

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

