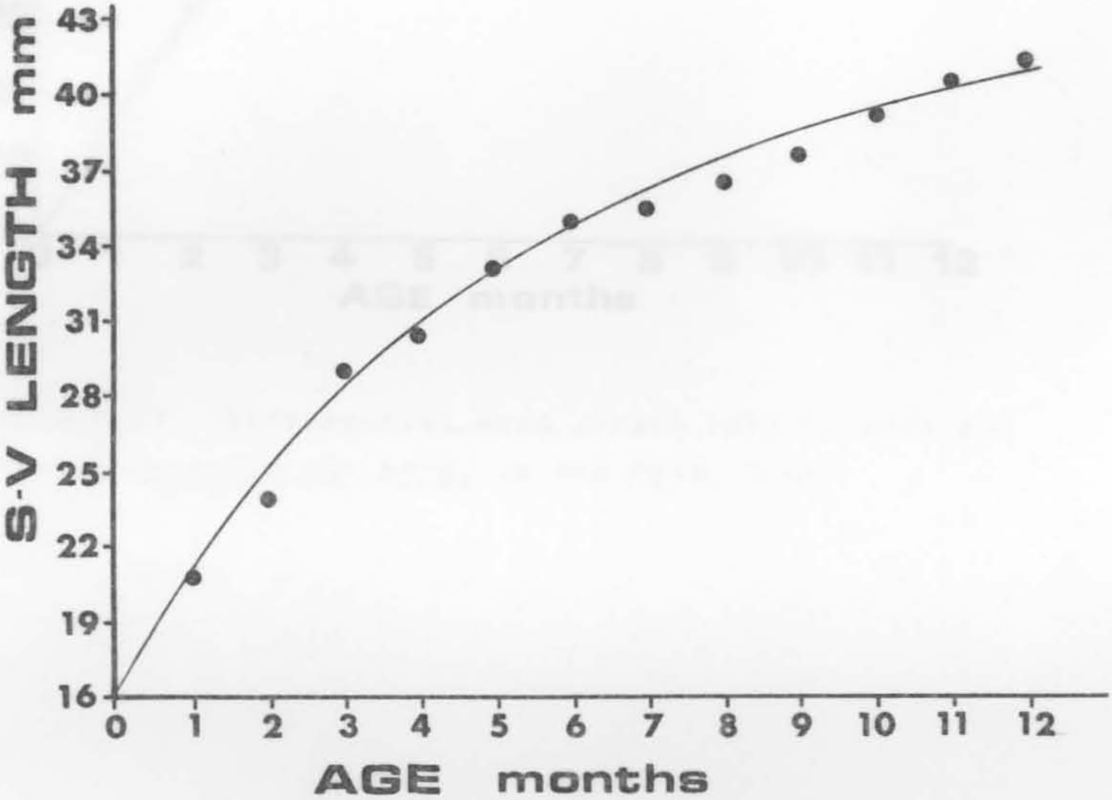


Figure 66. Mean growth rate of _Panaspis wahlbergi_ in the Study Area.

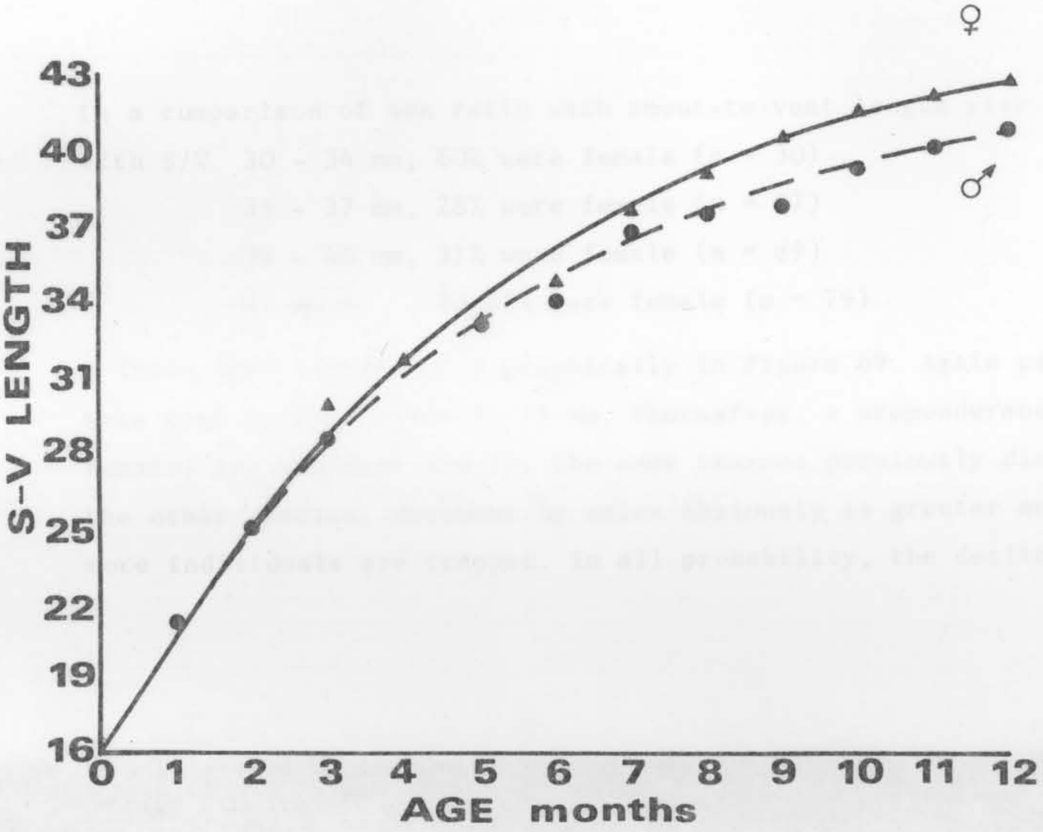


Figure 67. Differential mean growth rate of male and female Panaspis wahlbergi in the Study Area.

Growth is relatively rapid for the initial three months, but thereafter gradually slows down but never stops (Figure 66). A differential growth rate is also apparent with females reaching a greater size than males (Figure 67). Sexual maturity is achieved in eight months with a snout-to-vent length of 37 mm onwards. Figure 68 exhibits the range in size of gravid females. A slightly skewed poisson distribution is apparent - possibly on account of the relatively small sample. However, S/V length of between 41-43,0 mm are the most frequent with a peak at 42,0 mm. This would indicate a female between 8 - 11 months

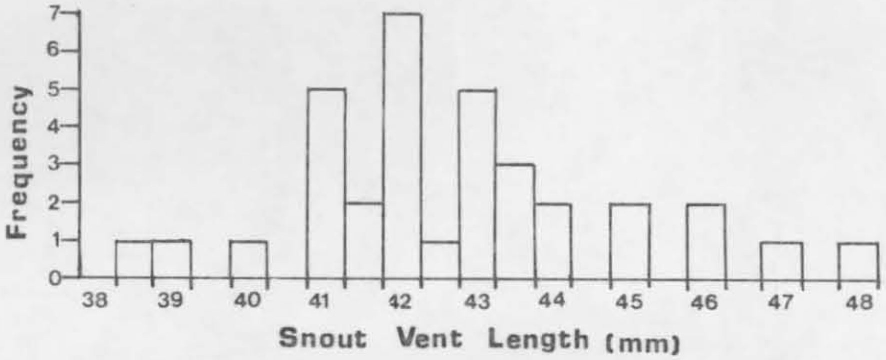


Figure 68. Size class frequency distribution of gravid _Panaspis wahlbergi_ in the Study Area.

In a comparison of sex ratio with snout-to-vent length size classes, those with S/V 30 - 34 mm, 60% were female (n = 30)
35 - 37 mm, 28% were female (n = 57)
38 - 40 mm, 31% were female (n = 89)
41 mm + 73,42% were female (n = 79)

These data are depicted graphically in Figure 69. Again parity is evident, this time in size class 31-35 mm. Thereafter, a preponderance of males and females are manifest and for the same reasons previously discussed under the other species. Movement by males obviously is greater and therefore more individuals are trapped. In all probability, the decline in the next size class, apart from being smaller animals, also indicate greater predation on males, as will be discussed later.

Figure 69. Frequency distribution of size classes and sex of Panaspis wahlbergi in the Study Area.

These data support Figure 67 but also show how variable the sex ratio can be. The largest lizards were females attaining a maximum length of 47,0 mm S/V whereas the largest male had a recorded length of 43,0 mm S/V. There also appears to be a differential mortality with adult females being found into April. This is, however, exceptional and most die by the end of April of the year following birth, at the age of 13 to 15 months. The males have a potential life span of 10 to 12 months. This is very similar to that of P.nimbaensis where the males reach on average 9,8 months and the females 13,1 months. From the size groups, four and possibly five categories can be recognised as follows:

Neonates, including hatchlings and juveniles up to the age of one month, therefore < 22 mm ;

Juveniles (23-28 mm) which are arbitrarily separated from subadults (29-36 mm); and

The adults which are arbitrarily separated into two groups.

Adult I (37-41 mm) mostly male and the smaller females, most of which do not appear to live beyond December of the year of hatching or the age of 11 months.

Adult II (42 +), mostly females which may live on for another two to four months.

Figure 70 shows the seasonal distribution of these categories during twelve months. The distinct brief breeding season is a feature of the lizard. Growth is rapid and mortality is probably high.

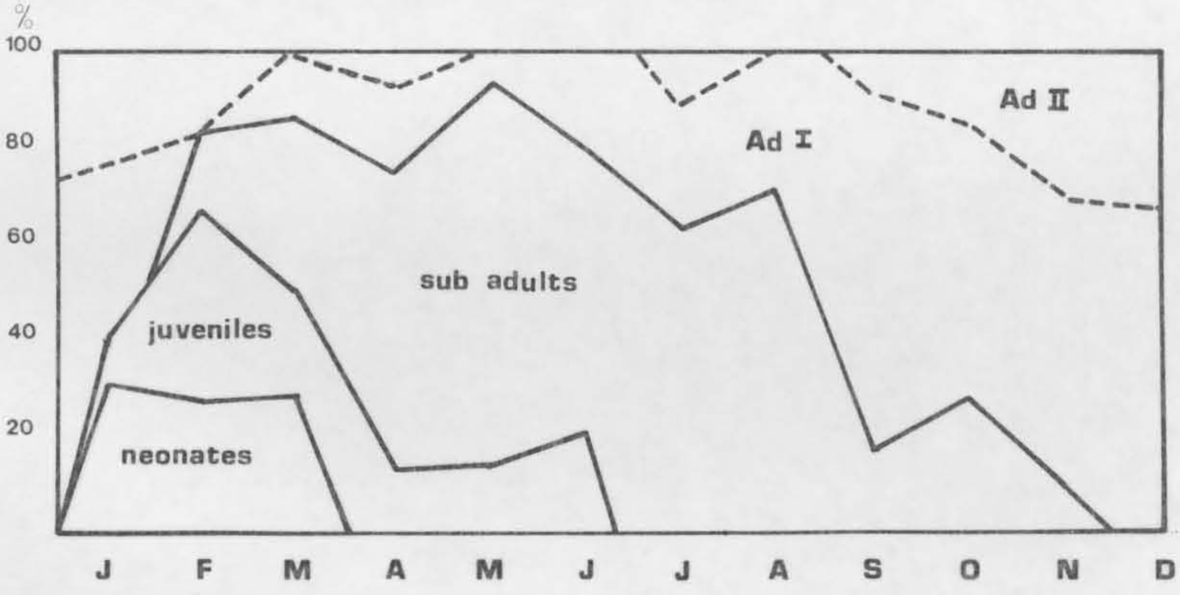


Figure 70. Relationship of five arbitrary age classes of <u>Panaspis wahlbergi</u> in the <u>Burkea africana</u> - <u>Eragrostis pallens</u> Study Area, May 1975 - May 1977.

Taking into account that not all regenerating tails are due to predation, it is nevertheless interesting to note the occurrence of this phenomenon during the year. Table 40 shows this distribution as follows:

Table 40. Seasonal variation in regenerating tails from captured lizards (May 1975 to May 1977).

| | Males | | Indeterminate | | Females | | |
|---|---|---|---|---|---|---|---|
| Month | Reg. | Nor. | Reg. | Nor. | Reg. | Nor. | % |
| January | 2 | 4 | 0 | 2 | 3 | 2 | 38,46 |
| February | 1 | 2 | 0 | 9 | 3 | 3 | 22,20 |
| March | 0 | 0 | 1 | 7 | 1 | 5 | 14,29 |
| April | 0 | 3 | 0 | 5 | 4 | 5 | 23,53 |
| May | 0 | 0 | 0 | 5 | 1 | 8 | 7,14 |
| June | 0 | 1 | 1 | 1 | 1 | 1 | 40,00 |
| July | 2 | 3 | 0 | 1 | 4 | 8 | 33,33 |
| August | 1 | 4 | 1 | 2 | 2 | 6 | 25,00 |
| September | 11 | 27 | 0 | 0 | 9 | 15 | 32,26 |
| October | 11 | 15 | 0 | 0 | 9 | 6 | 48,78 |
| November | 10 | 21 | 0 | 0 | 14 | 11 | 42,86 |
| December | 10 | 13 | 0 | 0 | 10 | 8 | 48,78 |

It can clearly be seen that there is a distinct increase towards the end of the year. This cannot only be ascribed to an increase in abundance and movements of the lizards but, possibly because the animals are larger they are more easily seen. Although the samples are relatively small, the relative percentage of regenerating tails in males and females also show an apparent disproportionate slant towards females (Table 41).

Table 41. Monthly variation in regenerating tails between male and female *Panaspis wahlbergi* on the Nylsvley Nature Reserve : May 1975 to May 1977.

| Month | Males | Females |
|---|---|---|
| January | 33,00% | 60,00% |
| February | 33,33% | 50,00% |
| March | 0 | 16,67% |
| April | 0 | 44,44% |
| May | 0 | 11,11% |
| June | 0 | 50,00% |
| July | 40,00% | 33,33% |
| August | 20,00% | 25,00% |
| September | 28,95% | 37,50% |

Table 41 (Continued)

| Month | Males | Females |
|---|---|---|
| October | 42,31% | 60,00% |
| November | 32,26% | 56,00% |
| December | 43,48% | 55,56% |

This slant is especially so towards the larger sized skinks and may hinge on their being more visible to predators, at this time of the year. No instances of intraspecific agonistic behaviour was seen during the study. Therefore, a relatively high predation pressure is being exerted on the population. Barbault (1974a) postulates that the population of Panaspis nimbaensis are controlled by two factors, namely drought (direct effect) and predation (delayed effect), the rate of mortality of different age classes evidence a considerable downward trend in the total fecundity of the population, with the recruitement of new adults and the average fecundity of females also decreasing.

Lygodactylus capensis (Cape dwarf gecko) is the most abundant lizard in the savanna ecosystem at Nylsvley. They are typical geckos and oviparous, laying two hard-shelled eggs at a time. These are originally soft-shelled but upon contact with the air, the shell hardens to its brittle consistancy. The eggs are normally joined at one end and, therefore, appear to be laid in pairs, altough there is only a single egg per oviduct. Occasionally single eggs may be laid. Egg size varies from 6,5-7,5 x 5,6-6,0 mm (n = 20). Mating appears to take place throughout the year. Observations were recorded in May, September and October. Mating was observed on one occasion when the male was seen lying on top of the female with fore-limbs clasping the female midway between the fore and hindlimbs. One of his hind-legs straddles the female near the cloaca and behind her hind-legs. The other hind-foot was supporting them on one side. The female's legs were spread out. No neck bite was observed. The male's tail was twisted under that of the female and the cloacas were in contact. Observed copulation lasted for a minimum of 16 min. but the animals had already begun prior to my arrival. On separating, both appeared to drag their cloacas and the male moved off with an arched tail while the cloacas are dragged on the branch, much the same as they do when they defecate. With the exception of January, February and March, the eggs are laid throughout the year (Figure 71) and there are two distinct periods, namely a long period from April to August and again from November to December. Although there are no data corresponding to the month of October at Nylsvley, it is evident from subsequent data that gravid females may also have been found during this month. However, the months of September and October show a low rate of egg-laying, which may be overemphasized at Nylsvley.

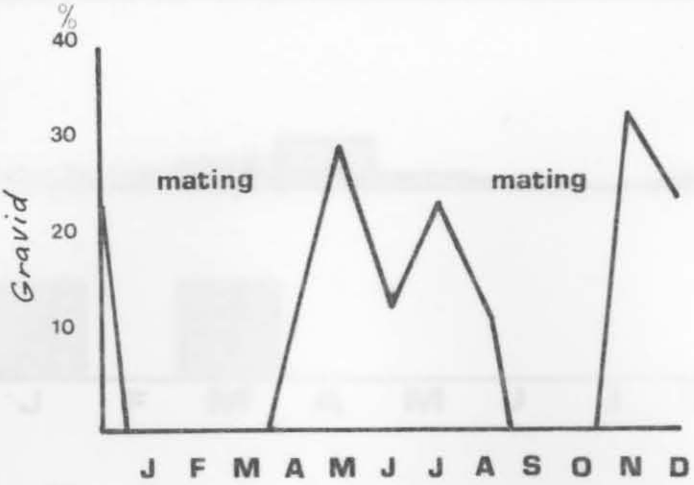


Figure 71. Distribution of breeding seasons of Lygodactylus capensis in the Study Area.

The eggs take two months to incubate and although most young hatch during January to March (Figure 72), it is apparent that hatchlings should also be found during mid-winter. It is not clear why this discrepancy occurred. There is a very even age distribution throughout the population (Figure 72)which indicates therefore that these animals live in excess of one season and possibly even two. The hatchlings or neonates only measure between 13,0 mm and 15,0 mm at birth with a mass of 0,09-0,10 g, but growth is relatively rapid and the geckos reach sexual maturity within eight months. Growth, however, continues (Figure 73) but after 10 months gradually declines, probably as a result of egg-laying at this time of the year. It is probable that the adults succumb after 15 months, but some enter the following reproductive season (See also Figure 72).

The longest age record of a marked gecko is that of a male captured and marked as a juvenile during June 1975 and was recovered at various intervals, finally totalling 634 days. Measurements range from 23,0 S/V on the initial capture, with a probable age of five months to 35,0 mm during April 1976, 308 days later, achieving a mean growth rate of 0,039 mm/day.

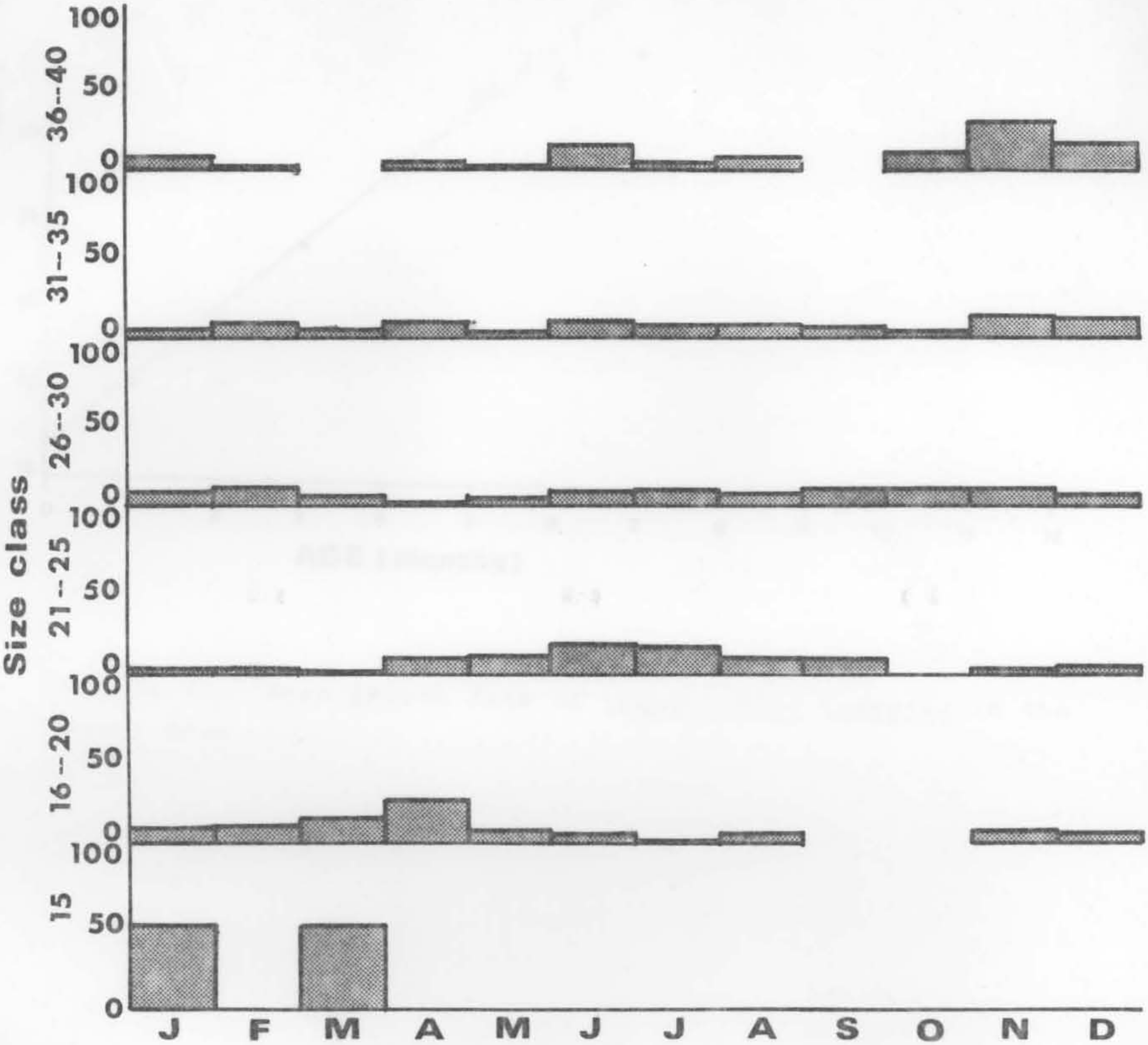


Figure 72. Monthly distribution of size classes of *Lygodactylus capensis* in the Study Area.

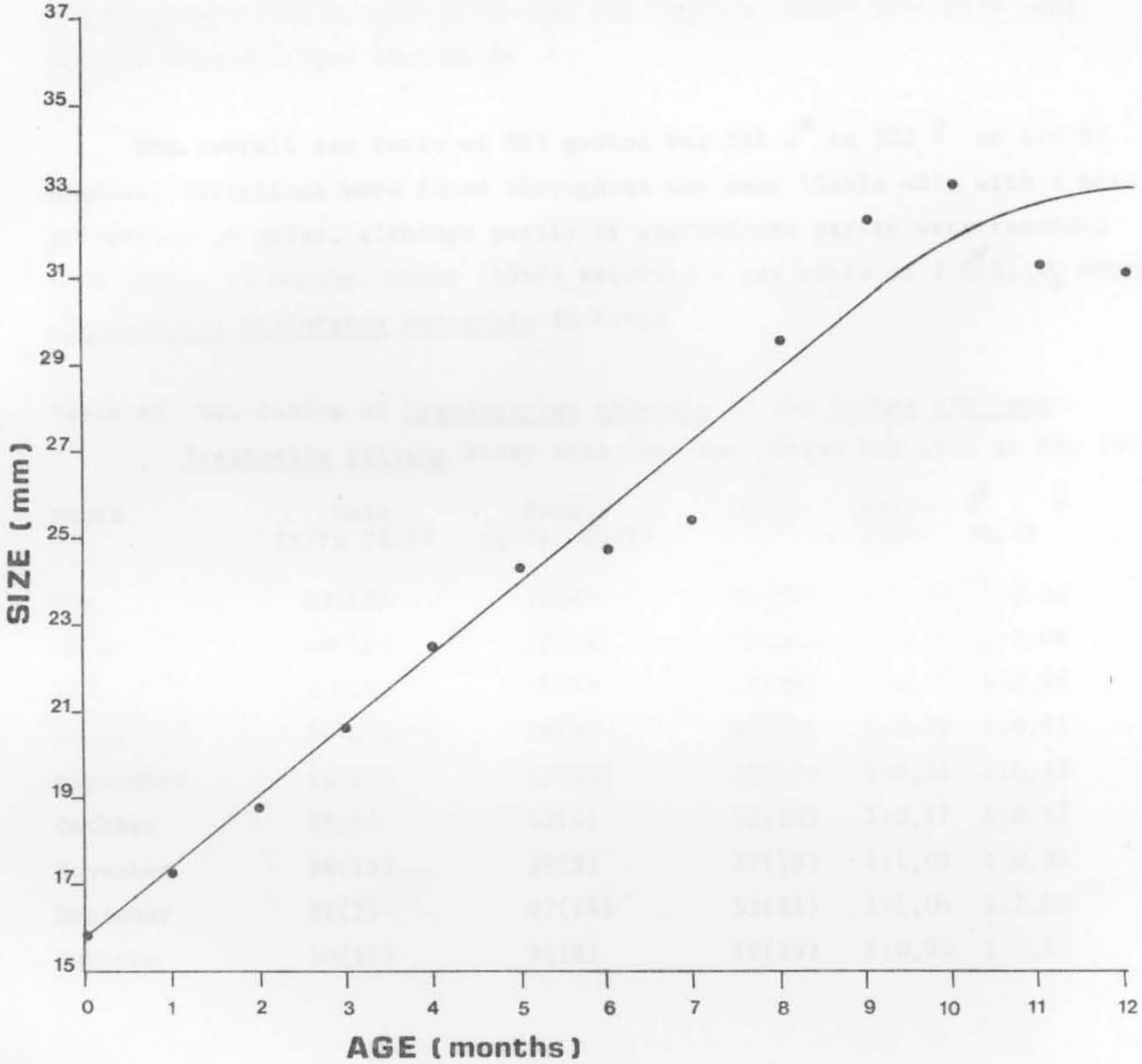


Figure 73. Mean growth rate of *Lygodactylus capensis* in the Study Area.

Thereafter, no further growth was measured over the following 326 days. This lizard was, therefore, 634 days plus approximately 150 days, 784 days old on the date of last capture (Figure 74). Various other geckos were captured over lesser lengths of time, achieving a mean growth rate of 0,047 mm/day (n = 71) with a range of 0,007 mm/day to 0,193 mm/day, depending on the age and size of the lizard (Figure 75). There is an apparent negative linear correlation between growth rate and size. However, two seasons, winter and summer, influence the growth rate. During winter the growth rate is low or ceases altogether, while during summer, growth rate may be exceptionally high even for adult animals. This accounts for the large scattering to be seen on the graph which almost obscures the relationship.

Figure 76 illustrates the distribution of size classes and the typical pattern observed among the other species of lizards is apparent. Parity is approached in the 21-25 mm size class but, thereafter, the males dominate until the largest size class is reached, which indicates that females become larger than males.

The overall sex ratio of 883 geckos was 561 ♂ to 322 ♀ or 1:0,57. However, variations were found throughout the year (Table 42), with a preponderance of males, although parity or approximate parity were recorded in a number of months. Greer (1967) recorded a sex ratio of 1 ♂:2,10♀ among *Lygodactylus picturatus keniensis* in Kenya.

Table 42. Sex ratios of *Lygodactylus capensis* in the *Burkea africana* - *Eragrostis pallens* Study Area over the period May 1975 to May 1976

| Month | Male | Female | Total | Ratio ♂ : ♀ | |
|---|---|---|---|---|---|
| | 75/76 76/77 | 75/76 &6/77 | | 75/76 | 76/77 |
| May | 19(16) | 14(8) | 33(24) | 1:0,74 | 1:0,50 |
| June | 40(15) | 15(16) | 55)31) | 1:0,37 | 1:1,06 |
| July | 31(16) | 24(9) | 55(25) | 1:0,77 | 1:0,56 |
| August | 25(11) | 18(9) | 43(20) | 1:0,72 | 1:0,82 |
| September | 23(19) | 12(10) | 35(29) | 1:0,52 | 1:0,52 |
| October | 21(6) | 12(4) | 33(10) | 1:0,57 | 1:0,67 |
| November | 38(13) | 39(5) | 77(18) | 1:1,03 | 1:0,38 |
| December | 26(7) | 27(14) | 53(21) | 1:1,04 | 1:2,00 |
| January | 10(11) | 9(18) | 19(29) | 1:0,90 | 1:1,63 |

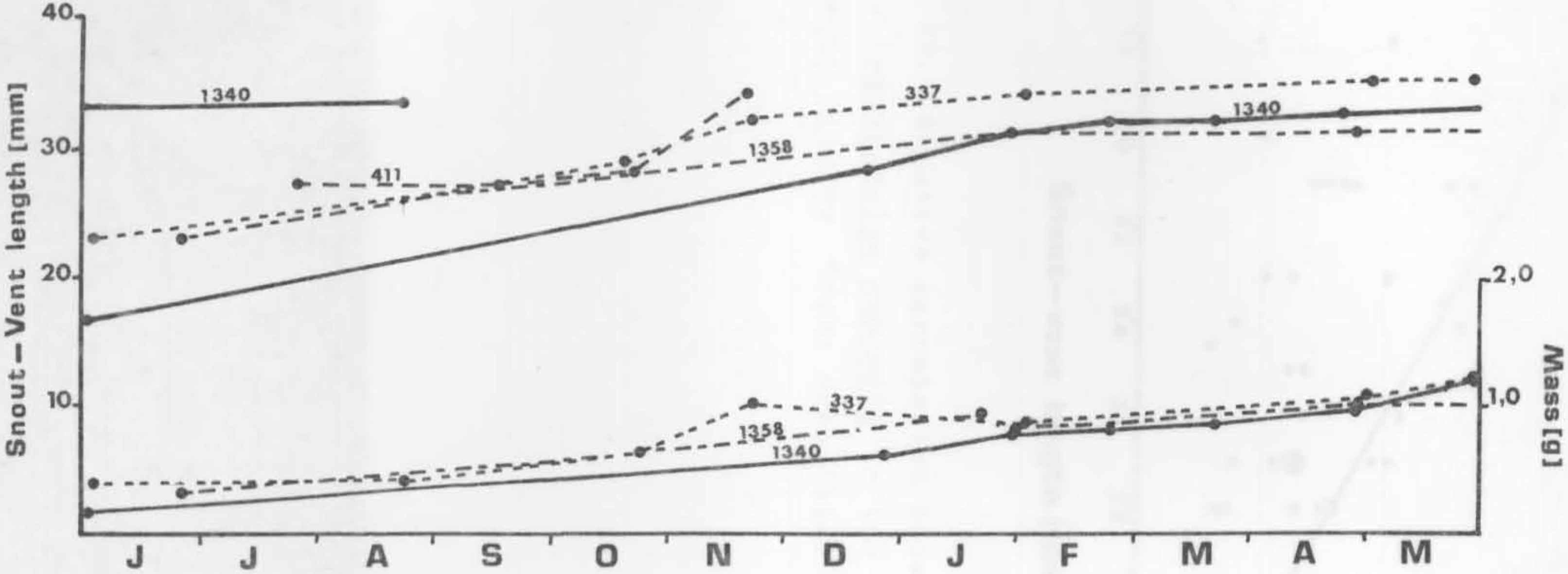


Figure 74. Growth exhibited by individual recaptured *Lygodactylus capensis* in the Study Area.

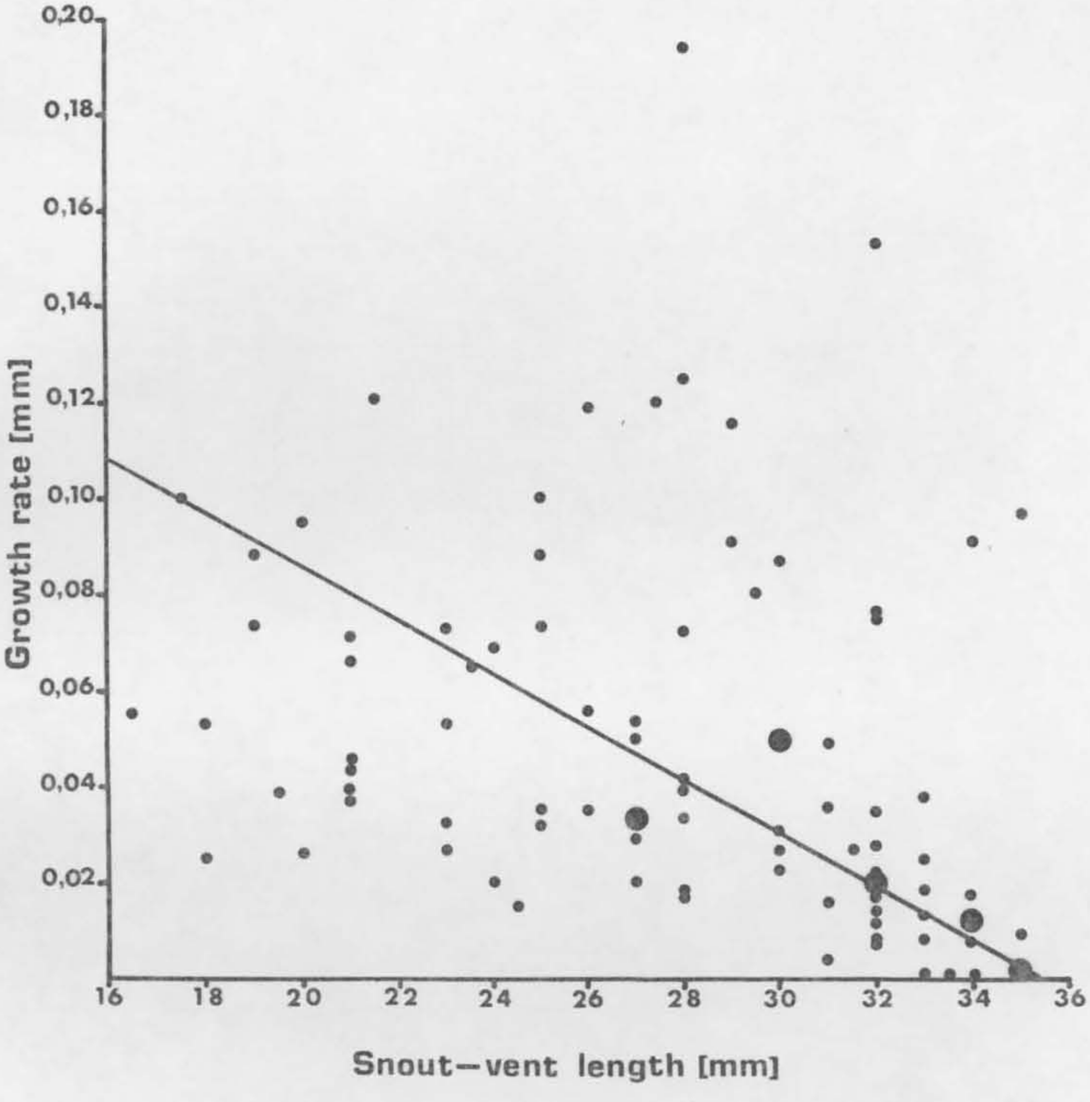


Figure 75. Negative correlation between growth rate and size of Lygodactylus capensis in the Burkea africana - Eragrostis pallens Study Area (Line drawn by eye).

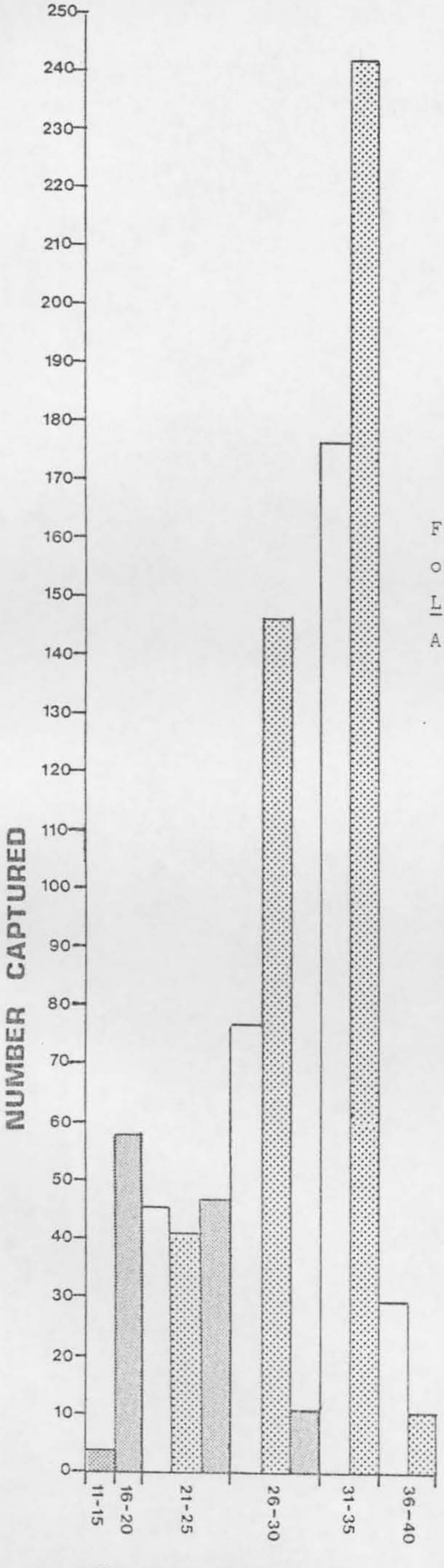


Figure 76. Frequency distribution of size classes and sex of _Lygodactylus capensis_ in the Study Area.

Table 42 continued.

| Month | Males 75/76 76/77 | Females 75/76 76/77 | Total | Ratio ♂ : ♀ 75/76 | 76/77 |
|---|---|---|---|---|---|
| February | 32(18) | 13(5) | 45(23) | 1:0,41 | 1:0,28 |
| March | 14(17) | 6(9) | 20(26) | 1:0,43 | 1:0,53 |
| April | 18(15) | 12(14) | 30(29) | 1:0,67 | 1:0,93 |
| Total | 397(164) | 201(121) | 598(285) | 1:0,51 | 1:0,74 |
| $\bar{x}$ | 33,1(13,7) | 16,75(10,1) | 49,85 | 1:0,68 | 1:0,51 |

Sexual dimorphism in this species, is restricted to the adults, whereby the males have a row of precloacal pores anterior to the vent. This, however, only appears when the animal is about six months of age with a S/V length of 27,0 mm. It is assumed that this coincides with the achievement of sexual maturity. Greer (loc.cit)states that this is also the case with the similar sized Lygodactylus picturatus keniensis where preanal pores appear in males at a snout/vent length of 26-27 mm. The smallest female with developing ova, found during this study was 28,0 mm S/V which is similar to that established by Greer (loc.cit.) Size and, therefore, age is important in determining fecundity. In a sample of 54 gravid females, plotted against S/V length, it is apparent that females with a S/V length of 33,0 mm have the highest frequency (Figure 77) and the total distribution exhibits a poisson distribution. Fecundity increases rapidly with age and decreases more abruptly.

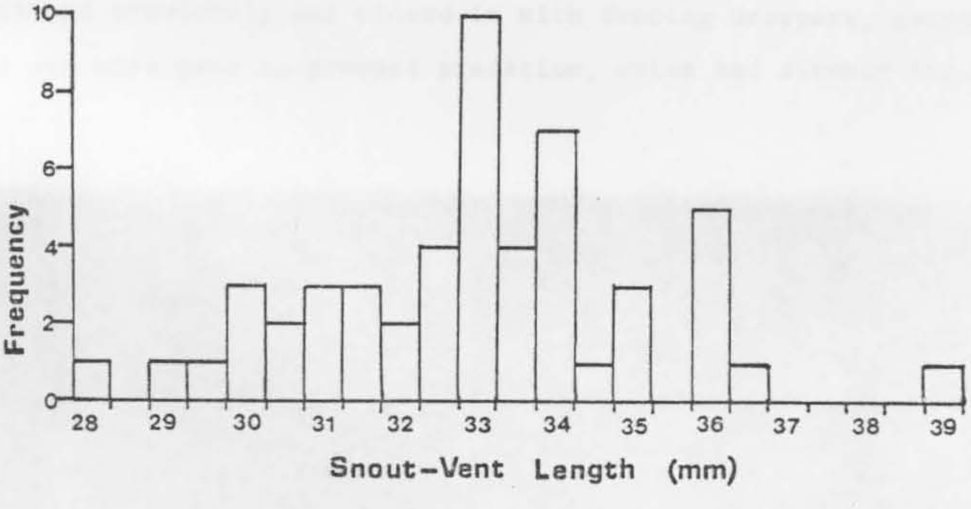


Figure 77. Size class frequency distribution of gravid Lygodactylus capensis in the Study Area.

The eggs are normally laid under loose bark on the bole or branches of the tree or stumps and also in any sheltering declevity especially those of woodborer beetles. Usually a single pair is found but if the site is particularly favourable, then up to seven pairs may be found together as well as the broken remains of older layings. Whether this is the work of a single female or that of more than one is not known, but it is presumed to be the latter.

Few data were obtained about the remaining species except that juveniles were captured during mid-summer, that is January,February and March. These include Pachydactylus bibronii, Agama atricollis, Chamaeleo dilepis and Gerrhosaurus flavigularis. An exception to this is the veld monitor (Varanus exanthematicus albigularis). The veld monitor was observed copulating during August and September. All observed instances of egg-laying (n = 5) during 1976 took place during November, while a nest which had been opened up by mongooses and contained dry egg shells was found early in December, also indicating a laying during November. Signs of digging and one animal actually involved were observed during September 1977, indicating an earlier season contrary to other species such as Ichnotropis which starts late. All nesting attempts were along the roads bordering on and in the Ecosystem Study Area. It appears that road construction creates conditions suitable for nesting sites. One female, however, was seen to dig at five different sites before selecting a sixth which proved suitable. Digging followed the pattern previously described for Ichnotropis capensis, after which she reversed back into the hole and deposited her eggs. The hole was 90-100 cm and approximately 30 cm below the surface. Egg-laying in this instance took a minimum of 100 min. and may take as long as 120 min. A total of twelve eggs was laid after which the female emerged, raked some soil back into the hole and then entered and tamped the soil down with her snout. This pattern predominated throughout the covering period which took 34 min. after which she moved off and investigated one of her previously dug holes, which she then also began closing but abandoned it and wandered away.

Cowles (1930) in a study of the Nile monitor (Varanus niloticus) observed an incubation period of 10 months, but in captivity eggs took three months to hatch (H. Erasmus pers. comm.). The nest of the veld monitor mentioned previously was closed in with fencing droppers, galvanised sheet iron and wire mesh to prevent predation, which had already begun one day after laying. The nest had been opened by mongooses, probably banded mongoose (*Mungos mungo*) and two eggs removed. However, I closed the nest again and left it as natural as possible for a period of 12 months after which on not finding any juveniles, the nest was opened up and the eggs opened. In some of the eggs only bones remained but others still had the decomposing remains of fully developed neonates. This indicates that the incubation period could be ten months. In addition, very small juveniles approximating hatchling size were captured during November, which also tends to support the above evidence. It is probable that under artificial conditions, hatching may take place very much sooner, as temperature and humidity do not fluctuate to the extent of that in the wild, where the eggs probably develop marginally during the winter months, if at all.

## Amphibians

It was already mentioned that large numbers of amphibians were resident in the *Burkea africana* - *Eragrostis pallens* savanna in the Study Area. They are completely seasonal in activity, being ultimately totally dependent on rainfall for activity, including reproduction. It was mentioned previously that there are eleven species resident in the Study Area but only three species are common. The most abundant is *Bufo garmani* or northern mottled toad. Although by virtue of its glandular skin it is able to move about on the soil surface before any of the other amphibian species, it is dependent on surface water for egg-laying and development.

As is the case with the lizards, *Bufo garmani* hibernates, but over an extended period from May to September. Once the toads emerge they forage for food but as soon as substantial rain has fallen, they move off down to the turf vlei. This appears to take place during October/November, but is variable as it depends on adequate rainfall to form pools in which breeding is possible. Mating occurs in situ as the males call to attract females and during amplexus the eggs are deposited in the water. While it is possible to sex the adults externally, this was not possible for the small immatures and juveniles. Sex ratios, therefore, only pertain to the adults. Sexual dimorphism is found with the male having a dark gular region as opposed to the marbled white of the female, while he also has pads on his thumbs with which he retains a hold on the female during aplexus. The mean sex ratio of adult toads over the months September to January, for the two years 1975/76 and 76/77 is 1♂ : 1,44 ♀ n = 320, although there is variation from month to month (Table 43). This variation is directly attributable to movement of these amphibians into and out of the Study Area.

Table 43. Sex ratios of *Bufo garmani* over the period May 1975 to May 1977 in the *Burkea africana* - *Eragrostis pallens* Study Area.

| Month | Male | Female | Total | Ratio (♂ : ♀) |
|---|---|---|---|---|
| May | 0 | 1 | 1 | 0:1 |
| September | 7 | 2 | 9 | 1:0,28 |
| October | 22 | 14 | 36 | 1:0,63 |
| November | 3 | 7 | 10 | 1:2,33 |
| December | 1 | 11 | 12 | 1:11,0 |
| January | 2 | 13 | 15 | 1:6,5 |
| February | 3 | 9 | 12 | 1:3,0 |
| March | 4 | 4 | 8 | 1:1,0 |
| April | 0 | 0 | 0 | 0:0 |
| May | 0 | 0 | 0 | 0:0 |
| September | 28 | 18 | 46 | 1:0,64 |
| October | 24 | 14 | 38 | 1:0,58 |
| November | 1 | 4 | 5 | 1:4,0 |
| December | 0 | 20 | 20 | 0:20,0 |
| January | 2 | 28 | 30 | 1:14,0 |
| February | 10 | 10 | 20 | 1:1 |
| March | 0 | 0 | 0 | 0:0 |
| April | 2 | 0 | 2 | 1:0,0 |
| May | 22 | 34 | 56 | 1:1,54 |
| Total | 131 | 189 | 320 | 1:1,44 ($\bar{x}$) |

*Bufo garmani* females lay 12 000 to 20 000 eggs, Taylor (1982), which hatch and metamorphose during November, December and January and the juvenile toads return to the Study Area during January and February (Figure 78). Depending on temperature and rainfall, the eggs hatch within 24 hrs and metamorphosis is completed in 64 days, with the juvenile toads being 9 mm in S/V length and a mass of 13 mgm, Taylor (*loc. cit.*). The toads then move further away from the pond and become increasingly nocturnal but grow at a rapid rate, reaching an average Snout/Vent length of 31 mm and a mass of 165 mgm in 21 days. It is at this stage that the toadlets enter the Study Area. According to Taylor (*loc.cit.*) therefore the toadlets achieve a growth rate of 1,05 mm/day.

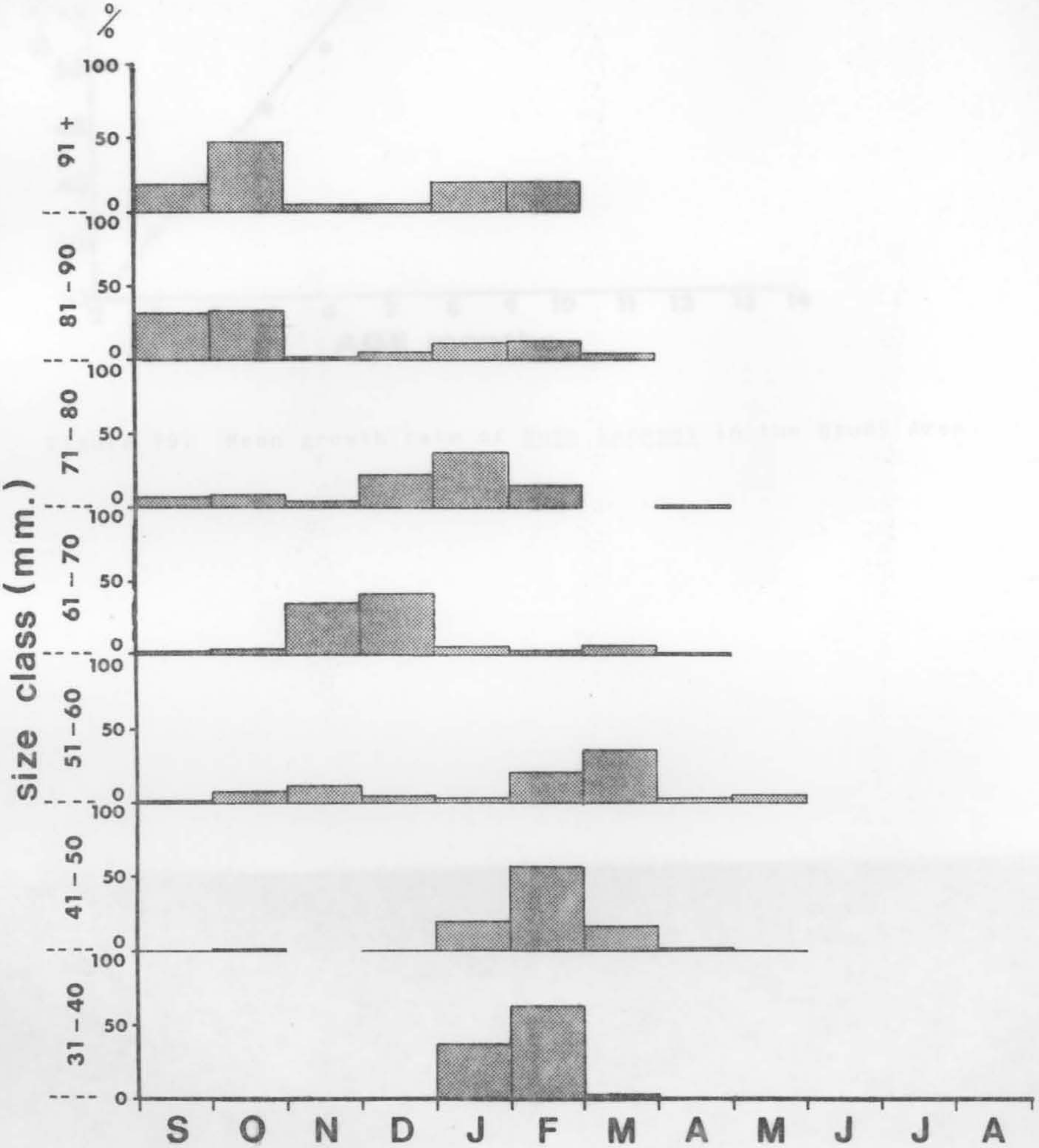


Figure 78. Monthly distribution of size classes of Bufo garmani in the Burkea africana - Eragrostis pallens Study Area.

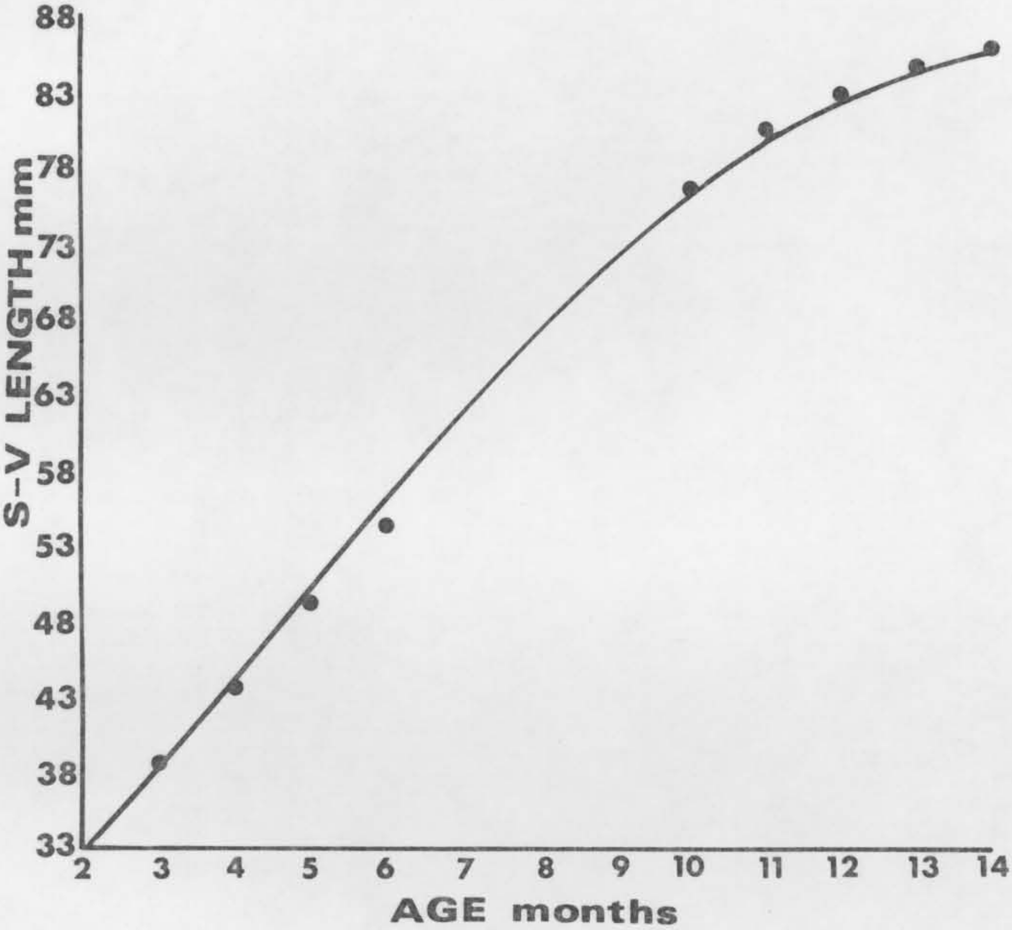


Figure 79. Mean growth rate of Bufo garmani in the Study Area.

Figure 78 shows the distribution of size classes according to the months of the year. Growth is relatively rapid from 33,0 mm snout-to-vent length to 86,0 mm within a period of 12 months (Figure 79) or approximately 0,145 mm/day. Sexual maturity is, therefore, achieved at the age of nine months and in readiness for the breeding season. Figure 80 shows the frequency distribution of size classes. The exclusion of the young animals which were not sexable from the Figure would have produced a more even distribution, although still somewhat skewed to the larger size classes.

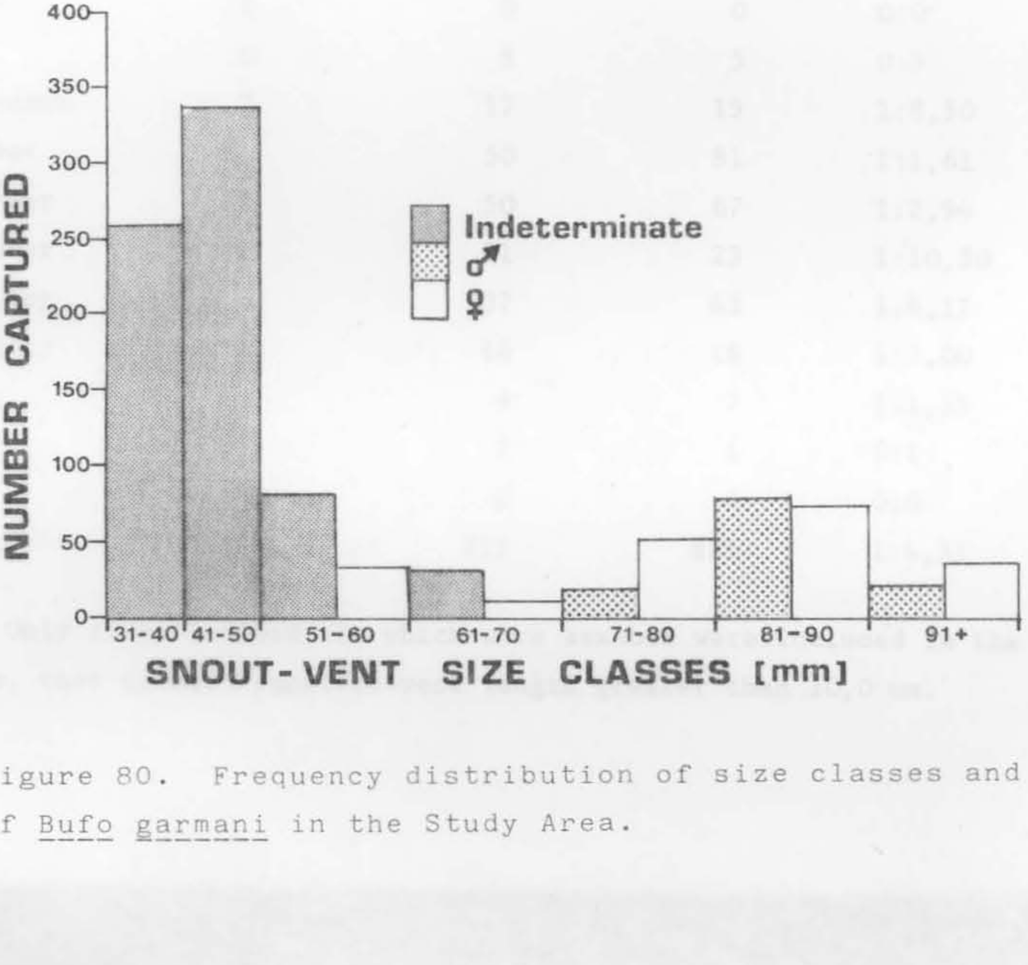


Figure 80. Frequency distribution of size classes and sex of Bufo garmani in the Study Area.

The other very abundant species is Kassina senegalensis or bubbling kassina, which is absolutely dependent on rainfall and surface moisture. Like the toads, they are therefore completely seasonal. Large numbers hibernate in the Burkea africana - Eragrostis pallens savanna. On account of the fact that metamorphosis and juvenile growth is rapid, the frogs actually enter the Study Area as subadults. This may account for the distribution of the smallest size class throughout the active season from September to May. However, these frogs also move down to the turf vlei during periods of heavy rainfall and breed in the shallow pools in the company of the previous species. Breeding probably takes place at the same time as the roads after which they return to the Study Area between November and March.

These amphibians also display a sexual dimorphism when adult. The male has a black gular plate while the female is immaculate. The mean male to female ratio is 1♂ : 4,51 ♀ . As with Bufo garmani, there is tremendous variation from month to month, which is directly correlated to rainfall. If rainfall is abundant then the Kassinas are abundant but if the period is dry then few frogs will venture forth. Table 44 shows the monthly fluctuations.

Table 44. Variations in sex ratio of Kassina senegalensis over the period May 1975 to May 1977 on the Nylsvley Nature Reserve.

| Month | Male | Female | Total | Ratio (♂ : ♀) |
|---|---|---|---|---|
| May | 2 | 4 | 6 | 1:2,00 |
| October | 2 | 19 | 21 | 1:9,50 |
| November | 36 | 111 | 147 | 1:3,08 |
| December | 23 | 120 | 143 | 1:5,21 |
| January | 12 | 97 | 109 | 1:8,08 |
| February | 15 | 104 | 119 | 1:6,93 |
| March | 5 | 63 | 68 | 1:12,60 |
| April | 0 | 0 | 0 | 0:0 |
| May | 0 | 5 | 5 | 0:5 |
| September | 2 | 17 | 19 | 1:8,50 |
| October | 31 | 50 | 81 | 1:1,61 |
| November | 17 | 50 | 67 | 1:2,94 |
| December | 2 | 21 | 23 | 1:10,50 |
| Janurary | 6 | 37 | 43 | 1:6,17 |
| February | 2 | 14 | 16 | 1:7,00 |
| March | 3 | 4 | 7 | 1:1,33 |
| April | 0 | 1 | 1 | 0:1 |
| May | 0 | 0 | 0 | 0:0 |
| Total | 159 | 717 | 875 | 1:4,51 |

Only those individuals which were sexable were included in the above Table, that is with snout-to-vent length greater than 30,0 mm.

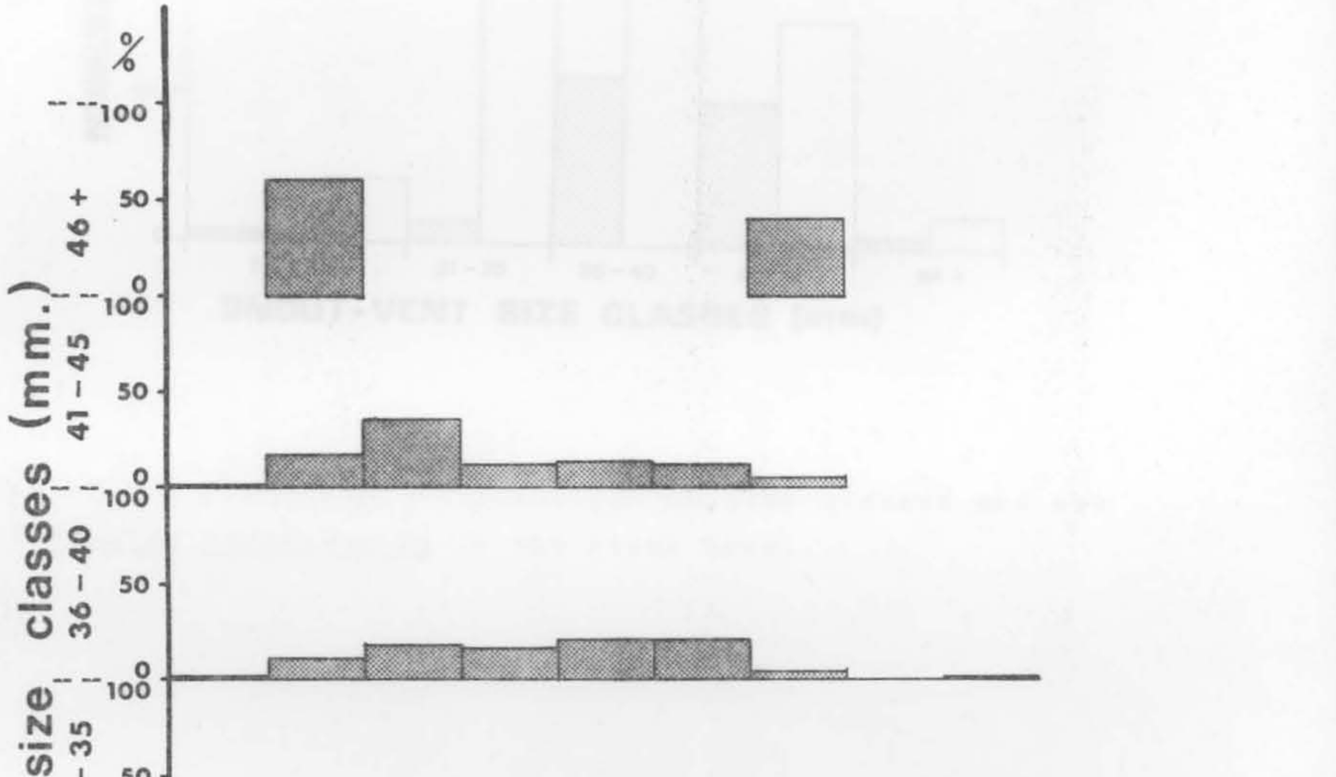


Figure 81. Monthly distribution of size classes of _Kassina senegalensis_ in the Study Area.

It can be seen that there is preponderance of females. Each female can potentially lay 400 eggs. This ensures that adequate numbers survive. According to Carruthers (1982), they breed between October and the end of January. Metamorphosis takes place after 50 to 60 days, which correlates well with the size classes captured in the Study Area over this period (Figure 69). The smallest individual to be captured was 22,0 mm snout-to-vent length, while the largest was a female 53,5 mm in size. Figure 81 shows the distribution of size classes within the population on a yearly basis, while Figure 82 exhibits the frequency of each size class, which approximates a poisson distribution.

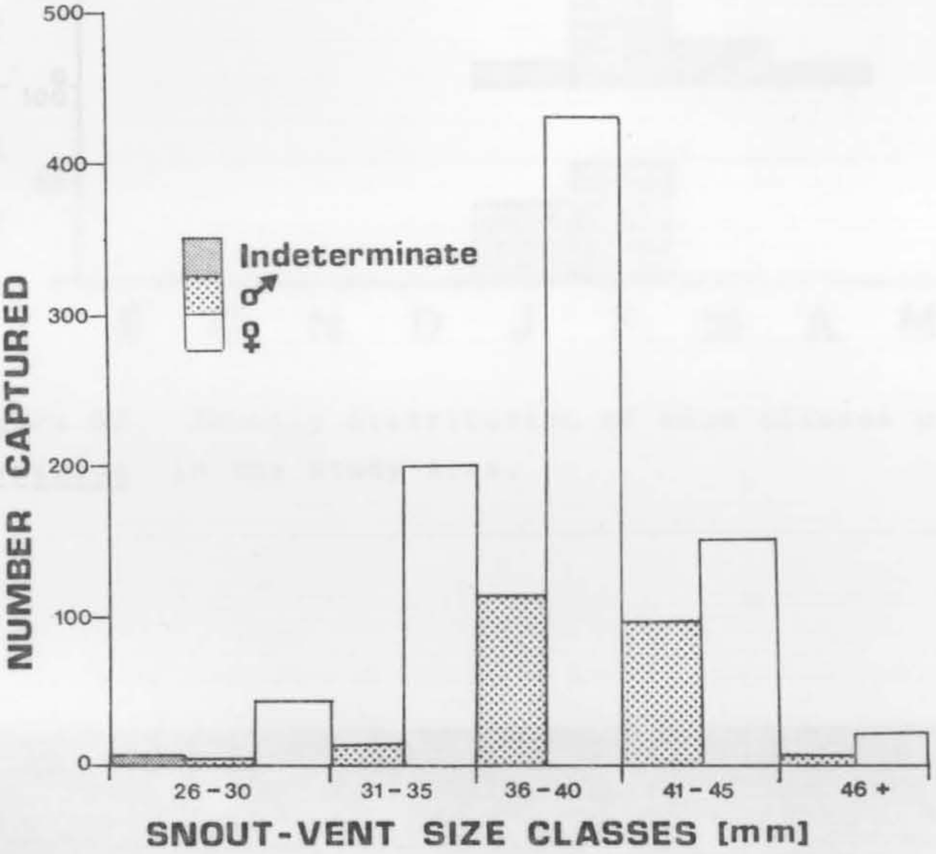


Figure 82. Frequency distribution of size classes and sex of Kassina senegalensis in the Study Area.

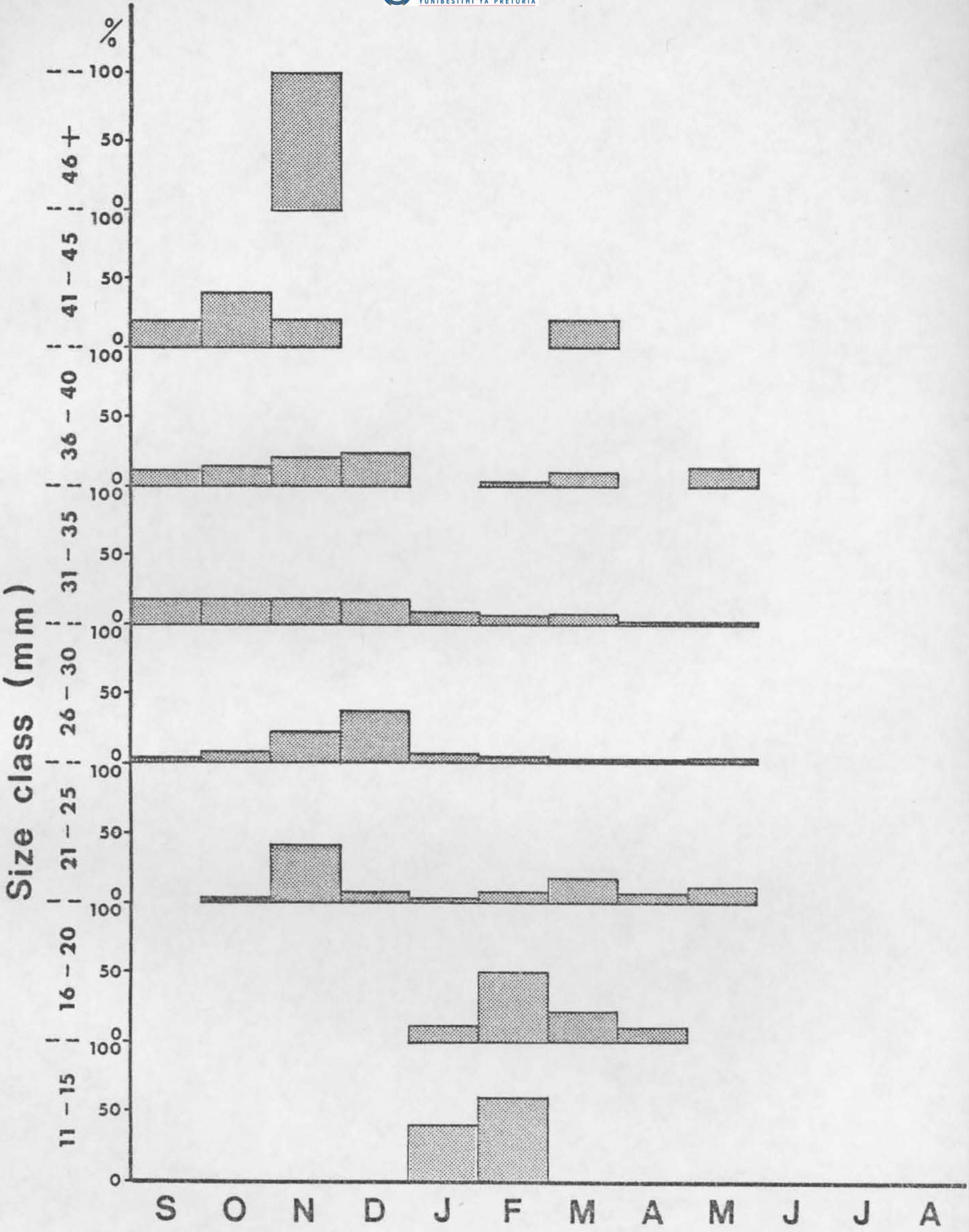


Figure 83. Monthly distribution of size classes of Breviceps adspersus in the Study Area.

The third most abundant amphibian in the Study Area is Breviceps a. adspersus, the common short-headed frog, which is a member of a unique genus of amphibian which are independent of surface water for reproduction. Wager (1960), Poynton & Pritchard (1976), give descriptions of mating, tunnelling and egg-laying. Egg number varies from 17 to 46 and eggs are deposited in the soil in a nest approximately 20,0 to 45,0 cm below the surface, depending on the degree of exposure of the nest. The female may often be found under cover within close proximity of the nest. Poynton & Pritchard (loc. cit.) mentioned that two burrows had double entrances placed 23 cm and 28 cm apart respectively. The average length of each fork was 21 cm and the total lengths of the burrows being 51 and 56 cm respectively. In both cases, a female inhabited one fork and the male the other, both being found about 30 cm below the surface. According to Wager (loc.cit.), incubation and metamorphosis take from six to eight weeks after ova deposition. These hatchlings, approximately 6,0 mm in size, then burrow out and disperse. Figure 83 shows the distribution of size classes over one calendar year. It can be seen that the smallest individuals are found during January and February, which indicates an ova deposition during December/January or at a time when rainfall has moistened the soil to a satisfactory depth to avoid excessive dehydration of the eggs. Figure 84 exhibits the frequency of each size class. A poisson distribution is apparent.

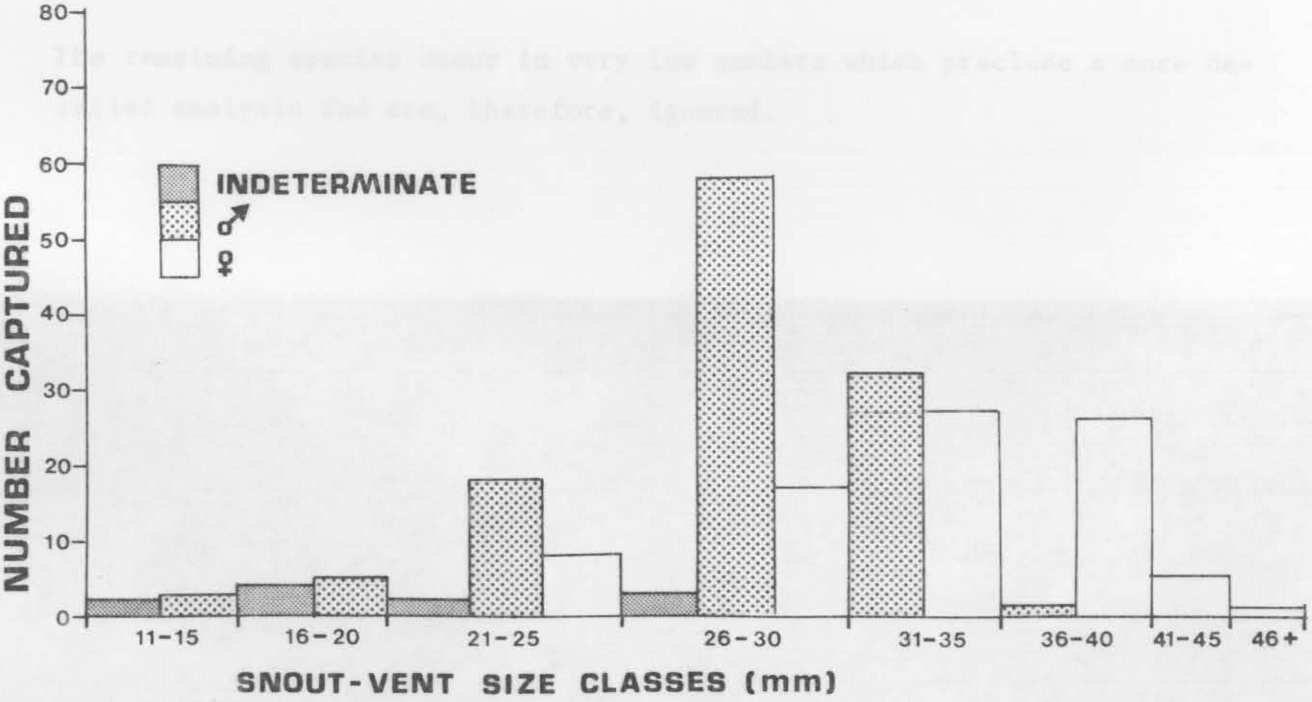


Figure 84. Frequency distribution of size classes and sex of Breviceps adspersus in the Study Area.

During the 1975/76 season, activity only started during October, whereas the 1976/77 season activity started in September. This is dependent on rainfall. During the rainy season the amphibians would be heard calling both during the day as well as during the evening or early morning, provided atmospheric humidity was high. However, it was mostly after thunder showers that they moved about on the surface foraging for termites and ants.

They display a limited chromatic sexual dimorphism consisting of a black throat in males as opposed to gray-black diffuse patterns in females. The latter also tended to be larger than the males. In a random sample of 20 males and 20 females, the males averaged 25,85 mm snout-to-vent length, as opposed to 35,2 mm for the females. This is no doubt important to the reproductive biology of the species as the male is attached during amplexus to the rear of the female by a chemical glandular exudate and the female burrows backwards down into the soil with the male attached to a level where the spherical nest site is hollowed out. Apparently the male also assists in this digging process, Wager (<u>loc</u>. <u>cit</u>.).

The mean sex ratio is 1♂: 0,71 ♀ but varies from month to month (Table 45). On account of the limited sample size (200), it was necessary to lump the data for the same months of different years.

Table 45. Sex ratio of <u>Breviceps</u> <u>a</u>. <u>adspersus</u> over the period May 1975 to May 1977 in the Nylsvley Nature Reserve.

| Month | Male | Female | Total | Ratio |
|---|---|---|---|---|
| May | 8 | 8 | 16 | 1:1,00 |
| September | 9 | 8 | 17 | 1:0,89 |
| October | 10 | 12 | 22 | 1:1,20 |
| November | 31 | 16 | 47 | 1:0,51 |
| December | 32 | 14 | 46 | 1:0,44 |
| January | 6 | 5 | 11 | 1:0,83 |
| February | 9 | 6 | 15 | 1:0,67 |
| March | 9 | 10 | 19 | 1:1,11 |
| April | 3 | 4 | 7 | 1:1,33 |
| Total | 117 | 83 | 200 | 1:0,71 |

The remaining species occur in very low numbers which preclude a more detailed analysis and are, therefore, ignored.

From the aforegoing it would appear that most amphibian species show a sex ratio slanted towards an abundance of females. This may be the result of a reproductive system which relies on the reaction of females to calling males and, therefore, ensures that a calling male will always make contact with a female in reproductive condition. At the same time it also enhances gene pool mixing. However, it does not explain the approach to parity exhibited by both _Bufo garmani_ and _Breviceps a. adspersus_. It may have to do with the possibility that a male may be able to mate with more than one female, particularly if for some reasons it is more sought after than another. Mention has already been made in this respect for _Bufo garmani_ and it probably pertains to the other species as well.

Of all amphibian species, _Breviceps adspersus_ is the only true resident of the _Burkea africana-Eragrostis pallens_ savanna, as it is present throughout the year whereas all the other species must leave in order to breed. Therefore there is always a loss to the _Burkea africana - Eragrostis pallens_ savanna by amphibians moving out of the area to breed.

# CHAPTER 7

# ECOLOGY

## HOME RANGE, MOVEMENT AND BEHAVIOUR

The previous chapters have all dealt with aspects of the life cycles of various reptiles and amphibians on the Nylsvley Nature Reserve. It was possible through observation and mark-recapture sampling to collect data on their home range size, movement and behaviour, during the two-year period of the study. While extensive movement by amphibians has been mentioned in the previous chapter, and is important to ensure breeding, large scale movements of the reptiles, particularly snakes, are not well documented. Movement consists basically of three types involved with food seeking, reproduction and exploration. At certain times of the year one activity may merge into the other, but each type has certain characteristic behaviour. There are only two territorial reptile species at Nylsvley while several species, notably lizards, possess definite home ranges. As the size of home ranges is dependant on frequency of sighting or capture, the data obtained pertains specifically to those species which occur in greater numbers.

### Snakes

Although a large number of snakes was captured during the two-year period, it was only possible to determine home range size for a single species, namely the vine snake (Thelotornis capensis). The vine snake is a unique species, being totally arboreal and exhibits a behaviour unlike that of other reptiles. Vine snakes are diurnal reptiles with acute sight and the widest binocular fields of vision known for any snake,Henderson & Binder (1981). In the Study Area a total of 147 vine snakes was captured over the period May 1975 to December 1977. Of these, 78 have been recaptured or re-sighted on at least one occasion, but some were found on five or more occasions. September 1975 provided the first indication of unusual behaviour. During the trapping period, a total of 18 snakes was found scattered in the south-east corner of the Study Area, mostly (78%) occupying Grewia flavescens shrubs. This aggregation was also seen during 1976 and 1977, where 12 and 15 vine snakes respectively, were found under similar conditions. Several were together copulating and sometimes three were found in the same bush. This predilection for Grewia flavescens shrubs is a marked feature of this snake during spring and early summer (Figure 85 and Table 46).

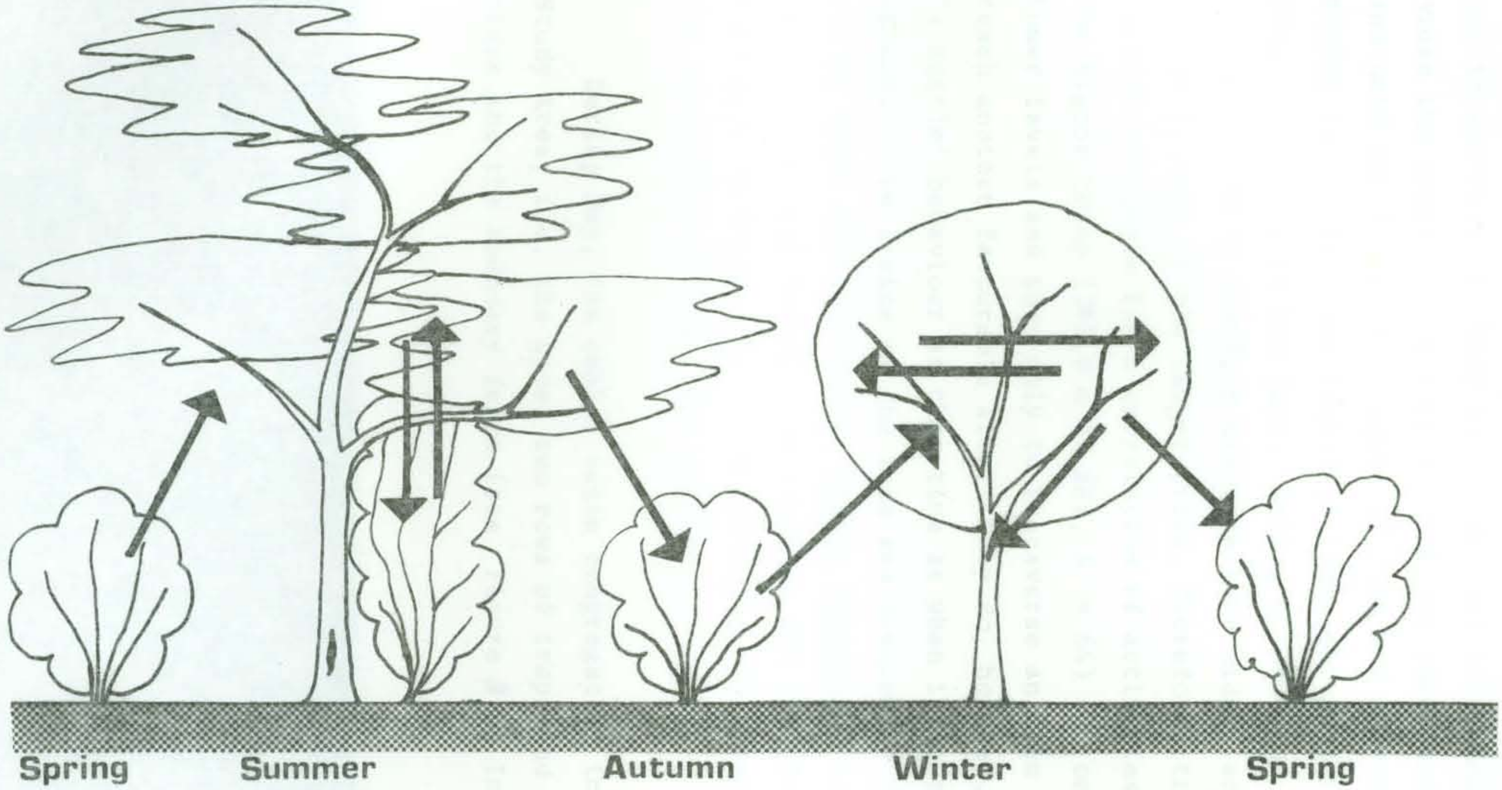


Figure 85. A schematic representation of seasonal movement of <u>Thelotornis capensis</u> in the <u>Burkea africana</u> - <u>Eragrostis pallens</u> Study Area.

Table 46. Seasonal tree species selection by *Thelotornis capensis* in the *Burkea africana* - *Eragrostis pallens* Study Area : May 1975 - May 1977, expressed as a percentage for each month.

| Tree Species | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Grewia flavescens* | 66,7 | 100 | 77,8 | 75,0 | 41,9 | 3,7 | 10,0 | 21,9 | 72,5 | 62,5 | 62,5 | 41,7 |
| *Strychnos pungens* | 0 | 0 | 0 | 0 | 9,7 | 72,84 | 65,0 | 32,9 | 5,9 | 0 | 0 | 0 |
| Others | 33,3 | 0 | 22,2 | 25,0 | 48,4 | 23,5 | 25,0 | 45,2 | 21,6 | 37,5 | 37,5 | 58,3 |

The snakes chose on average low positions in these shrubs (75,4% $<$1,5 m, N = 51) and may be found in a variety of positions but normally with the body and head outstretched within the shrub. Occasionally they would be seen with the fore-quarter or third of the body protruding rigidly from the bush. On being approached, all movement is followed by tilting the head so as to keep the approacher in view.

They rely to such a degree on their camouflage ability that they allow one to encircle the body with thumb and fore-finger without moving, provided the snake is not touched. At the same time, the tongue is protruded and held out for short lengths of time and movement in and out is very slow. During summer they may remain in these shrubs for relatively short periods, occasionally up to two days. During October and November and then on until March, these reptiles disperse more widely and are difficult to find in the foliage of the larger trees. Therefore, there are relatively few records available for a correlation of activities. However, they take to the higher trees ($>$2,0 m 21,88%, N = 64) and only rarely descend to the lower levels and then only to transverse an open piece of ground and so reach another favourable site. They do, however, exhibit a type of 'shuttle' behaviour at this time as when it is hot they descend from the canopy to the inside of the tree and frequently into shrubs below the canopy where there is shade. *Grewia flavescens* is frequently found scrambling up into the larger tree canopies and the snakes are often found under such circumstances. This, therefore, is responsible for the high ratings for this shrub during these months.

During May, the snakes begin congregating in the upper portion of the Study Area, i.e. the upper two rows of traps and that section between these traps and the boundary fence (see Figure 3). In contrast to September, they move into Strychnos pungens trees with its sharp-tipped, virtually evergreen foliage. Here most spend the winter, although when it is particularly cold, they enter holes in trees and hibernate under these conditions. Many, however, remain outside virtually throughout the winter and may be found day after day in the same tree or group of trees, some specimens remaining for up to three months in the same tree. Many do not truly hibernate as they exhibit diurnal movement, moving out onto the extended branches of the tree to bask on the east side in the morning, returning possibly to the centre during the middle of the day, and out on the west side in the afternoon. Others disappear during July and actually may enter holes in trees even at soil level and hibernate as they do not emerge until spring. This then is the typical scene during the winter months. They therefore have, in effect, seasonal home ranges, which in winter may only be the perimeter of the foliage of the tree or trees and, therefore, only measures several square metres in extent.

However, their summer ranges are far more extensive and vary from about five to eleven hectares. In some instances, individuals make exploratory moves extending 300 m or more from their normal haunts. However, they do return in due course. Size of home ranges was delimited by a line mid-way between the sighting and the next series of traps, i.e. an extra 50 m all round. Only those snakes with five or more sightings were included in these calculations. The average home range size was 4,6 ha n = 19 (Figure 86) and a considerable overlapping was found. The distribution of these snakes within the Study Area can be seen in Figure 87 using frequency of occurrence at the various trapping sites. It will be remembered that observations on these snakes are based on sightings and not captures in traps. It will be noticed that there is a centre of abundance in the upper part of the Study Area which appears to be particularly favourable to the vine snakes with a larger surrounding area where vine snakes were also found to be relatively abundant. The distribution appears largely to be correlated with the density of shrubs and trees in this portion of the Study Area.

Further to the west, along the downslope towards the turf vlei, the trees open up and a denser grass cover is found, while Grewia flavescens and Strychnos pungens become far fewer and in the case of the latter almost non-existant. There are possibly two reasons for this anomaly. One is that lower down the slope the cold intensifies although the slope is

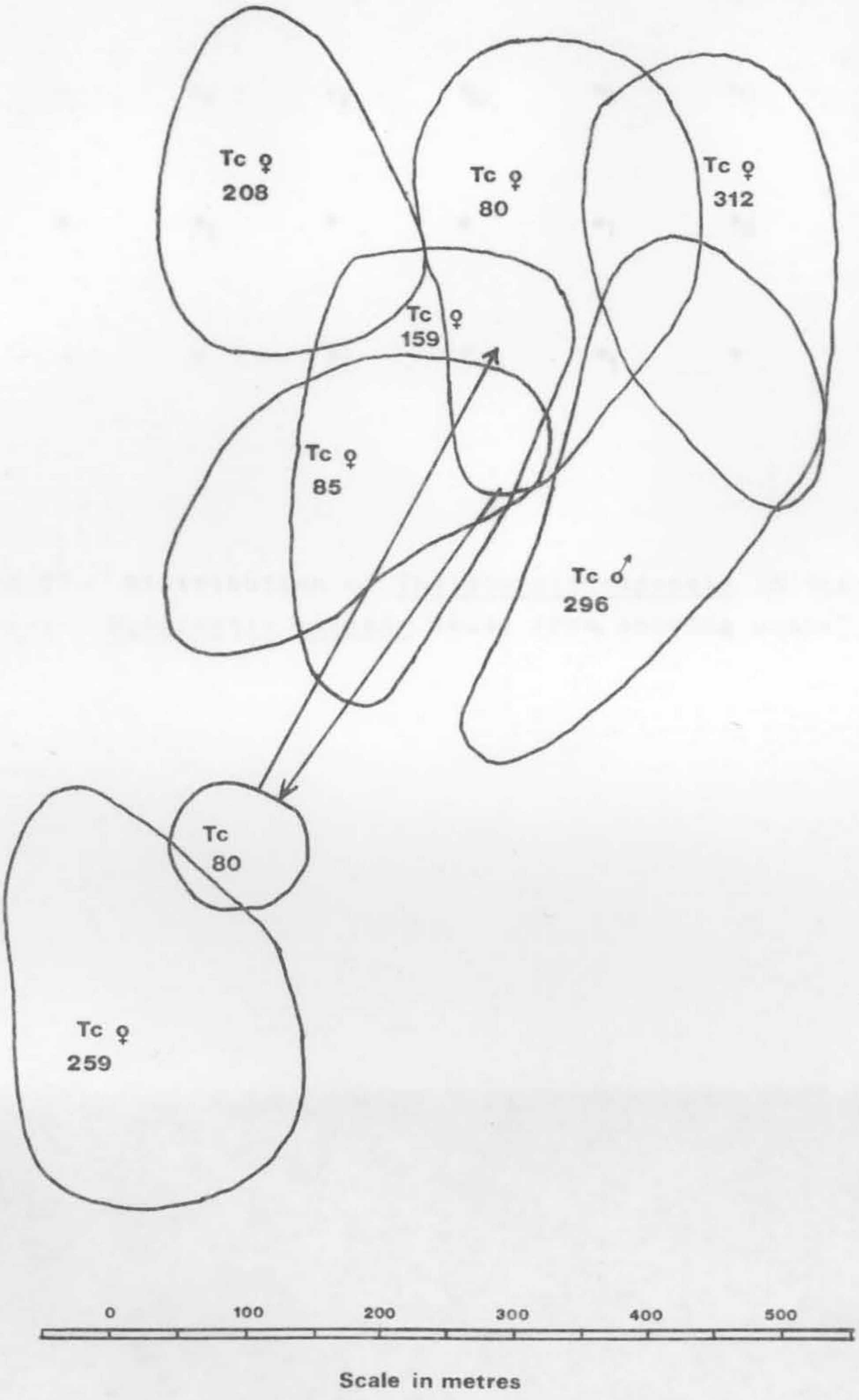


Figure 86. Home ranges of Thelotornis capensis in the Study Area.

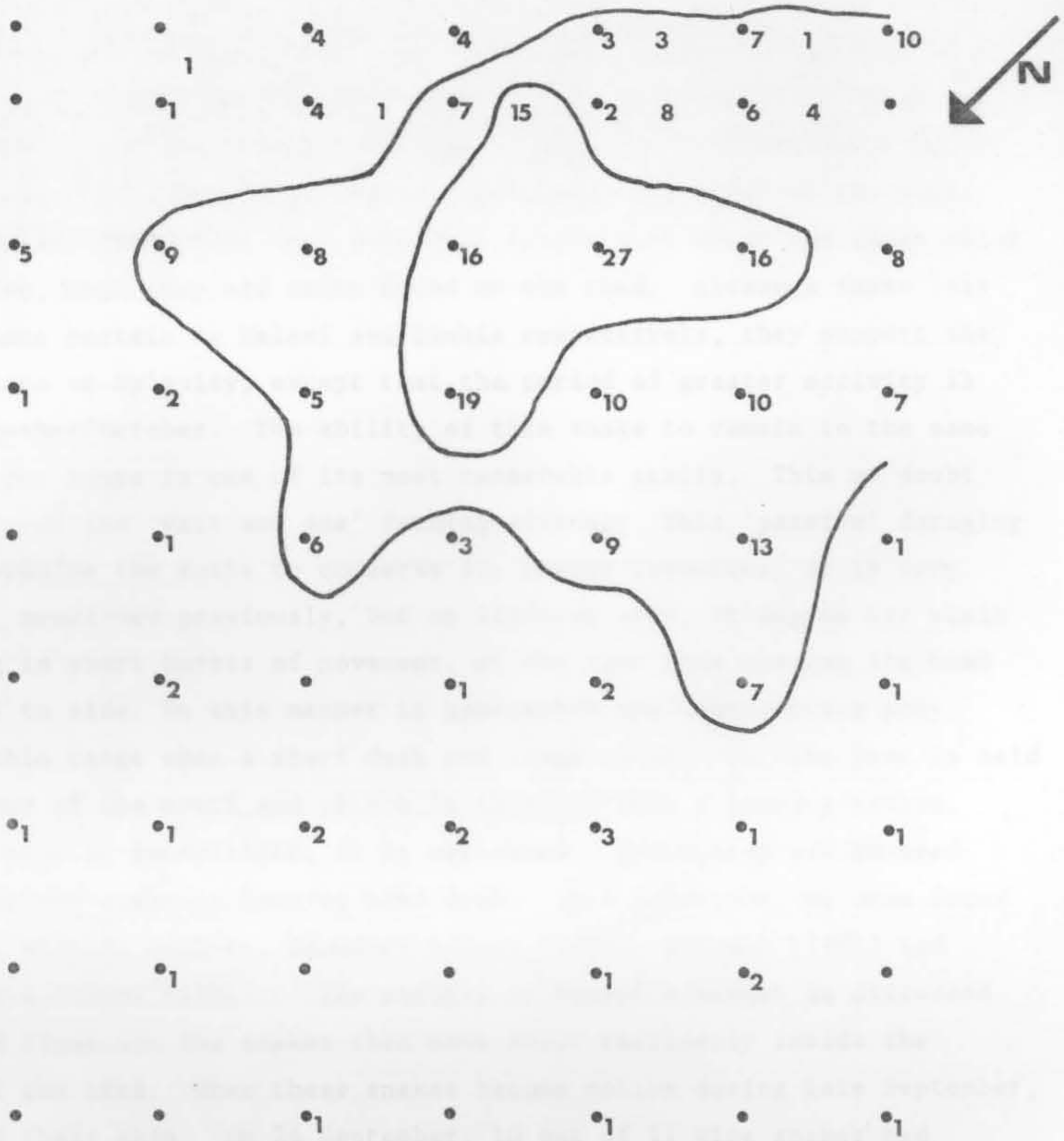


Figure 87. Distribution of _Thelotornis_ _capensis_ in the _Burkea_ _africana_ - _Eragrostis_ _pallens_ Study Area, showing anomalies.

very gradual, or secondly, the impeded drainage affects the growth of the two woody species which feature so prominently in the life style of this snake in the Study Area.

It is, however, probable that the small temperature differences as well as the fact that Strychnos pungens is evergreen during winter are responsible for the movement of these snakes to the top end of the Study Area. Extensive searches, both below and outside the Study Area reveal that this is definitely a preferred site. Figure 88 shows the distribution of these snakes according to sightings and capture over 3-month periods. It is clearly discernible how the pattern changes from highly localised during autumn and winter, to being widespread during spring and summer.

Sweeney (1971), also found that vine snakes remain in one area for several days and may 'wander' in a limited area on a number of trees. He concluded that the occurrence of Thelotornis was dependent on climatic conditions and that they were rare at seasonally dry times of the year. Wilson (1965), found that they were most active just after the first rains have fallen, when they are often found on the road. Although these last observations pertain to Malawi and Zambia respectively, they support the observations on Nylsvley, except that the period of greater activity is late September/October. The ability of this snake to remain in the same position for hours is one of its most remarkable traits. This no doubt forms part of its 'wait and see' feeding strategy. This 'passive' foraging pattern enables the snake to conserve its energy resources. It is very alert as mentioned previously, but on sighting prey, it begins its stalk by moving in short bursts of movement, at the same time swaying its head from side to side. In this manner it approaches the unsuspecting prey, until within range when a short dash and lunge secures it. The prey is held in the rear of the mouth and poison is injected with a chewing action. Once the prey is immobilized, it is swallowed. Swallowing can proceed even while the snake is hanging head down. This behaviour has been documented by several authors, Broadley & Cock (1975), Sweeney (1971) and Henderson & Binder (1981). The ability to remain extended is disturbed when wind blows and the snakes then move about restlessly inside the canopy of the tree. When these snakes become active during late September, most shed their skin. On 26 September, 10 out of 11 vine snakes had sloughed. Sloughing is not correlated with growth per se, but appears to be an irregularly timed mechanism of removing dead skin layers.

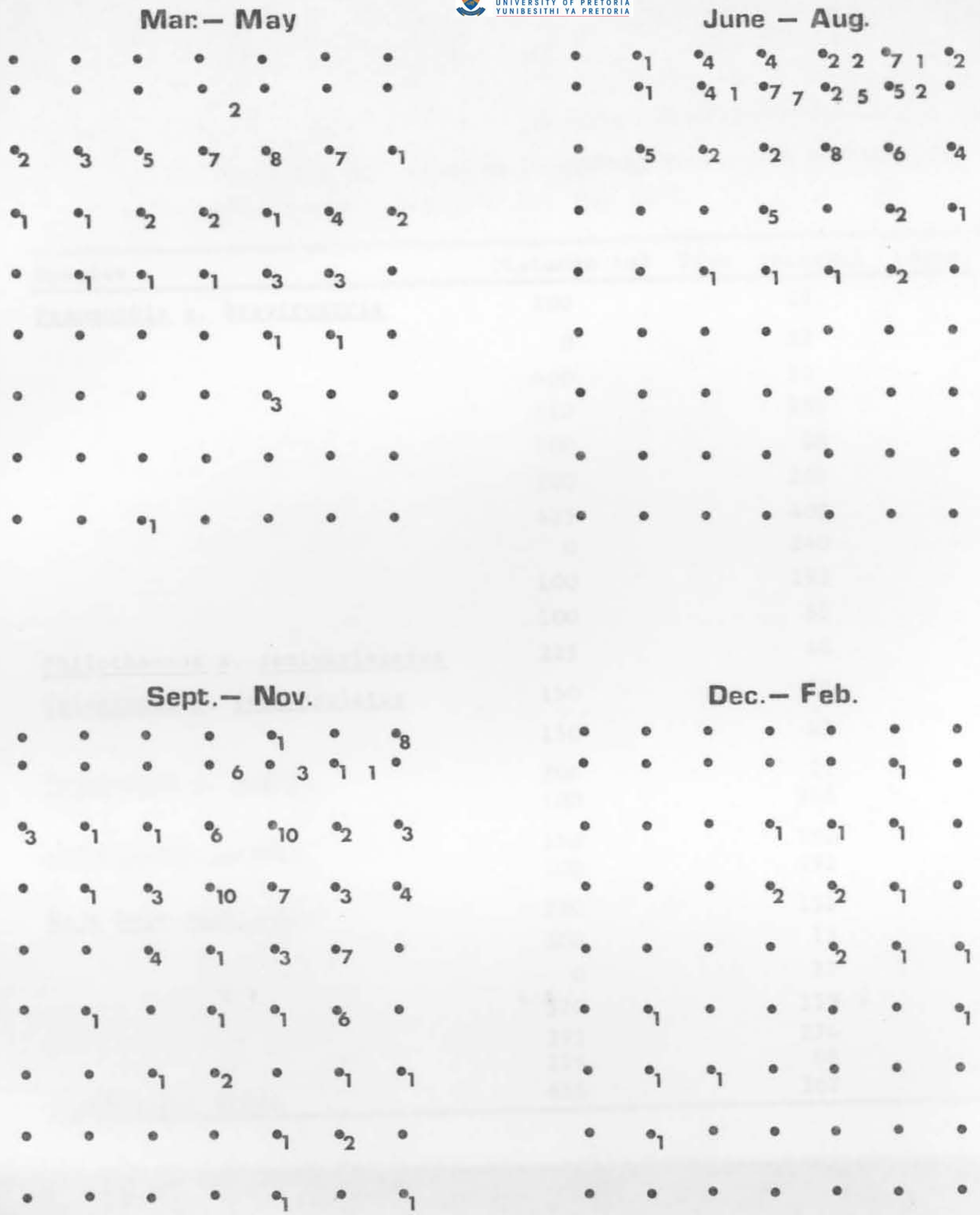


Figure 88. Seasonal variation in the distribution of *Thelotornis capensis* in the Study Area.

In contrast to the 'percher' attitude of the vine snake, the other species actively forage. This is particularly so of the short-snouted sand snake (Psammophis s. brevirostris), which is an active diurnal snake. It moves about slowly while foraging, but if prey is sighted, it follows with an accellerated dash, catching its prey. It is extremely agile and the head follows each movement of the prey. The prey is also held until dead or immobilised after which it is swallowed, usually head first. These snakes do not appear to have home ranges, as they disappear for long periods, only to reappear in traps 100 m from where they were originally trapped. A total of 82 individuals were captured, of which 12 were recaptured on single occasions. As the times of capture/recapture were widely separated, it is therefore only possible to present the distances between these times, as the shortest route between the points. This is actually applicable to all the species (Table 47).

Table 47. Distances between sites of capture and recapture of snakes in the Burkea africana - Eragrostis pallens savanna on the Nylsvley Nature Reserve : May 1975 to May 1977.

| Species | Distance (m) | Time interval (days) |
|---|---|---|
| Psammophis s. brevirostris | 200 | 29 |
| | 0 | 32 |
| | 400 | 20 |
| | 510 | 189 |
| | 100 | 28 |
| | 100 | 207 |
| | 635 | 409 |
| | 0 | 240 |
| | 100 | 293 |
| | 100 | 85 |
| Philothamnus s. semivariegatus | 225 | 46 |
| Telescopus s. semiannulatus | 150 | 32 |
| | 150 | 47 |
| Dasypeltis s. scabra | 200 | 21 |
| | 100 | 346 |
| Lycophidion capense | 150 | 150 |
| | 200 | 192 |
| Naja haje annulifera | 200 | 131 |
| | 500 | 13 |
| | 0 | 77 |
| | 320 | 355 |
| | 395 | 274 |
| | 225 | 88 |
| Dispholidus typus | 655 | 362 |

| Species | Distance (m) | Time interval (days) |
|---|---|---|
| Crotaphopeltis h. hotamboeia | 100 | 37 |
| | 100 | 30 |
| | 150 | 219 |

It is apparent that the results are highly variable, with indications and contraindications of a home range. It was previously discussed that some American snakes, such as the Racers which have similar habits, have extended 'home ranges' up to 700 m in diameter, which may indicate a similar situation among the sandsnakes. However, it does not explain why 85% of the short-snouted sandsnakes captured were never seen again. Similar arguments can be made for the other species with equally poor recapture results, but when recaptured are only short distances from the site of original capture. The only other snake species recaptured which travels over long distances is the Egyptian cobra (Naja haje annulifera) but this is to be expected as the larger species need a greater foraging range in which to locate prey.

Therefore, although there are indications of possible home ranges, these are in effect largely obscured by the great turnover of these snakes during the trapping period. It is illogical to assume that most snakes become trap-shy after their initial capture, but it is difficult to account for this trend.

## Lizards

Almost as varied as the snakes, the lizards are represented by species with similar foraging strategies as those of the snakes. The most active forager is the Cape rough-scaled lizard (Ichnotropis capensis) which moves about actively foraging, often in short bursts of movement followed by a slower cursorial inspection of an area. If prey such as a grasshopper is disturbed and bounds away, the lizard will follow very rapidly. Similarly, during its search for termites and spiders, it digs and scrapes among the leaves often quite vigorously. They course the area extensively and from recaptures it was possible to ascertain the extent of their home range. The mean home range size is 622,5 square metres (n = 12). No agonistic behaviour was observed and in fact few interactions occurred, although home ranges overlapped (Figure 89). When two lizards met they touched each other with their tongues, after which they parted and continued foraging.

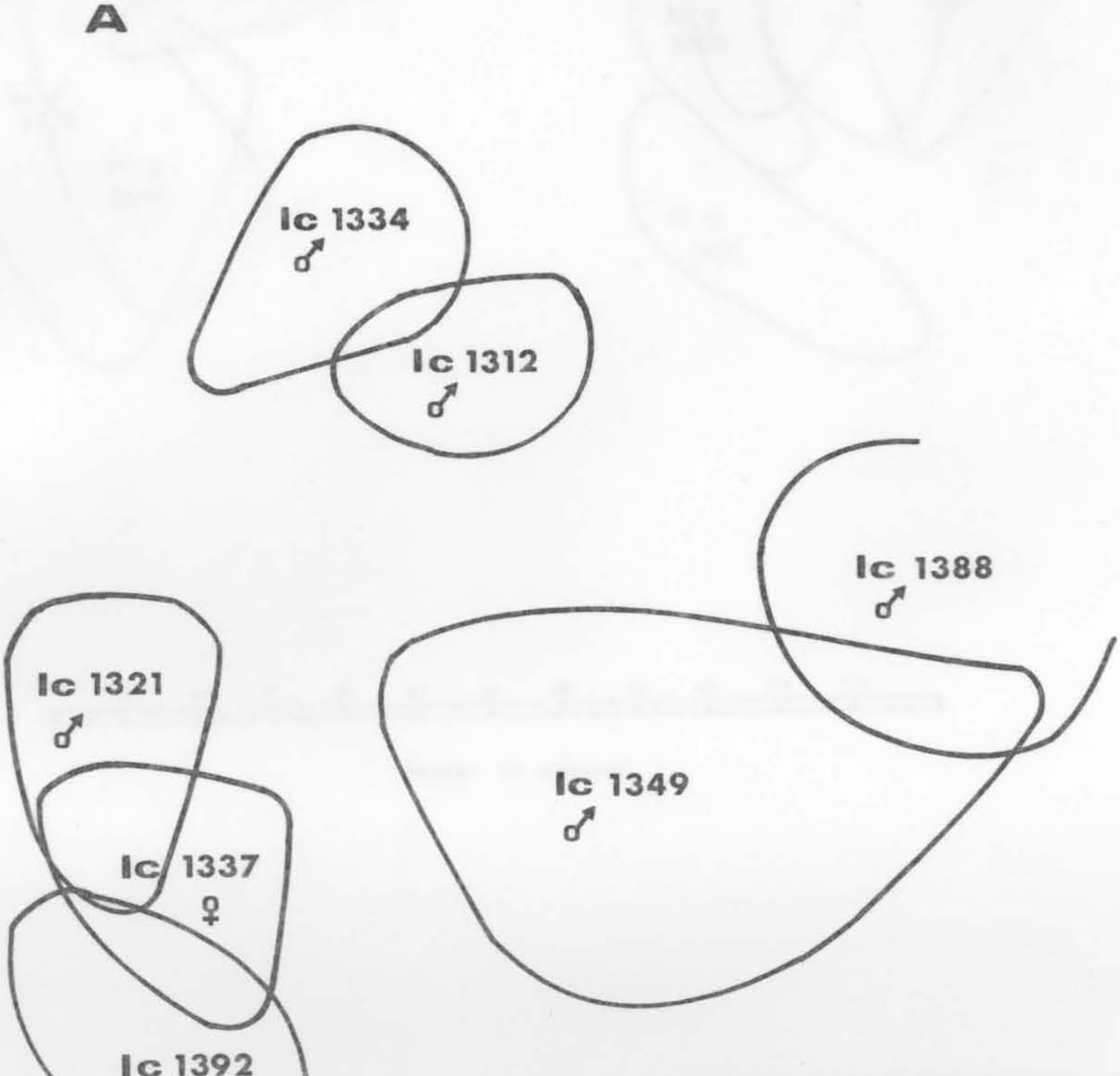
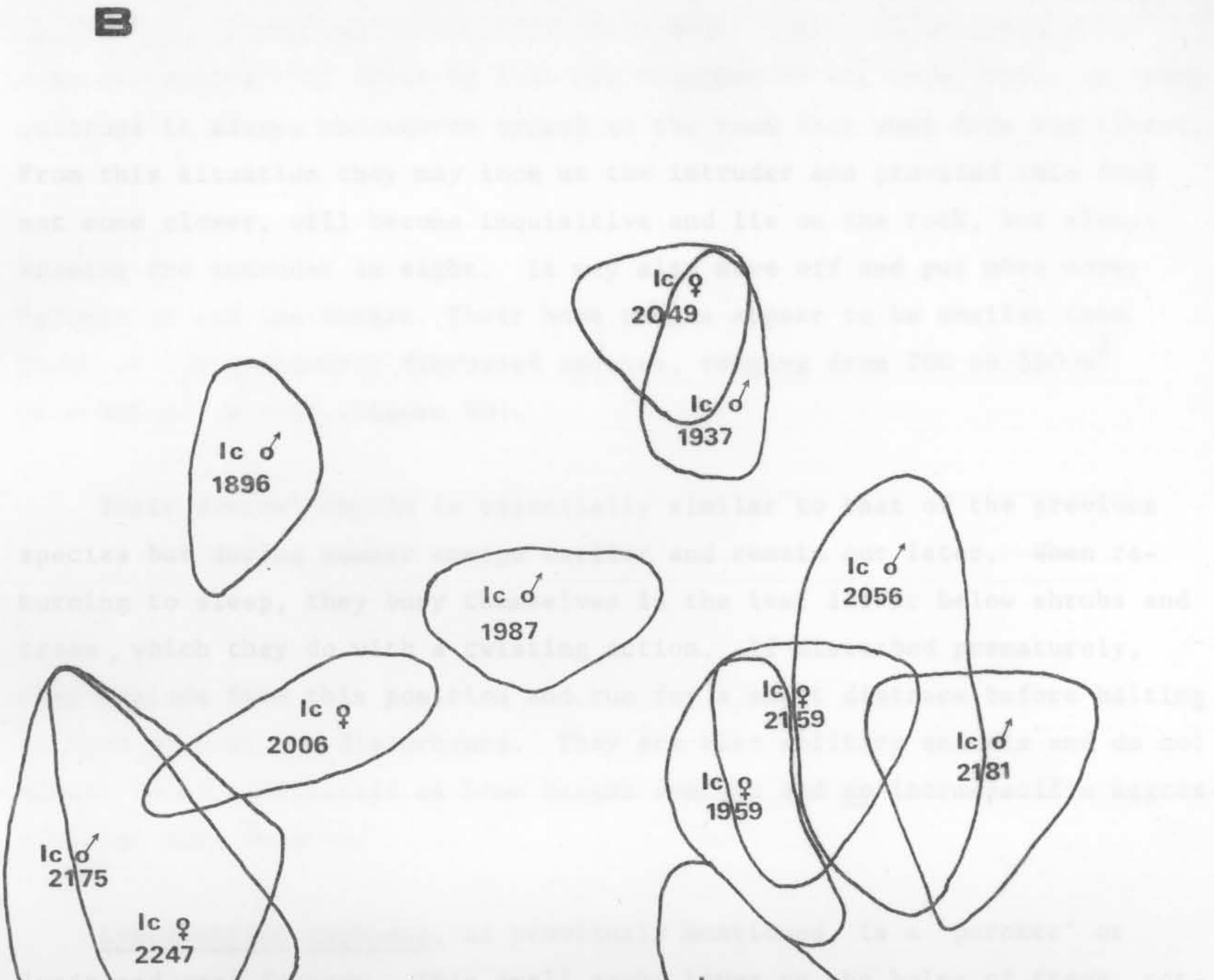


Figure 89. Home ranges of Ichnotropis capensis in the Burkea africana - Eragrostis pallens Study Area (A) 1976 (B) 1977.


B
Ic ♀ 2049
Ic ♂ 1937
Ic ♂ 1896
Ic ♂ 1987
Ic ♂ 2056
Ic ♀ 2006
Ic ♀ 2159
Ic ♂ 2181
Ic ♀ 1959
Ic ♂ 2175
Ic ♀ 2247
Ic ♀ 1871
0 10 20 30 40 50 60 70 80 90 100
Scale in metres

During the heat of the day, i.e. 12h00 -14h00, these lizards stayed in the shade of shrubs and if disturbed ran swiftly off but returned to shade as soon as possible. They begin foraging during summer at 07h00 and apart from the noon period, are active until 17h00. During the winter, the few individuals which are active, emerge later and are already dormant by 16h00. The lizards live down burrows and partially bury themselves in the loose soil under logs where they lie semi-curled up and become almost totally torpid.

In contrast to the foraging strategy of the previous lizard, Mabuya varia (variable skink) is intermediate between the 'active' forager and the 'passive forager, such as the Cape dwarf gecko. It therefore hunts as well as 'hawks'. Its movements are usually in the form of a short, fast dash across open ground, taking cover under grass clumps, logs, shrubs and rocks, which it then uses as vantage points from which to survey the surrounding area. The boles of trees are frequently used for this purpose to a height of one metre, but more often lower down. If threatened, it does not hesitate to climb up into the branches of the tree, while on rocky outcrops it always manoeuvres around to the rock face away from the threat. From this situation they may look at the intruder and provided this does not come closer, will become inquisitive and lie on the rock, but always keeping the intruder in sight. It may also move off and put more cover between it and the threat. Their home ranges appear to be smaller than those of the previously discussed species, ranging from 200 to 550 $m^2$ ($\bar{x}$ = 389 $m^2$ n = 5), (Figure 90).

Their diurnal rhythm is essentially similar to that of the previous species but during summer emerge earlier and remain out later. When returning to sleep, they bury themselves in the leaf litter below shrubs and trees , which they do with a twisting action. If disturbed prematurely, they explode from this position and run for a short distance before halting to look back at the disturbance. They are also solitary animals and do not appear to be territorial as home ranges overlap and no intraspecific aggression has been observed.

Lygodactylus capensis, as previously mentioned, is a 'percher' or 'wait and see' forager. This small gecko lives on the boles of trees, rotting logs, and stems of shrubs. It is diurnal, spending the day moving about up and down its habitat, but mostly may be seen within 1,5 m of the ground, where it may cling upside-down, maintaining an alert look-out for

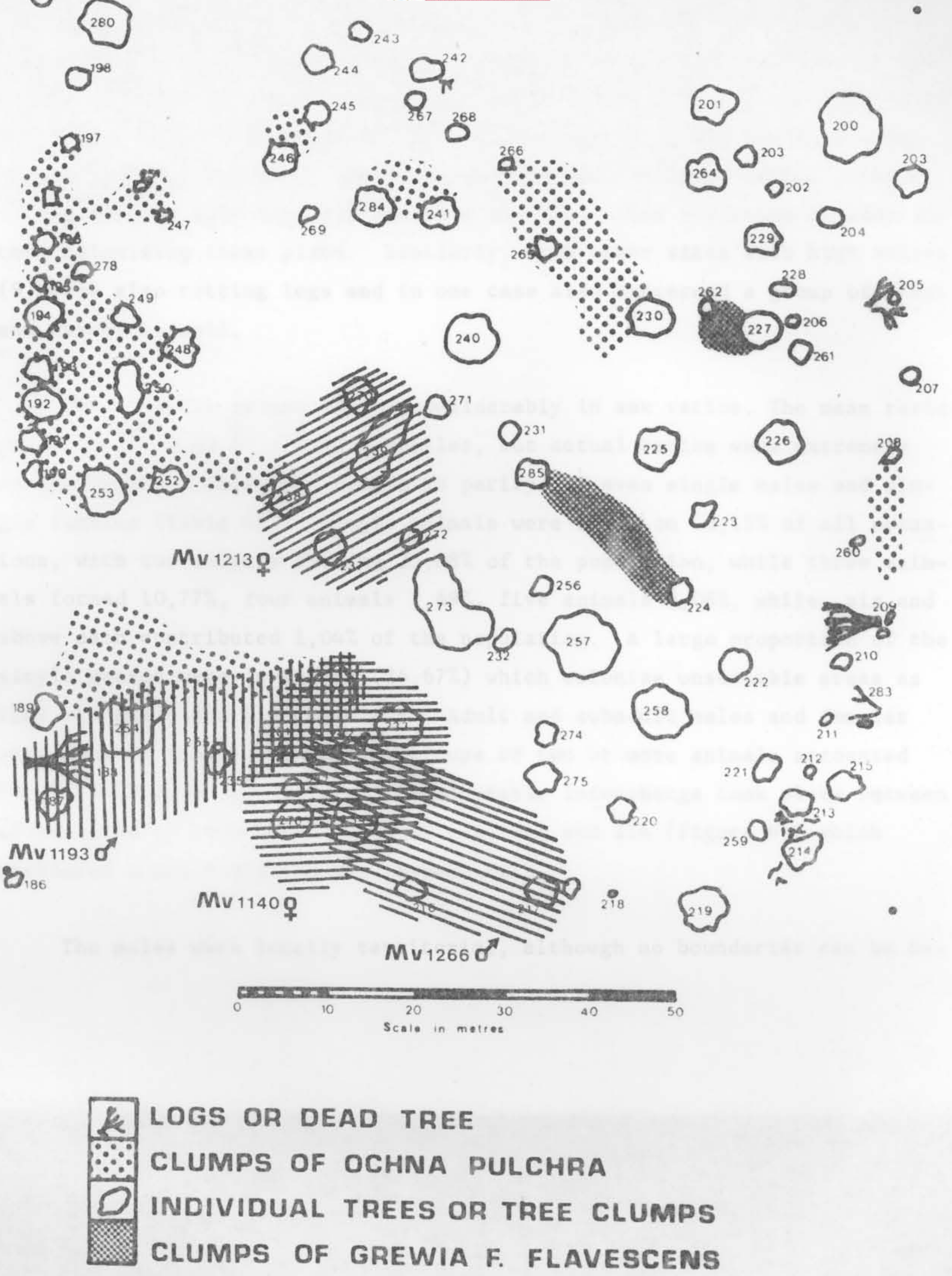


Figure 90. Home ranges of _Mabuya varia_ within the _Lygodactylus capensis_ Intensive Study Area.

passing prey. Once movement is sighted, it may dash down and snap up its prey as much as 60 cm from its retreat.

They appear to prefer trees such as Burkea africana, because these are normally partially rotten and woodboring beetles have excavated numerous tunnels while there is usually much loose bark under which the lizards can hide. It has already been mentioned that in an area of one hectare, these geckos occupy 69% of all the trees, but 100% of all the available habitat. Adults keep to the best sites while the juveniles frequently are found in shrubs where they sleep at the base in the leaf litter adpressed to the stem. The adults live in the holes and crevices of the bole. As such, the Cape dwarf gecko lives in small family groups with a mean of 2,49 (n = 172) individuals per site. However, when assessing the numbers of individuals captured at each number over a six-month period, then a different picture is apparent. Single animals occur with the greatest frequency followed by pairs, threes and fours respectively. The largest number of individuals captured at any one site was 13, which was a rotting Lannea discolor log which had been chopped down while surveying lines during 1974 or approximately one year earlier. This indicates to what extent colonising takes place. Similarly, both other sites with high values (9) were also rotting logs and in one case also concerned a group of trees and shrubs as well.

These family groups varied considerably in sex ratios. The mean ratio was 1,00 ♂ : 0,63 ♀ : 0,32 juveniles, but actual ratios were extremely varied from 5,0 males per female to parity and even single males and single females (Table 48). Single animals were found on 46,15% of all occasions, with two animals forming 23,08% of the population, while three animals formed 10,77%, four animals 7,69%, five animals 3,08%, while six and above each contributed 1,04% of the population. A large proportion of the single geckos were juveniles (26,67%) which colonize unsuitable areas as they are small and inconspicuous. Adult and subadult males and females were equally single. Therefore groups of two or more animals accounted for 53,85% of the population. Considerable interchange took place between sites close to each other, such as nos. 213 and 214 (Figure 91) which harboured 8 and 9 individuals respectively.

The males were locally territorial, although no boundaries can be de-

Table 48. Adult and juvenile complement of *Lygodactylus capensis* inhabiting different sites in the Intensive Study Area : June - December 1975.

| Number of sites | Number of adult males | Number of adult females | Number of Juveniles |
|---|---|---|---|
| 1 | 7 | 2 | 0 |
| 1 | 3 | 1 | 0 |
| 1 | 5 | 1 | 2 |
| 1 | 4 | 1 | 0 |
| 3 | 1 | 1 | 0 |
| 3 | 0 | 2 | 0 |
| 1 | 4 | 3 | 0 |
| 6 | 2 | 0 | 0 |
| 11 | 1 | 0 | 0 |
| 1 | 6 | 6 | 1 |
| 1 | 4 | 1 | 1 |
| 2 | 2 | 1 | 0 |
| 11 | 0 | 1 | 0 |
| 1 | 2 | 2 | 0 |
| 1 | 2 | 0 | 1 |
| 1 | 3 | 2 | 0 |
| 2 | 1 | 1 | 1 |
| 1 | 3 | 5 | 2 |
| 1 | 1 | 1 | 2 |
| 1 | 0 | 0 | 2 |
| 1 | 1 | 0 | 2 |
| 8 | 0 | 0 | 1 |
| 1 | 1 | 2 | 1 |
| 1 | 1 | 0 | 1 |
| 1 | 3 | 0 | 0 |
| 1 | 2 | 1 | 1 |
| 1 | 0 | 1 | 1 |
| 66 | 84 | 53 | 27 |

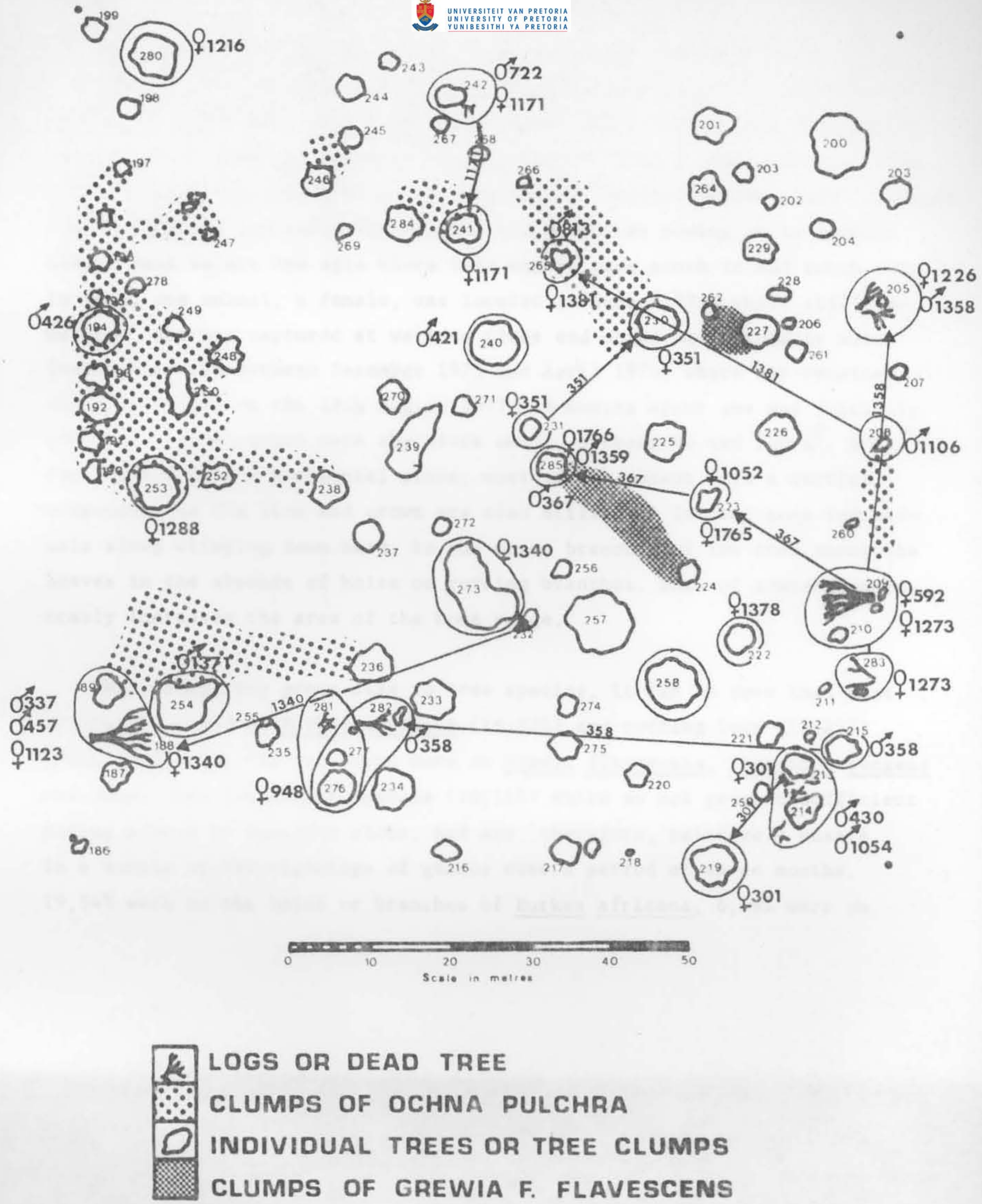


Figure 91. Home ranges and movement of marked Lygodactylus capensis in the Intensive Study Area.

fined as the only interactions seen were in close proximity of a basking or foraging adult. He would threaten all who came close by raising his body, blowing out his gular region and lashing his tail. If this display did not succeed, then he would advance on the intruder and if the latter did not flee, then a lateral threat posture was assumed followed by an attack. The animals grasped any portion of the body, frequently the tail or leg and attempt to overthrow the opponent. Once one individual had surrendered it would flee only to be pursued extensively by the victorious male. There is what amounts to be a hierarchical system operating, with the dominant males and females having the most favoured basking and foraging sites, while the remainder are scattered elsewhere.

While most individuals stayed at one site, occasionally moving to another close by site from 10 to 20 m away, on some occasions individuals moved distances of 50 m or more. The reason for such moves is not readily apparent. In some instances, a juvenile grows up in a small shrub or tree which is then unsuitable for the adult and it therefore moves until it finds a site. Here it may abide for several months before moving on to another site. Many select one site where they may be seen month in and month out. In fact, one animal, a female, was located in June (1975) while still immature. She was captured at various times and moved to a probably more favourable site between December 1975 and April 1976, where she remained until last seen on the 19th August 1977, 26 months after she was initially captured. Home ranges were therefore small, between 40 and 100 $m^2$. However, apart from a horizontal plane, most of the geckos have a vertical component, as the stem and crown are also utilized. In fact some individuals sleep clinging down head, to the upper branches of the tree among the leaves in the absence of holes or rotting branches. This of course considerably increases the area of the home range.

When comparing group size to tree species, it can be seen that most groups are found on <u>Burkea africana</u> (16,92%) and rotting logs (13,85%) while single lizards are found more on <u>Grewia flavescens</u>, <u>Strychnos pungens</u> and other less favourable species (26,15%) which do not present sufficient hiding places or roosting sites, and are, therefore, relatively unsafe. In a sample of 329 sightings of geckos over a period of three months, 19,54% were on the boles or branches of <u>Burkea africana</u>, 6,69% were on

Terminalia sericea, 4,56% on Strychnos pungens, 2,13% on Ochna pulchra with various other species occurring in the one hectare study plot in lesser amounts. However, the overwhelming majority choose to spend the day on rotting logs mostly lying on the ground but also dead trees upright. Sixty-two percent of the geckos were found in these situations. However, many of these were small logs lying at the foot of trees or bush clumps, but at the same time those found on living trees and shrubs were often on dead branches or other dead wood. It is significant that they actually choose the rotting logs as these provide better shelter, not camouflage as the boles of Burkea, Terminalia and others, match the colour of the geckos, which in any event are also capable of colour change by lightening or darkening the skin to suit the background. There is probably an additional advantage in that there are numerous insects and other arthropods found around rotting logs, therefore supplying food as well, such as beetles, ants and spiders, which feature prominantly in their diet (Figure 32).

It was seen on examination of stomach samples that feeding activity took place mainly during the afternoon (Figure 34). This observation is supported by the general activity pattern of the geckos which indicates a period of greater activity during the late afternoon (Figure 92) based on the numbers of geckos per minute during the gecko-sampling periods.

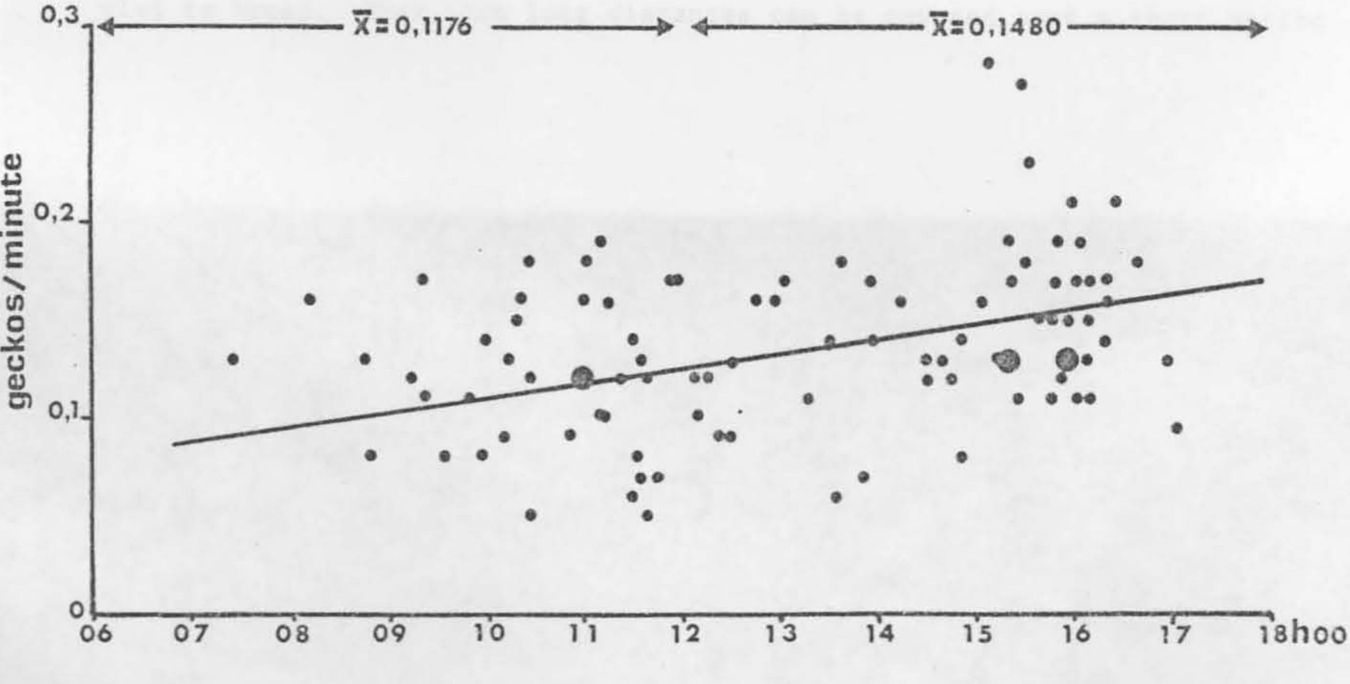


Figure 92. Correlation of activity of Lygodactylus capensis with time of day in the Study Area.

Although Panaspis wahlbergi were relatively common in the Study Area, no details of movements could be determined because of the infrequency of capture. They do, however, appear to be local and probably do not have large home ranges.

Similar comments are pertinent for the remainder of the lizard species of which some, such as Pachydactylus bibronii left their rocky retreat for up to four metres, being captured in traps that distance away. This means that foraging takes place some distance from the rocky outcrops. During the day they are restricted to crevices between rocks which they live in, in pairs or small groups.

Lygosoma sundevallii was also not captured with any frequency but was determined to be nocturnal as they were only captured in the traps during the night while tracks also indicated nocturnal movement. These lizards are sand dwellers, living under rotting logs and stones during the day but emerging by night to change location and forage.

## Amphibians

Although movement by amphibians and in particular Bufo garmani and Kassina senegalensis took place, recaptures were few and only supported the allegation that they move between the turf vlei and the Study Area. No trapping was carried out between the Study Area and the vlei. This can be seen in Table 49 from which it is apparent that despite the paucity of recaptures, a trend is visible. Activity during the months, August, September, and to a lesser degree, October and November, appears to be downslope, that is towards the turf vlei, while during middle and late summer, the reverse situation is noted. This pertains only Bufo garmani, as movement by Kassina senegalensis appears to be random.

It is also apparent that some of the movements took place over considerable lengths of time. This further confuses the issue, as obviously no movement took place during the four dry and cold months of the year, so that the distances covered could have been prior to hibernation or they could have been thereafter. The time of activity was always used as the time of recapture and, therefore, no finite conclusions can be made, but merely serves to indicate support for the theory that they go to the turf vlei to breed. That such long distances can be covered over a short period of time is evidenced in Table 49 and distances of over 100 m per day are by no means unusual.

It is also apparent that in several instances recaptures were effected in the same place despite long time intervals, which indicates some homing ability. This is supported by Taylor (loc.cit.) who tested toads' homing capabilities. He obtained 57 recoveries involving 36 *Bufo garmani* after release at the site of capture. He went on to release these toads at varying distances from their original capture site and returns involved distances of 500 to 1 000 m in various directions. In some instances, the toads covered the 500 m in from two to four days, and one released 1 000 m away was back home in five days. Another took 209 days before it eventually arrived back. There is, therefore, no doubt that a homing instinct exists, although the recovery rate was considerably less with 12 recoveries involving nine individuals. What is unusual is that all such recoveries were males and that they had to circumvent several obstacles including ponds where other individuals were calling.

The kassinas were also capable of long distance movement over short periods of time (Table 50). Movement appears to be somewhat random and in fact rarely westwards towards the turf vlei, which is an interesting phenomenon, but for which there is no explanation except that other breeding sites must also be available. None are found in the Ecosystem Study Area as a whole. Movements may, therefore, be more extensive than originally thought. It is possible that a large scale flux of these frogs takes place and this involves large scale replacement of individuals annually.

Table 49. Movement of _Bufo garmani_ in the _Burkea africana_ - _Eragrostis pallens_ Study Area from recapture results : May 1975 - May 1977.

| Date | Distance (m) | Direction | Time (days) |
|---|---|---|---|
| November | 325 | SW | 35 |
| | 100 | W | 35 |
| December | 100 | E | 39 |
| | 500 | E | 22 |
| | 100 | E | 18 |
| January | 0 | same place | 31 |
| | 100 | E | 3 |
| | 0 | same place | 54 |
| February | 62 | SW | 28 |
| | 40 | NE | 2 |
| | 100 | E | 2 |
| | 420 | E | 24 |
| | 430 | E | 3 |
| | 600 | S | 23 |
| | 0 | same place | 25 |
| | 0 | same place | 31 |
| | 230 | E | 3 |
| | 0 | same place | 28 |
| | 26 | NE | 6 |
| | 0 | same place | 1 |
| | 80 | E | 3 |
| | 21 | SE | 2 |
| March | 0 | same place | 2 |
| | 75 | W | 23 |
| | 375 | E | 24 |
| | 15 | E | 2 |
| | 100 | ESE | 24 |
| | 535 | NNE | 27 |
| | 325 | E | 27 |
| | 60 | S | 27 |
| April | 65 | SW | 4 |
| | 130 | S | 39 |

| Date | Distance (m) | Direction | Time (days) |
|---|---|---|---|
| May | 20 | E | 41 |
| August | 10 | SW | 2 |
| September | 540 | W | 317 |
| | 290 | E | 213 |
| | 0 | same place | 2 |
| | 45 | SW | 29 |
| | 15 | W | 2 |
| | 60 | NW | 1 |
| | 10 | SW | 154 |
| | 5 | SW | 220 |
| | 121 | SW | 5 |
| | 10 | W | 213 |
| October | 90 | W | 195 |
| | 500 | NNW | 218 |
| | 230 | E | 219 |
| | 100 | E | 6 |
| | 55 | SW | 196 |
| | 280 | SW | 6 |
| | 20 | E | 215 |
| | 25 | W | 2 |
| | 100 | W | 2 |
| | 130 | E | 2 |
| | 40 | S | 26 |
| | 100 | S | 4 |
| | 20 | SE | 5 |
| | 35 | NE | 5 |
| | 40 | E | 29 |
| | 46 | E | 30 |

Table 50. Movement of *Kassina senegalensis* in the *Burkea africana* - *Eragrostis pallens* Study Area from recapture results.

| Date | Distance (m) | Direction | Time (days) |
|---|---|---|---|
| November | 55 | NE | 2 |
| " | 12 | NE | 2 |
| " | 0 | same place | 2 |
| " | 35 | SE | 28 |
| December | 425 | SE | 23 |
| " | 200 | SE | 7 |
| January | 370 | E | 49 |
| " | 0 | same place | 2 |
| " | 22 | SE | 2 |
| " | 100 | S | 2 |
| February | 200 | S | 5 |
|  | 140 | SE | 391 |
| September | 450 | N | 241 |
| October | 150 | ESE | 244 |
|  | 200 | NNE | 5 |
|  | 10 | N | 2 |
|  | 20 | SW | 22 |
|  | 60 | N | 21 |
|  | 0 | same place | 2 |
|  | 230 | W | 2 |
|  | 200 | N | 2 |
|  | 135 | NE | 3 |
|  | 200 | E | 2 |
|  | 100 | E | 2 |
|  | 375 | SE | 5 |
|  | 80 | Se | 5 |
|  | 70 | SW | 5 |
|  | 34 | SE | 5 |
|  | 50 | N | 7 |

# CHAPTER 8

# DISCUSSION

## A COMPARISON OF THE HERPETOFAUNA IN DIFFERENT HABITAT TYPES IN TEMPERATE AND TROPICAL AREAS

The various adaptations and mode of life of the reptiles and amphibians have been discussed. However, to examine individual species narrowly would be to neglect them as integral parts of a community. They should, therefore, also be considered in a broader context and compared with simiiar groups of reptiles and amphibians in other ecological zones.

A biotic community is an assemblage of organisms living together and interacting at all trophic levels. Consequently a community is not limited to specific taxa and, therefore, to speak of a 'herpetological community' by definition is not an ecologically meaningful entity,(Heatwole 1977), but rather to call these segments of the community 'herpetofaunal assemblages'. Barbault (1976b) terms these units 'herpetocenoses'. Inger & Colwell (1977) refer in their paper to the ecological organization of the herpetofauna which they examined in Thailand. Whatever connotation one applies to these terms, it is essentially a number of similar organisms and their interactions both with their environment as well as among themselves, and within which the Nylsvley Ecosystem Study was partitioned. In this discussion the term herpetofaunal assemblage will be adhered to as outlined previously.

The nature of the organization of species of reptiles and amphibians in an assemblage and the factors affecting such structure is an important aspect. It has long been accepted that numbers of species of reptiles and amphibians increase from higher to lower latitudes. This is exemplified by a comparison of species in temperate and tropical localities (Table 51).

Table 51. Comparison of species numbers of amphibians, lizards and snakes in different habitat types in temperate and tropical areas, Barbault (1975, 1976a) and Inger *et al* (1977).

| Habitat | Amphibians | Lizards | Snakes | Total |
|---|---|---|---|---|
| Nylsvley N.R. Tvl. | 24°39'S | 28°42E | 630 mm | 1110 m alt. |
| *Burkea africana* savanna | 11 | 17 | 21 | 49 |
| *Combretum apiculatum* savanna | 7 | 16 | 17 | 40 |
| *Acacia tortillis* savanna | 12 | 12 | 19 | 43 |

| | | | | |
|---|---|---|---|---|
| *Acacia tortilis* savanna | 12 | 12 | 19 | 43 |
| Nyl river floodplain | 15 | 4 | 6 | 25 |
| Total species in all habitats | 17 | 23 | 29 | 69 |
| *Lamto, Ivory Coast | 6°13'N | 5°02'W | 1280 mm | ± 140 m alt. |
| Herbaceous savanna | 13 | 5 | 21 | 39 |
| Wooded savanna | 16 | 8 | 26 | 50 |
| Total species in savanna | 24 | 8 | 29 | 64 |
| Total species in all habitats | 38 | 17 | 40 | 95 |
| *Sakaerat NE Thailand | 14°30'N | 101°55'E | 1500 mm | ± 140 m alt. |
| Evergreen forest | 19 | 28 | 29 | 76 |
| Deciduous forest | 20 | 18 | 27 | 65 |
| Total species in all habitats | 25 | 31 | 47 | 103 |

However, as is apparent from Table 51, it is not sufficient to look at basic latitudinal differences between the faunas but also to take into consideration the structure of the habitat whether forest, savanna or desert. A forest offers a greater diversity of microhabitats, for example, than possibly a desert. Altitude, climate and substrate are also important factors. Rainfall is one of the most important limiting factors including too much or too little. Seasonal differences in this commodity are extremely important. The high rainfall areas of north-eastern Thailand exhibit the greatest number of lizards and snakes while the amphibians are most abundant at Lamto. This may be due to the greater seasonality of the former as opposed to the latter, where virtually only one month of the year is on average relatively dry. This is also reflected by the amphibians which are more diverse at Lamto than at Sakaerat. The relative paucity of lizards in the savanna at Lamto is very marked when compared to Sakaerat and Nylsvley. The diversity and structuring of the habitats are no doubt responsible for the differences while rainfall also plays a role. The high rainfall appears to limit species diversity of lizards at Lamto although Thailand in contrast exhibits a greater diversity because it experiences a longer dry season. Evergreen forest in particular exhibits a lizard species diversity unequalled by any of the other habitats under discussion (Table 51). The geckos, agamas and skinks have obviously adaptively radiated under these conditions. The first and last groups show a wide tropical distribution but both also exhibit two primary centres of radiation, one in African and one in the Indoaustralian regions while the agamids have extensively radiated into different habitats, Goin, Goin & Zug (1978). Diversity was apparently favoured at Sakaerat, particularly with arboreal species (Table 52).

Table 52. A comparison of the habitats of lizards in the three areas under discussion.

| | Lamto | | | | Sakaerat | | | | Nylsvley | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | T | A | F | R | T | A | F | R | T | A | F | R |
| Geckonids | 0 | 5 | 0 | 0 | 3 | 8 | 0 | 0 | 2 | 1 | 0 | 1 |
| Agamids | 0 | 0 | 0 | 1 | 1 | 7 | 0 | 0 | 1 | 1 | 0 | 0 |
| Chameleonids | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Scincids | 5 | 2 | 1 | 0 | 8 | 2 | 1 | 0 | 3 | 1 | 2 | 1 |
| Lacertids | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| Gerrhosaurids | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| Varanids | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| | 6 | 9 | 1 | 1 | 13 | 17 | 1 | 0 | 14 | 4 | 2 | 3 |

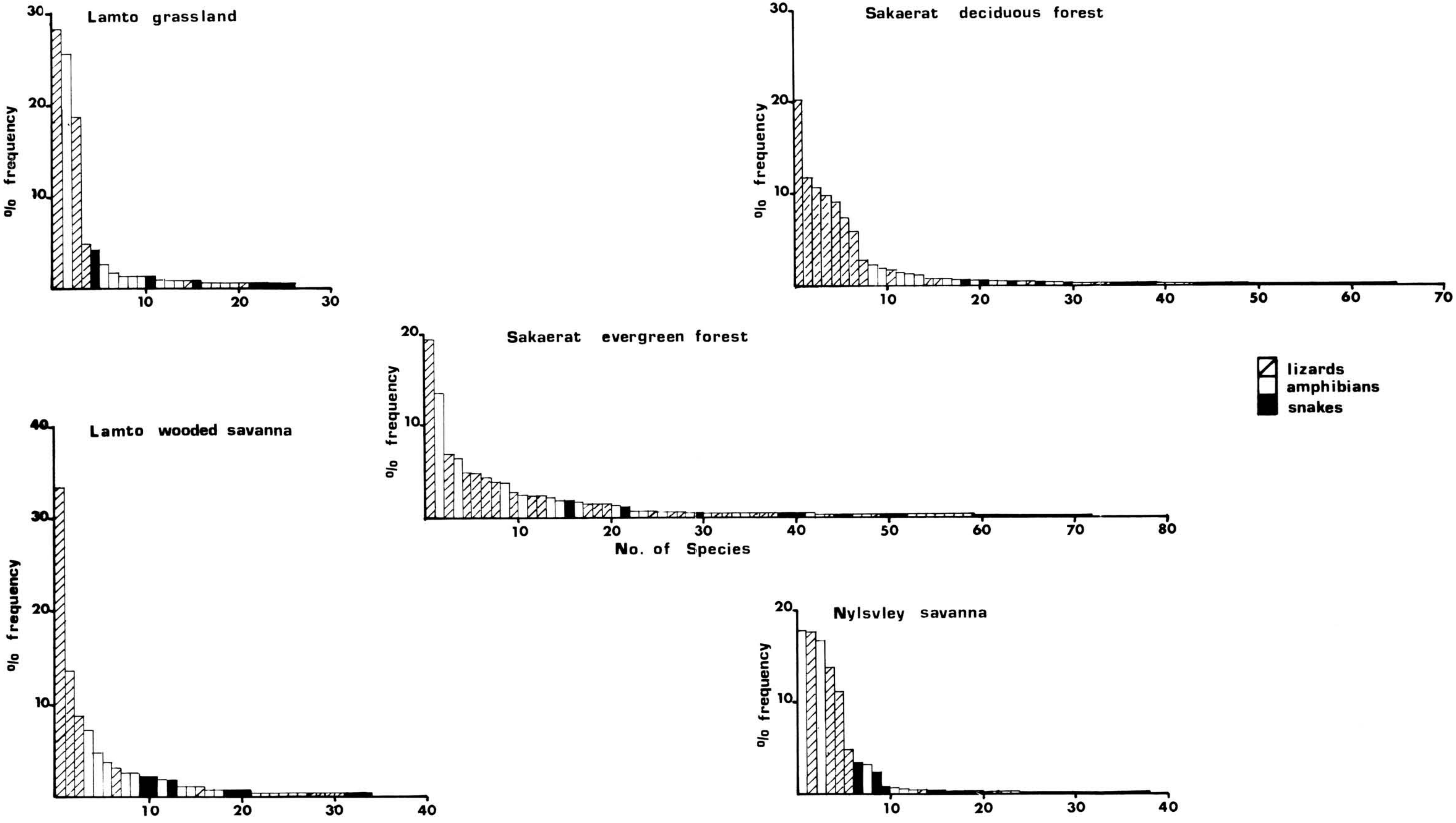
T = terrestrial, A = arboreal, F = fossorial, R = rupicolous

Lamto and Sakaerat exhibit similar trends whereas Nylsvley showed the greatest terrestrial diversity while arboreal niches are lacking. Both Lamto and Sakaerat offer a greater diversity of arboreal niches. However, neither of the latter two areas exhibit rupicolous niches. At Lamto an agamid is principally found around human habitation and therefore appears to have occupied a niche not exploited by other forms. Similarly on the Nylsvley Nature Reserve, *Mabuya s. punctatissimus* occurs principally around human habitation and is rarely seen in the field and is then only arboreal. Nylsvley Nature Reserve, however, exhibits a greater number of terrestrial forms which indicate that the diversity of this habitat is greater than that offered by the other two areas. There are generally few taxonomical similarities between the African and Asian areas under discussion. Only three amphibian, three lizard and four snake genera have counterparts in Asia, while species and generic similarities between the Nylsvley Nature Reserve and Lamto are of a high order. Three species and five genera (45%) of amphibians, one species and seven genera (77%) of lizards and seven species and sixteen genera (53%) of snakes are shared by these two areas. Unfortunately a complete list of amphibians has not been seen so that relative values are approximate. One species of amphibian Kassina senegalensis and one species of snake Psammophis sibilans are common and abundant in both areas.

Figure 93 illustrates the equitability of the areas under comparison. It is apparent that both the Deciduous Forest in NE Thailand, as well as the deciduous Burkea africana savanna on the Nylsvley Nature Reserve are more equitable than either of the other habitat types. Both the Evergreen forest in NE Thailand as well as the Wooded Savanna at Lamto exhibit between the first two and the last two sites. However, in all instances illustrated, from 1 to 7 species dominate the assemblages, the remaining species being relatively uncommon. This is typical of tropical species and herpetofaunal assemblages.

Although the Nylsvley Nature Reserve lies at a considerably higher altitude than the other areas, it does nevertheless exhibit a greater degree of equitability which is in contrast to what Heatwole (loc.cit.) mentions. There does appear to be some correlation with other factors including rainfall and no doubt number of dry months in the year. The high rainfall areas depicted in Figure 93, all exhibit a similar trend with the exception of the Deciduous Forest where a greater degree of equitability was also apparent as mentioned previously. This is in contrast to what has been documented for Thailand and probably has been overlooked.

Differences between the Thailand and African herpetofaunal assemblages are also apparent. For instance, the Evergreen Forest in NE Thailand is dominated by lizards and amphibians while the Deciduous Forest is almost exclusively dominated by lizards. Although the former is largely true in the African context, snakes are more important than they are in the Asiatic context and feature more prominently. With regard to species diversity the Thailand examples show an incredible array including large numbers of rare or uncommon species which is not equalled in the African context. The Nylsvley Nature Reserve in this regard tends to exhibit an abrupt decline between the common and the not so common species and therefore not as gradual as that of the other species. Pianka (1975, from Inger & Colwell 1977)



Lamto grassland

Sakaerat deciduous forest

Sakaerat evergreen forest

Lamto wooded savanna

Nylsvley savanna

Figure 93. Equitability of different areas under comparison.

finds a positive relationship between species richness and environmental predictability which would predict greater diversity in the Tropics declining away from the Tropics although other factors may also be important.

Inger & Colwell (loc.cit.) maintain that interactions among species are important in the patterning of communities. While the physical-chemical environment demands certain minimum physiological adaptations for entrance into a community, every species must also pass the much more demanding criteria imposed by the biotic environment, particularly necessities such as finding food, coping with predation and reproducing successfully, which will be discussed presently.

Pianka (1977) states that provided that all else being equal, Assemblages with fewer different resources will support fewer species thereby indicating the basic difference between the Burkea africana Savanna and the Acacia Savanna on the Nylsvley N.R. However, although exhibiting fewer niches, there are more of each niche so that continuity is greater which therefore enables a greater density and biomass of each species which is a feature of the Acacia Savanna. This may also be the case at Lamto where there are three basic vegetation types of which the study utilized two, namely herbaceous savanna or grassland and wooded savanna including palms and other trees. Secondly, the number of species which can co-exist within an Assemblage decreases as the diversity of utilization of resources by an average species increases. Thirdly, the amount of niche overlap will affect the number of species able to exist within an environment. Fourthly, in spite of having the similarities discussed previously, the species diversity in Assemblages can still differ in the extent to which they actually support as many different species as possible or until 'saturated'. Resources seldom go unused for very long and it is perhaps the reason why such low density species, such as Mabuya capensis and Psammophis angolensis suddenly appear within the Assemblage.

Species diversity is enhanced by within-habitat partitioning of space. Considerable variations exist in the manner in which reptiles use space. In this study one snake and three lizard species are discussed, each with different requirements but generally only occupying home ranges without being territorial. Diversity of microhabitats and their use are responsible for this diversity. It is probably for this reason that the Burkea africana herpetofaunal assemblage is as diverse as that of Lamto. Differences between these areas are largely due to latitude, rainfall and habitat diversity. Latitude,as we have seen, tends to promote stability of climate the closer one gets to the Equator. Rainfall tends to enhance specific group differences such as a greater diversity of amphibians and also snakes at both Lamto and Thailand. Lizards in contrast are more diverse at Nylsvley than at Lamto, because of the greater number of niches rather than a saturation of niches. Lizards appear to diversify in a more arid environment as Pianka (1969) for example observed 39-40 species living sympatrically in parts of Australian desert areas. On the other hand, lizard species diversity in Thailand are very high as a result of the 5-6 month dry period.

Habitat, microhabitat and niche occupation may lead to physiological and anatomical adaptations such as the expanded digits of the arboreal lizards and frogs while burrowing forms develop elongated cylindrical bodies and degeneration of limbs. Snakes too have achieved a tremendous degree of variation in this respect. The snakes on the Nylsvley Nature Reserve have adapted well to their environment. Considering the ratio of tail length to : snout/vent length, a function of their anatomical adaptations correlate it with the ways in which these reptiles use space, (Figure 94).

Arboreal snakes approach a 1:1 ratio of tail to snout/vent length closest as the tail is extremely useful when moving through the tree canopy and as anchorage. The sandsnakes exhibit a close ratio which is explained by their active foraging habit which ensures adequate purchase against objects to acquire a greater speed when chasing after swift moving prey. The puff adder, however, approximates the burrowing species which again is correlated with its feeding strategies, of lying in wait along rodent tunnels in thick grass cover and acting like a mouse trap. The burrowing species and especially Typhlops are well adapted to a subterranean life. The blunt head with the large scale to force through the soils assisted by a cylindrical body, while the short blunt tail enables the animals to reverse inside the burrows, all go to make the blind snakes ultra specialised. Numerous other adaptations exist which determine the success of survival.

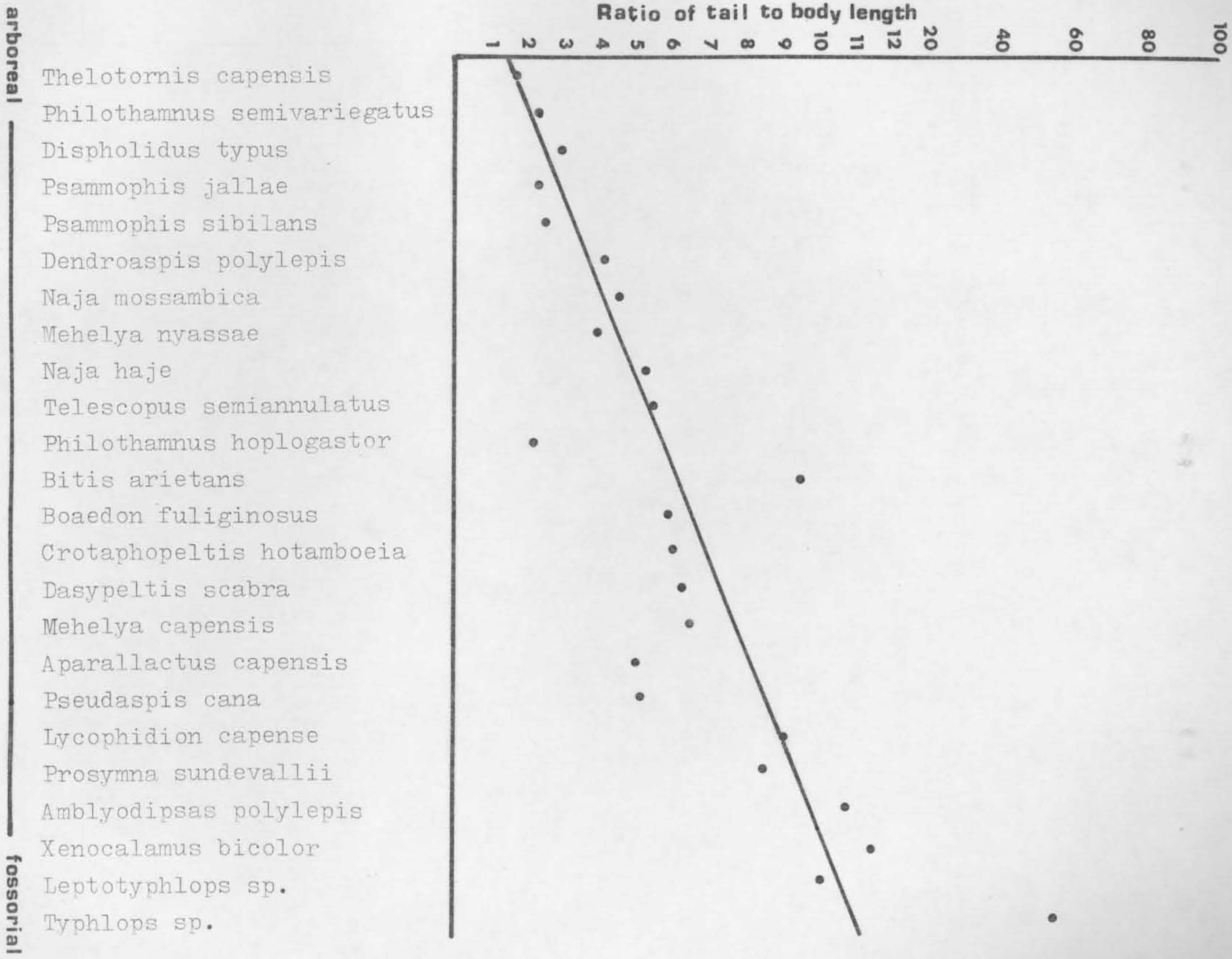


Figure 94. Ratio of tail length to snout/vent length as a function of the snakes adaptations to their respective microhabitats and niches.

Species diversity and numbers are important in a comparison of areas but in themselves are not enough. It is also essential to determine their biomass per unit of habitat if community structure is to be fully understood. Although biomass values have been reported for a few individual species of herpetofauna, the biomass of entire herpetofaunal assemblages have scarcely been studies, Heatwole (loc.cit.).He quotes the work of Barbault as an exception. Previous discussions in other Chapters have centred around the work of Barbault at Lamto on the Ivory Coast. Here mean annual biomass of snakes was 150 g/ha, lizards 89,59 g/ha and amphibians 179,42 g/ha with highest values occurring during the wetter parts of the year. A similar situation exists in the Burkea africana Savanna, where the longer dry season precluded amphibian activity, while cooler weather affected lizard and snake activity and, therefore, biomass. Seasonal influences on biomass included mortality and reproduction as some species exhibited annual life cycles. Similar situations were also apparent at Lamto where the maximum mean life expectancy after maturity (6 months of age) is about nine months for female Mabuya maculilabris, Barbault (1976a). Mean annual biomass of snakes in the Burkea africana savanna was 93,36 g/ha, for lizards 64,36 g/ha and amphibians 593,4 g/ha.

Barbault (loc.cit) suggests that the high predation pressure undergone by small tropical lizards produces selection for increasing fecundity rather than for increased adult survivorship. Although the data are fragmented, a similar situation exists in the Burkea Savanna except that the situation is compounded by the long, cold and dry winter months which suppresses growth rate of immature animals.

Type of habitat may be important in biomass stability. Barbault (1967, in Heatwole 1977) found that total biomass of terrestrial lizards showed large seasonal fluctuations; low values occurred following fires after which they rose and reached a peak by the end of the rainy season; by contrast arboreal lizards did not reflect a similar trend. This situation too is apparent on the Nylsvley Nature Reserve with the exception that fires were very rare so that seasonal turnover was rather more a function of climate, reproduction and predation. However, the arboreal and long lived Cape dwarf gecko did not fluctuate as much as did the terrestrial species which is in agreement with Barbault's conclusions.

In contrast the amphibians in the *Burkea* Savanna are mostly dependent on moisture. Maiorana (1976, in Heatwole 1977) states that many species are dependent on standing water or its proximity for reproduction and suggested that predation pressure on larvae and competition among them for such aquatic environments are probably intense. Therefore in the equable tropics conditions favouring reproduction are extended throughout most of the year and amphibians become temporally segregated using breeding water sequentially in time, thereby avoiding competition. Therefore, more species can co-exist than in seasonal environments, where favourable conditions do not persist long enough for temporal segregation of more than a few species. This view is supported by Barbault (1976b, c) and is illustrated by the number of amphibians at Lamto and at Sakaerat in NE Thailand in comparison to the *Burkea africana* Savanna. In the former, a greater and more widespread rainfall with a very short, if any, dry season, enables the amphibians to breed at different times and in a greater number and variety of habitats in comparison to either Sakaerat where the dry season persists for five to six months and the Nylsvley Nature Reserve where the dry season may last six months, while at least one month within the rainy season will also be relatively dry. Here the amphibians breed when the rains come and breeding therefore varies from year to year. If the rainfall is erratic then a poor survival rate is achieved, as opposed to a successful season when adequate water bodies are formed. Larval mortality is great in the seasonal rainfall areas and, therefore, important in regulating population densities. This is borne out by the differences in numbers of amphibians captured in the Study Area over the 1975/76 season when compared with those of the 1976/77 season (Chapter 4.) Fluctuations in numbers being largely a function of immigrating juveniles, particularly during the months of January, February and March, which are a feature not experienced to such a degree at Lamto.

Habitat selection is not confined only to breeding sites but also includes aspects such as food and shelter, particularly from predators. It was mentioned in Chapter 7 that juvenile and subadult *Lygodactylus capensis* were most commonly found on shrubs and trees which offer marginal shelter from predation and therefore results in spatial separation of the immature or ontogenetic stages. This enables a population to inhabit all

available habitat such as the Cape Dwarf gecko (Figure 25) does. Similarly, the fact that nocturnal snakes are most prevalent in the *Burkea* savanna and yet feed mostly on diurnal lizards, indicates that shelter is a possible limiting factor. Skinks have been observed sheltering under leaf litter surrounding *Ochna* and *Grewia* shrubs and their reaction if molested of bursting out of their cover and running off a short distance before stopping to look at the origin of the disturbance is indication of the predation pressure involved. Most snake species at Nylsvley feed on lizards and fewer on amphibians (Chapter 5), while at Lamto most species feed on amphibians as their availability extends throughout the year. This can be attributed purely to rainfall which on the one hand appears to depress lizard diversity, such as in West Africa, but in contrast enhances diversity in Thailand to the extent that it supercedes amphibian diversity.
It is apparent that both diversity of habitats and evolution play an important role in determining species diversity.

Resource partitioning among the lizards and amphibians appears to be similar. Food does not appear to be a limiting factor. The differing sizes, different feeding times and even the different emphasis on different invertebrate orders preclude competition. Some show a degree of dietary restriction, such as the agamids, which feed on ants (*Hymenoptera*:*Formicidae*), similarly *Ichnotropis capensis* feeds mostly on termites in the Study Area, as has been found by Broadley (1979) in Zimbabwe. *Panaspis wahlbergi* also feeds on termites but avoids competition by being able to forage deeper in the leaf letter than does *Ichnotropis*. Some predation pressure is exerted on the snake-eyed skink by the variable skink. Most lizard species are, however, opportunistic feeders as can be seen from Tables 15-18 (Chapter 5). The amphibians, although competing for food with the lizards, are nocturnal and, therefore, temporally and spatially avoid competition with lizards. Considerable overlap is experienced in their feeding behaviour but because the amphibians differ greatly in size and are mostly dependent on moisture before they become active, are able to gorge themselves should the climate and food availability become favourable. This is an adaptation not found among the lizards, which are in any event independent of moisture, except for breeding, to a limited degree.

Competition between amphibian species is avoided by differences in food and a few species are ant and termite specialists. This situation is reflected at Lamto where even more species including sympatric ones have adopted a similar approach, Barbault (1976 c).

Home ranges were determined for three lizard and one snake species. Home range size is to a degree determined by various other factors, such as food availability, shelter, breeding sites and so forth. Turner, Jennrich & Weintraub (1969, in Stamps 1977) observed a positive relationship between body mass and home range size in lizards and noted that males had larger home ranges than females. This appears to be somewhat contradictory as female mass is usually greater than that of males so that the situation should be the reverse. However, size of animal may also have a bearing on the amount of food ingested, leading back to a resource/home range size relationship.

The lizards observed on the Nylsvley Nature Reserve did not exhibit territoriality and only the dwarf gecko was observed to defend an area in his immediate vicinity, which indicates a movable site depending on whether it is used for basking, foraging or possibly shelter, although no interactions concerning the latter were observed. Both the lacertid, the Cape rough-scaled lizard as well as the variable skink displayed overlapping home ranges as did the vine snake. Unfortunately the work of Barbault at Lamto did not provide comparable results. Broadley (loc.cit.) also demarcated home ranges for the Cape rough-scaled lizard on the basis of recaptures but owing to the relative paucity of recaptures the results are highly variable but home ranges appear to be considerably smaller.

In conclusion a great deal more remains to be learned about herpetofaunal assemblages and ecosystems so that patterns and origins of species diversity, number and biomass as well as their biotic and abiotic interactions can be understood more fully. In the present study of an Assemblage the results suggest that snake species diversity is governed by habitat structure and water either directly or more probably indirectly through changes in prey community diversity. On the other hand, lizard species diversity is dependent on the diversity of habitat structure, and in biomass on the seasonality of the climate and predation. The amphibians are solely dependent on moisture and therefore breeding sites which are vital to these animals in the dry Burkea Savanna.

# CHAPTER 9

# CONCLUSIONS

It was stated in the Introduction that the Study formed part of the Savanna Ecosystem Project. The aims of this Study were threefold:

to determine species diversity and distribution of reptiles and amphibians in the Nylsvley Nature Reserve;

to determine the population size and biomass of reptiles and amphibians in the Ecosystem Study Area;

to determine the inter-relationships between the reptiles and amphibians and their physical and biotic environment.

Discussions pertaining to these aspects were made in previous Chapters and, therefore, this Chapter will deal solely with conclusions derived from the results of this Study.

Species diversity and distribution of reptiles and amphibians on the Nylsvley Nature Reserve can be attributed to a combination of floristic and edaphic conditions, of which the former is also a function of the latter. Nevertheless, through structural and plant species diversity, reptile and amphibian habitat niche separation is enhanced. Differences in herpetofaunal diversity between the different vegetation types on the Nylsvley Nature Reserve are evident and is greatest in the _Burkea africana_ - _Eragrostis pallens_ Savanna.

However, when species diversity is compared to other Ecosystems, as discussed in Chapter 8, it is apparent that climatic factors must be taken into consideration and in fact form the basis for species diversity and distribution. The low rainfall, vegetation and edaphic structural conditions are responsible for the greater diversity of terrestrial lizards in the Nylsvley Nature Reserve in comparison to the other two areas discussed. Lizards appear to be more tolerant of environmental extremes and increase in diversity in arid environments, but temperature remains the controlling factor.

The Nylsvley Nature Reserve and the Study Area, although situated south of the tropics, have a diversity more commensurate with more tropical regions which may be explained by the habitat and structural diversity of the area which enhances diversity despite the limiting climatic factors.

Population density and biomass are low in comparison to other areas with the exception of the amphibians where it is higher, which factor can be attributed both to the climate with dry and cold winters, as well as the sandy nature of the soil and its higher elevation as mass migration into the Study Area takes place annually.

All three populations, i.e. snakes, lizards and amphibians display fluctuations in density and biomass, both monthly as well as annually. These fluctuations are attributable to differences in rainfall and temperature, which affect reproductive success, food availability and movement, which in turn affect reproductive potential and survival. The necessity of the amphibians to move out of the area to breed (with one exception) and to congregate around localized water bodies in large concentrations, must make them vulnerable to predation and this is confirmed by the low return of marked adult amphibians. The large influx of young toads must also sustain a high mortality, as many snakes feed on them, while hibernation during winter and dehydration during migration back into the Study Area must also be excessive. Biomass and density fluctuations are due to emigration, immigration, rainfall and drought.

Five orders of invertebrates form the main food of the lizards and amphibians. It is apparent that most reptiles and amphibians are opportunistic feeders, feeding on the most abundant and easily attainable invertebrates at any one time. Some degree of specialization has taken place, particularly on invertebrates such as the Hymenoptera (Formicidae) and Isoptera (Termitidae) because they are abundant yet relatively unexploited food sources. Therefore, there are several snake, lizard and amphibian species which are myrmecophagous. Most snakes are also opportunistic but a few are relatively stenophagous, such as the blind and thread snakes, centipede-eater and egg-eater.

The lizards, with the exception of the common chameleon, do not display unique anatomical adaptations for prey capture or storage. Amphibians on the other hand have the ability to distend their stomachs considerably and can, therefore, gorge themselves should the opportunity arise. This is a result of the variable and erratic precipitation and is therefore advantageous under these conditions.

It is, however, apparent that there is sufficient prey biomass to support the reptiles and amphibians and this therefore cannot be considered as a limiting factor influencing abundance and biomass.

The pronounced seasonality of the climate has induced various reproductive strategies to allow for climatic variations experienced in the Study Area.

Reptile reproductive activity starts mainly in Spring in accordance with a rise in temperature. Most eggs are laid during early to mid-summer and the young hatch during mid-to-late summer. This coincides with a peak in food availability and the juvenile reptiles and amphibians are able to hibernate in good condition. Hatchling egg-eaters emerge during September at a time when bird eggs are most prevalent.

Similarly, the amphibians are well adapted to the variable climate. As soon as heavy rain has fallen, they migrate to open water in which they breed. Although outside the Study Area, pools form an integral part of the amphibians' survival strategy. Hatching of eggs and larval development proceeds rapidly and juveniles re-enter the Study Area approximately 1-1,5 km distant at an approximate age of two months.

Large numbers of eggs are laid and the success of this strategy is evident in the large immigration of juveniles into the Study Area. Contrast this to the only amphibian breeding in the Study Area, the common short-head frog which only lays 10-20 eggs in a hole in the ground in which larval development and metamorphosis takes place. It is apparent that most of the water-dependent amphibians have based their reproductive strategy on a 'hit and miss basis; while the largely water-independent frog ensures survival by laying small clutches of large eggs, thereby expending less energy.

Growth in both reptiles and amphibians is initially fairly rapid, particularly in summer but because of low temperatures and resulting reduced metabolic activity during winter, a step-like growth pattern is evident.

There is a negative correlation between growth rate and S/V size. Two strategies are apparent, one, a population turnover on an annual basis and two, the long-lived species. Both appear to be equally successful. If the long-lived species do not reproduce during one year, it will not unduly affect the population, whereas the position of the annual reptiles is more critical. They overcome this by laying relatively large clutches of eggs and more than one clutch may be laid during a season, so that at least some members of one clutch are able to survive the variations in climate.

Only one species of reptile or amphibian on the Nylsvley Nature Reserve lays eggs throughout the year, namely Lygodactylus capensis. Clutch size is small but as the eggs are hard-shelled, they can withstand most climatic conditions and in fact a peak in egg-laying occurs during winter, indicating the success of their adaptation.

Movement, home ranges and territoriality are all governed by food availability, shelter and the chance to reproduce. Few species in the Study Area exhibit territoriality, some have home ranges. Overlap in home ranges between individuals of the same species as well as of different species indicate that these aspects are not limiting, although shelter may well be. Movements by snakes appear to be random and therefore possibly exploratory.

In conclusion it can be stated that the Ecosystem Study Area is unique in the diversity of its herpetofauna. This is due to increased structure of the habitat but is rigidly controlled by the seasonality of the climate; in particular temperature and rainfall against which the reptiles and amphibians have developed various strategies to ensure the survival of the species. These strategies are mainly apparent in their reproductive methods, as well as other aspects of their life style.

It is apparent from the relative densities and biomass of these animals in the Burkea africana Savanna that their impact as a whole on the Ecosystem is minimal, but they are still an integral part of the community and who knows what would happen should this group of lower vertebrates be removed from this system. They do form a link in the trophic chain and therefore in this respect may be important. They support a large number of predators, including birds, mammals, insects, reptiles and amphibians while they again prey on invertebrates and other vertebrates.

This process from climate to vegetation to invertebrates and so forth, up the trophic chain, to the decomposers, forms a continuous ring and should one of the links be removed, the system could collapse. The flow of energy will be interrupted and ultimately a more depauperate system will develop. This is the process of desertification.

# SUMMARY

This study formed part of the initial phase of the co-operative study to determine the structure and functioning of a Savanna Ecosystem. This study, therefore, was aimed at determining diversity, biomass, structure and functioning of reptile and amphibian species in the Burkea africana - Eragrostis pallens Savanna. Studies were initiated during May 1975, lasting until May 1977. The Nylsvley Nature Reserve as a whole contains a wide diversity of reptiles and amphibians, and this is exemplified by the Study Area which showed the greatest number of species, including 11 amphibians and 41 reptiles.

On account of mark-recapture limitations, it was only possible to determine population size of each group of the herpetofauna such as amphibians, snakes and lizards, with two exceptions, namely the Cape dwarf gecko and the vine snake, which were censussed separately. Population size and biomass fluctuated throughout the year as well as annually with a mean of 58,79 amphibians /ha with a biomass of 593,4 g/ha, 3,08 snakes /ha with a biomass of 93,36 g/ha and 62,27 lizards /ha with a biomass of 64,36 g/ha. The Cape dwarf gecko contributed considerably to the mean lizard density and biomass, with 55,1 geckos/ha and a biomass of 41,87 g/ha.

Reptiles and amphibians are dependent on a certain minimum temperature and rainfall for activity to take place. A mean minimum of 10°C is essential before activity takes place while rain is essential for amphibian activity.

Both reptiles and amphibians feed mainly on prey of the same five invertebrate orders which indicates that food is not a limiting factor. Competition is avoided temporally, spatially and with size of prey. A degree of specialization among some lizards and amphibians is apparent and is centred around the Hymenoptera (Formicidae) and Isoptera (Termitidae). Some snakes also show a degree of specialization.

Breeding strategies are aimed at overcoming seasonal climatic variations. The virtual synchronization of egg laying over a period of two months and the hatching of the young at a

time most beneficial to the young are important in reproductive success. Amphibians show two different reproductive strategies. One is reliant on movement out of the Study Area to seasonally inundated pans in which large quantities of eggs are laid in the hope that some survive. The other is independent of surface water but instead lays small clutches of large eggs in an underground nest dug by both the male and female.

Growth is generally rapid but slows down in winter. A differential growth rate is apparent between the sexes.

Home ranges and territoriality are discussed. Home ranges vary in size from 4,6 ha for the vine snakes and 40 sq m. for the Cape dwarf gecko. On account of overlap of home ranges, competition for food is unlikely.

Reptiles and amphibians or herpetofaunal assemblages at Nylsvley are discussed according to their food and feeding, reproduction and growth, as well as their spatial requirements. Frequent comparisons are made with similar studies and how these reflect on the situation in the _Burkea africana_ Savanna. Finally, the conclusion hinges around the structure and functioning of such a herpetofaunal assemblage, and the origins and maintenance of such an organization. Factors contributing include habitat structure, both biotic and abiotic, while latitude also has a role.

# OPSOMMINGS

Die studie het deel uitgemaak van die begin fase van die ko-operatiewe studie om die struktuur en funksionering van 'n Savanna Ekosisteem te bepaal. Die doelwit was om diversiteit, biomassa asook struktuur en funksioneering van reptiel en amfibie spesies in die *Burkea africana* - *Eragrostis pallens* Savanna te bepaal. Opnames is gedurende Mei 1975 geloots en het tot Mei 1977 geduur.

Die Nylsvley Natuurreservaat as 'n geheel toon 'n groot verskeidenheid amfibieë en reptiele en dit is bekragtig deur die Studie Gebied wat die grootste samestelling van dié diere in die reservaat het, naamlik 11 amfibie en 41 reptiel soorte.

As gevolg van merk-hervangs tegnieke en die inherente besprekinge daarvan, was dit slegs moontlik om bevolkingsgrootte vir die drie groepe naamlik slange, akkedisse en paddas te kon evalueer, met twee uitsonderings naamlik die van die gewone dwerggeitjie en die van die takslang wat afsonderlik gemonitor is. Bevolkingsgrootte en biomassa het deur die jaar gewissel sowel as jaarliks met 'n gemiddeld van 58,79 amphibieë /ha met 'n biomassa van 593,4 g/ha, 3.08 slange /ha met 'n biomassa van 93,36 g/ha, en 62,27 akkedisse /ha met 'n biomassa van 64,36 g/ha. Die gewone dwerggeitjie het heelwat toe die gemiddelde akkedis digtheid en biomassa bygedra met 55,1 geitjies /ha en 'n biomassa van 41,78 g/ha.

Reptiele en amfibieë is afhanklik van 'n sekere minimum temperatuur en reënval vir aktiwiteit. 'n Gemiddeld minimum van 10°C is essentieël voordat reptiel aktiwiteit plaasvind, terwyl die amfibieë reënval benodig voordat hulle aktief word.

Beide reptiel en amfibië vreet hoofsaaklik diere van dieselfde vyf ongewerwelde ordes wat daarop dui dat voedsel nie 'n beperkende faktor is nie. Kompetisie word vermy deurdat die diere op verskillende tye en plekke, asook verskillende prooi grotes, vreet. 'n Mate van spesialiseering word onder party akkedisse en amfibie soorte gevind wat hoofsaaklik Hymenoptera (Formicidae) en Isoptera (Termitidae) vreet. Sommige slang soorte toon ook 'n mate van voedsel spesialiseering.

Teel strategieë is daarop gemik om seisoenale klimaatsvariasies te oorkom. Die eierlê periode, wat feitlik oor 'n tydperk van twee maande gesinchroniseer word, asook die uitbroei van die kleintjies in 'n tyd wat tot voordeel van hulle is, is belangrik vir teelsukses. Die ampfibieë toon twee verskillende teel strategieë. Die een is afhanklik van beweging uit die Studiegebied na seisoenale panne waarin groot hoeveelhede eiers gelê word met die hoop dat party oorleef. Die ander soort is onafhanklik van opgaar water, en lê klein broeisels, groot eiers in 'n ondergrondse nes wat deur beide mannetjie en wyfie gegrawe word.

Die groeivermoë is oor die algemeen vinnig maar stadiger gedurende die winter. 'n Verskillende groei tempo word deur mannetjie en wyfie reptiele gehandhaaf.

Tuisgebiede en territorialiteit word bespreek. Tuisgebiede wissel in grootte van 'n gemiddeld van 4,6 ha vir die takslang tot 40 vk.m. vir die gewone dwerggeitjie. As gevolg van oorvleueling van tuisgebiede word kompetisie vir voedsel onwaarskynlik.

Reptiele en amfibieë of herpetofaunistiese samestellings op die Nylsvley Natuurreservaat is bespreek ten opsigte van voedsel en voeding, voorplanting en groei sowel as die ruimte wat hul benodig. Verskeie vergelykings word met soortgelyke studies gemaak, en hoe dié vergelyk met die situasie in die *Burkea africana* Savanna.

Laastens is die bespreking en gevolgtrekkings omtrent die struktuur en funksionering van so 'n herpetofaunistiese samestelling saamgevat, asook die oorsprong en behoud van so 'n samestelling. Faktore wat hiertoe bydra sluit die habitat struktuur van beide biotese sowel as abiotiese komponente in, terwyl breetegrade ook 'n rol speel.

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## APPENDIX A

Incidence of prey per lizard species in the <u>Burkea africana</u> Savanna

| | Lizard species | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| No. of stomachs | 99 | 187 | 174 | 15 | 4 | 1 | 2 | 1 | 1 | 1 |
| Prey | * Ic | Mv | Lc | Pw | Ni | Nto | Gf | Aa | Pb | Aat. |
| Araneae | 31 | 41 | 52 | 11 | 2 | | 1 | | 1 | |
| Salticidae | | 1 | | | | | | | | |
| Solifugae | | 1 | | | | | | | | |
| Isoptera | 6 | 3 | 4 | 3 | | | | | | |
| Hodotermitidae | 1 | 2 | 1 | | | | | | | |
| Terminitidae | 28 | 8 | 8 | 1 | | 1 | | | | |
| Diplopoda | 3 | 6 | 4 | | | | | | | |
| Chilopoda | 2 | | | | | | | | | |
| Diptera | 1 | 2 | 2 | 1 | | | | 1 | | |
| Culicidae | | 4 | 8 | | | | | | | |
| Acilicidae | | 1 | 1 | | | | | | | |
| Tipulidae | | 1 | | | | | | | | |
| Calliphoridae | | | 1 | | | | | | | |
| Coleoptera | 14 | 35 | 36 | 1 | 2 | | | | | 1 |
| Elateridae | 7 | 7 | 7 | | | | | | | |
| Cleridae | | | 4 | | | | | | | |
| Buprestidae | 2 | 5 | 6 | | | | | | | |
| Curculionidae | 3 | 10 | | | | | | | | |
| Chrysomelidae | | 4 | 2 | | | | | | | |
| Eumopinae | | 1 | | | | | | | | |
| Hispinae | 1 | 1 | | | | | | | | |
| Scarabeidae | 1 | 3 | | | | | | | | |
| Ontophagus | | 1 | | | | | | | | |
| Melolonthinae | 1 | 2 | | | | | | | | |
| Coccinellidae | | 1 | 2 | | | | | | | |
| Lyctidae | | 1 | 3 | | | | | | | |
| Tenebrionidae | 2 | 2 | | | | | | | | |
| Carabidae (larvae) | 1 | | | | | | | | | |
| Bostrychidae | | | 1 | | | | | | | |
| Brentidae | | | 1 | | | | | | | |
| Staphylididae | | | 1 | | | | | | | |
| Melyridae | | | 2 | | | | | | | |

APPENDIX A (Continued)

| Prey * | Ic | Mv | Lc | Pw | Ni | Nto | Gf | Pa | Pb | Aat. |
|---|---|---|---|---|---|---|---|---|---|---|
| Mollusca | | | 1 | | | | | | | |
| Homoptera | | 5 | 2 | 2 | | | | | | |
| Cercopidae | | | 1 | | | | | | | |
| Jassidae | 1 | 1 | 8 | 1 | | | | | | |
| Pseudococcidae | | | 3 | | | | | | | |
| Aphididae | | | 3 | | | | | | | |
| Lepidoptera (larvae) | 8 | 14 | 25 | 1 | | | | | | |
| (adults) | 1 | 6 | 8 | | | | | | | |
| Orthoptera | 4 | 7 | 3 | | | | | | | |
| Acrididae | 12 | 55 | 14 | | 1 | | 1 | | 1 | |
| Gryllidae | 4 | 5 | 1 | | | | | | | |
| Tettigonidae | 1 | | | | | | | | | |
| Hemiptera | 3 | 18 | 13 | 1 | | | | | 1 | |
| Lygaeidae | | 3 | 1 | | | | | | | |
| Pentatomidae | 1 | 2 | | | | | | | | |
| Hymenoptera | | | 4 | | | | | | | |
| Apidae | | | 1 | | | | | | | 1 |
| Formicidae | 2 | 5 | 15 | 1 | | | | | | |
| Camponotus | 1 | 1 | 4 | | | | | | | |
| Pheidole | | 1 | 2 | | | | | | | |
| Crematogastor | | | 8 | 1 | | | | | | |
| Braconidae | | 1 | | | | | | | | |
| Isoptera | 1 | 3 | 1 | | | | | | | |
| Pseudoscorpiones | | | 4 | | | | | | | |
| Psocoptera | | | 1 | | | | | | | |
| Dictyoptera | | | | | | | | | | |
| Blattidae | | 8 | | | | | | | | |
| Mantidae | 1 | 3 | 2 | | | 1 | | | | |
| Odonata | | 4 | 1 | | | | | | | |
| Heteroptera | | | | | | | | | | |
| Reduviidae | | 2 | | | | | | | | |
| Neuroptera | | | | | | | | | | |
| Myrmeleontidae (nymph) | 1 | 1 | | | | | | | | |
| Chrysopidae | | | 1 | | | | | | | |
| Acarina | | | 2 | | | | | | | |
| Scincidae | | 2 | | | | | | | | |

* Ic = *Ichnotropis capensis* Pw = *Panaspis wahlbergi* Gf = *Gerrhosaurus flavigularis*

Mv - *Mabuya varia* Ni = *Nucras intertexta* Aa = *Agama aculeata*

Lc = *Lygodactylus capensis* Nto = *Nucras taeniolata ornata*

Pb = *Pachydactylus bibronii* Aat = *Agama atricollis*

APPENDIX B.

Incidence of prey per amphibian species in the savanna ecosystem.

| | | Amphibian species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Number of stomachs | | 53 | 39 | 1 | | 1 | 10 | 5 | 6 | 5 |
| Prey | * | Ks. | Ba. | B. gut. | Bg | Bc | Pb | Pn | Cb | Tc |
| Araneae | | 32 | 3 | 0 | 8 | 0 | 1 | 1 | 0 | 1 |
| Lycosidae | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hemiptera | | 8 | 0 | 0 | 9 | 1 | 0 | 0 | 0 | 0 |
| Reduviidae | | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| Hereroptera | | | | | | | | | | |
| Lygaeidae | | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hymenoptera | | | | | | | | | | |
| Vespidae | | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Formicidae | | | 14 | 1 | 0 | 0 | 5 | 2 | 5 | 0 |
| Camponotus | | 12 | 11 | 0 | 30 | 1 | 3 | 0 | 0 | 0 |
| Pheidole | | 1 | 16 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| Crematogaster | | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| Orthoptera | | | | | 2 | 0 | 0 | 0 | 0 | 0 |
| Acrididae | | 15 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 0 |
| Gryllidae | | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mantidae | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera | | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Acilicidae | | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lepidoptera | | | | | | | | | | |
| larvae | | 14 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| adults | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Coleoptera & larvae | | 15 | 2 | 1 | 26 | 1 | 0 | 0 | 0 | 0 |
| Chrysomelidae | | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Nitidulidae | | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Histeridae | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Buprestidae | | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Curculionidae | | 1 | 1 | 0 | 11 | 0 | 0 | 0 | 0 | 0 |
| Lyctidae | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Tenebrionidae | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Elateridae | | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Scarabaeidae | | | | | 1 | 0 | 0 | 0 | 0 | 0 |
| Melolonthinae | | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

APPENDIX B (Continued)

| | Ks. | Ba. | B. gut | Bg | Bc | Pb | Pn | Cb | Tc |
|---|---|---|---|---|---|---|---|---|---|
| Lampyridae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Carabidae | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Isoptera | | | | | | | | | |
| Termitidae | 11 | 14 | 0 | 4 | 0 | 0 | 0 | 2 | 0 |
| alates | 6 | 4 | 1 | 0 | 0 | 2 | 1 | 0 | 0 |
| Hodotermitidae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| alates | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Dictyoptera | | | | | | | | | |
| Blattidae | 4 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Homoptera | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Jassidae | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Acarina | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dermaptera | | | | | | | | | |
| Forficulidae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Pseudoscorpiones | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Solifugae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Chilopoda | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Mollusca | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Diplopoda | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Psocoptera | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |

Ks = *Kassina senegalensis* Ba = *Breviceps adspersus*

B.gut = *Bufo gutturalis* Bg = *Bufo garmani*

Bc = *Bufo carens* Pb = *Phrynomerus bifasciatus*

Pn = *Phrynobatrachus natalensis* Cb = *Cacosternum boettgeri*

Tc = *Tomopterna cryptotis*

**Lygodactylus capensis**

| | | | | | | |
|---|---|---|---|---|---|---|
| | 6 | 5 | 3 | 3 | 6 | |
| | 4 | 2 | 2 | 9 | | 2 |
| 5 | 3 | 4 | 2 | 2 | 7 | 4 |
| 5 | 3 | 8 | 8 | | 4 | 5 |
| 4 | 6 | 9 | 5 | 9 | 6 | 8 |
| 2 | 8 | 7 | 8 | 16 | 2 | 5 |
| 7 | 8 | 5 | 6 | 8 | 10 | 7 |

**Bufo garmani**

| | | | | | | |
|---|---|---|---|---|---|---|
| 31 | 30 | 27 | 15 | 16 | 5 | 9 |
| 21 | 47 | 35 | 23 | 16 | 13 | 12 |
| 16 | 15 | 20 | 31 | 3 | 15 | 13 |
| 38 | 31 | 9 | 24 | 6 | 10 | 13 |
| 35 | 45 | 16 | 14 | 13 | 13 | 14 |
| 27 | 27 | 16 | 6 | 16 | 7 | 8 |
| 22 | 8 | 12 | 14 | 7 | 12 | 11 |

**Mabuya varia**

| | | | | | | |
|---|---|---|---|---|---|---|
| 8 | 9 | 19[a] | 7 | 7 | 16 | 6 |
| 7 | 30 | 6 | 6 | 12 | 11 | 7 |
| 20 | 24 | 13 | 13 | 3 | 8 | 8 |
| 18 | 16 | 2 | 6 | 6 | 4 | 6 |
| 12 | 26 | 11 | 9 | 6 | 3 | 4 |
| 6 | 33 | 12 | 12 | 7 | 14 | 6 |
| 7 | 5 | 1 | | 6 | 9 | 6 |

**Breviceps adspersus**

| | | | | | | |
|---|---|---|---|---|---|---|
| 4 | 2 | | 2 | 1 | 1 | 1 |
| | 2 | | | 5 | | 6 |
| 1 | | 1 | 7 | 1 | 1 | 3 |
| 3 | 3 | 3 | 5 | 6 | | |
| 6 | 2 | 1 | 4 | 2 | 6 | 4 |
| 5 | 2 | 8 | 2 | 6 | 7 | 4 |
| 1 | 4 | 11 | 5 | 5 | 3 | 7 |

Appendix C. Distribution of various reptiles and amphibians in the Study Area showing anomalies, May 1975 - May 1977.

**Dasypeltis s. scabra**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● | ● | ● 2 | ● | ● | ● | ● |
| ● | ● 1 | ● | ● | ● | ● 1 | ● |
| ● 3 | ● 1 | ● 1 | ● | ● | ● | ● |
| ● | ● | ● 1 | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● 1 | ● | ● 1 | ● | ● 1 | ● 1 | ● |
| ● 2 | ● 1 | ● 1 | ● 2 | ● 1 | ● | ● |

**Aparallactus capensis**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 1 | ● | ● | ● | ● | ● 1 | ● |
| ● | ● | ● 1 | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● 1 | ● | ● | ● 3 | ● | ● | ● |
| ● | ● | ● | ● 1 | ● | ● | ● |
| ● | ● 2 | ● | ● | ● | ● 2 | ● 1 |
| ● | ● | ● | ● | ● 3 | ● 1 | ● |

**Phrynomerus bifasciatus**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 2 | ● | ● | ● 1 | ● 1 | ● 1 | ● 1 |
| ● | ● | ● 1 | ● | ● | ● 2 | ● |
| ● 2 | ● | ● 1 | ● | ● 1 | ● | ● |
| ● 1 | ● 2 | ● | ● | ● | ● | ● 1 |
| ● 1 | ● | ● 2 | ● 3 | ● 1 | ● 3 | ● |
| ● 1 | ● 2 | ● 3 | ● | ● | ● | ● 1 |
| ● 4 | ● 2 | ● | ● 1 | ● | ● | ● |

**Prosymna sundevallii**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● | ● | ● 1 | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● 1 |
| ● | ● | ● | ● | ● | ● | ● |
| ● | ● 1 | ● | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● | ● | ● 1 | ● | ● | ● 1 | ● 3 |
| ● | ● | ● | ● | ● | ● | ● |

**Lycophidion capense**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 1 | ● | ● 1 | ● 2 | ● | ● | ● |
| ● | ● | ● 1 | ● | ● | ● 3 | ● |
| ● 1 | ● | ● | ● 1 | ● | ● | ● |
| ● | ● | ● 1 | ● | ● | ● | ● |
| ● | ● 1 | ● 2 | ● | ● | ● | ● |
| ● | ● 1 | ● | ● | ● | ● 1 | ● |
| ● | ● | ● 1 | ● 1 | ● | ● 1 | ● |

**Lygosoma sundevallii**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 1 | ● 1 | ● 3 | ● 2 | ● | ● | ● |
| ● | ● 4 | ● 1 | ● 1 | ● | ● | ● |
| ● | ● | ● | ● | ● | ● 1 | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● 2 | ● | ● | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |

**Ichnotropis capensis**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 2 | ● 5 | ● 5 | ● 21 | ● 15 | ● 4 | ● 11 |
| ● 1 | ● 6 | ● 19 | ● 6 | ● 26 | ● 20 | ● 21 |
| ● 7 | ● 8 | ● | ● 5 | ● 1 | ● 7 | ● 18 |
| ● 4 | ● 13 | ● 11 | ● 9 | ● 11 | ● 22 | ● 22 |
| ● 14 | ● 11 | ● 16 | ● 12 | ● 10 | ● 21 | ● 14 |
| ● 10 | ● 15 | ● 9 | ● 8 | ● 8 | ● 12 | ● 37 |
| ● 5 | ● 20 | ● 10 | ● 11 | ● 23 | ● 21 | ● 28 |

**Panaspis wahlbergi**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 4 | ● 2 | ● 1 | ● 4 | ● | ● 2 | ● 2 |
| ● 1 | ● 8 | ● 7 | ● | ● | ● 1 | ● |
| ● 2 | ● 2 | ● | ● 1 | ● | ● 4 | ● 3 |
| ● 5 | ● 1 | ● 2 | ● 7 | ● 2 | ● 1 | ● 2 |
| ● | ● 2 | ● 3 | ● 7 | ● 5 | ● 5 | ● |
| ● 6 | ● 7 | ● 5 | ● | ● 7 | ● 5 | ● 2 |
| ● 5 | ● 6 | ● | ● | ● 11 | ● 4 | ● |

**Kassina senegalensis**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 18 | ● 9 | ● 23 | ● 12 | ● 6 | ● 12 | ● 14 |
| ● 11 | ● 22 | ● 13 | ● 23 | ● 13 | ● 12 | ● 20 |
| ● 17 | ● 34 | ● 35 | ● 23 | ● 7 | ● 9 | ● 13 |
| ● 18 | ● 18 | ● 24 | ● 18 | ● 6 | ● 11 | ● 9 |
| ● 29 | ● 17 | ● 26 | ● 12 | ● 14 | ● 12 | ● 26 |
| ● 17 | ● 39 | ● 11 | ● 12 | ● 23 | ● 19 | ● 13 |
| ● 46 | ● 18 | ● 23 | ● 11 | ● 7 | ● 12 | ● 15 |

**Psammophis s. brevirostris**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● | ● 2 | ● 1 | ● 2 | ● 5 | ● 1 | ● |
| ● 1 | ● 2 | ● 3 | ● 3 | ● 1 | ● 4 | ● 1 |
| ● 4 | ● | ● 2 | ● 2 | ● 2 | ● | ● 1 |
| ● 1 | ● 3 | ● 3 | ● 2 | ● 1 | ● 1 | ● 4 |
| ● 1 | ● 1 | ● 3 | ● 2 | ● 1 | ● 2 | ● 2 |
| ● 3 | ● 1 | ● 1 | ● 4 | ● 3 | ● 2 | ● 3 |
| ● 2 | ● 5 | ● 2 | ● 2 | ● 1 | ● 5 | ● 6 |

**Naja haje annulifera**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● | ● | ● 1 | ● | ● | ● | ● 1 |
| ● 2 | ● | ● | ● | ● 1 | ● 1 | ● |
| ● | ● | ● 2 | ● | ● 1 | ● 1 | ● |
| ● | ● | ● | ● | ● | ● 1 | ● |
| ● | ● 1 | ● 1 | ● 1 | ● | ● 1 | ● |
| ● 1 | ● 1 | ● 1 | ● | ● | ● 1 | ● 1 |
| ● 3 | ● | ● 2 | ● | ● 1 | ● | ● 2 |

**Crotaphopeltis hotamboeia**

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 1 | ● 2 | ● | ● 1 | ● | ● 1 | ● 4 |
| ● | ● | ● | ● 1 | ● | ● | ● |
| ● 2 | ● | ● 2 | ● | ● 1 | ● 1 | ● 1 |
| ● | ● | ● 1 | ● | ● | ● 1 | ● 2 |
| ● 1 | ● 1 | ● 1 | ● | ● | ● 1 | ● 1 |
| ● 3 | ● 2 | ● | ● | ● 1 | ● 4 | ● 2 |
| ● 2 | ● | ● 1 | ● 4 | ● 1 | ● | ● 1 |

### Philothamnus semivariegatus

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|---|---|---|---|---|---|---|
| ● | ● 2 | ● 1 | ● | ● 1 | ● | ● |
| ● | ● | ● 1 | ● | ● | ● 1 | ● 1 |
| ● 1 | ● | ● | ● | ● | ● | ● 1 |
| ● | ● | ● | ● 1 | ● | ● 1 | ● |
| ● | ● | ● | ● | ● 1 | ● | ● |
| ● | ● | ● | ● | ● | ● | ● 1 |
| ● | ● 1 | ● 1 | ● 1 | ● | ● 1 | ● |

### Phrynobatrachus natalensis

| | | | | | | |
|---|---|---|---|---|---|---|
| ● | ● | ● | ● | ● 1 | ● 1 | ● |
| ● | ● | ● 1 | ● | ● | ● 1 | ● |
| ● 1 | ● | ● 1 | ● 1 | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● | ● | ● | ● | ● 1 | ● | ● |
| ● 1 | ● | ● | ● | ● 3 | ● | ● |
| ● 1 | ● | ● 1 | ● | ● | ● | ● |

### Bufo carens

| | | | | | | |
|---|---|---|---|---|---|---|
| ● 1 | ● | ● | ● | ● | ● | ● |
| ● | ● | ● | ● 1 | ● | ● | ● |
| ● | ● | ● 1 | ● | ● | ● | ● 2 |
| ● | ● | ● | ● | ● | ● | ● |
| ● | ● | ● 1 | ● | ● 1 | ● | ● |
| ● | ● 3 | ● | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |

### Cacosternum boettgeri

| | | | | | | |
|---|---|---|---|---|---|---|
| ● | ● | ● | ● | ● 1 | ● | ● 1 |
| ● 2 | ● | ● | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● | ● | ● | ● 1 | ● | ● | ● |
| ● | ● | ● 1 | ● | ● 1 | ● | ● |
| ● | ● | ● 1 | ● 1 | ● | ● | ● |
| ● | ● 2 | ● | ● | ● | ● 1 | ● |

### Tomopterna cryptotis

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|---|---|---|---|---|---|---|
| ● 3 | ● | ● 3 | ● 1 | ● 1 | ● | ● |
| ● 4 | ● 1 | ● | ● | ● | ● | ● |
| ● 1 | ● | ● | ● 1 | ● | ● | ● |
| ● 1 | ● 3 | ● 2 | ● | ● | ● | ● 1 |
| ● 1 | ● | ● 1 | ● | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● 3 | ● | ● | ● | ● | ● | ● 3 |

### Mehelya nyassae

| | | | | | | |
|---|---|---|---|---|---|---|
| ● | ● | ● | ● | ● | ● 1 | ● |
| ● | ● 2 | ● 1 | ● | ● 1 | ● 1 | ● 3 |
| ● 1 | ● 1 | ● | ● | ● | ● | ● |
| ● 1 | ● | ● | ● | ● | ● | ● |
| ● | ● 1 | ● | ● 1 | ● | ● | ● |
| ● | ● | ● | ● | ● | ● | ● |
| ● 1 | ● 3 | ● | ● | ● 1 | ● | ● |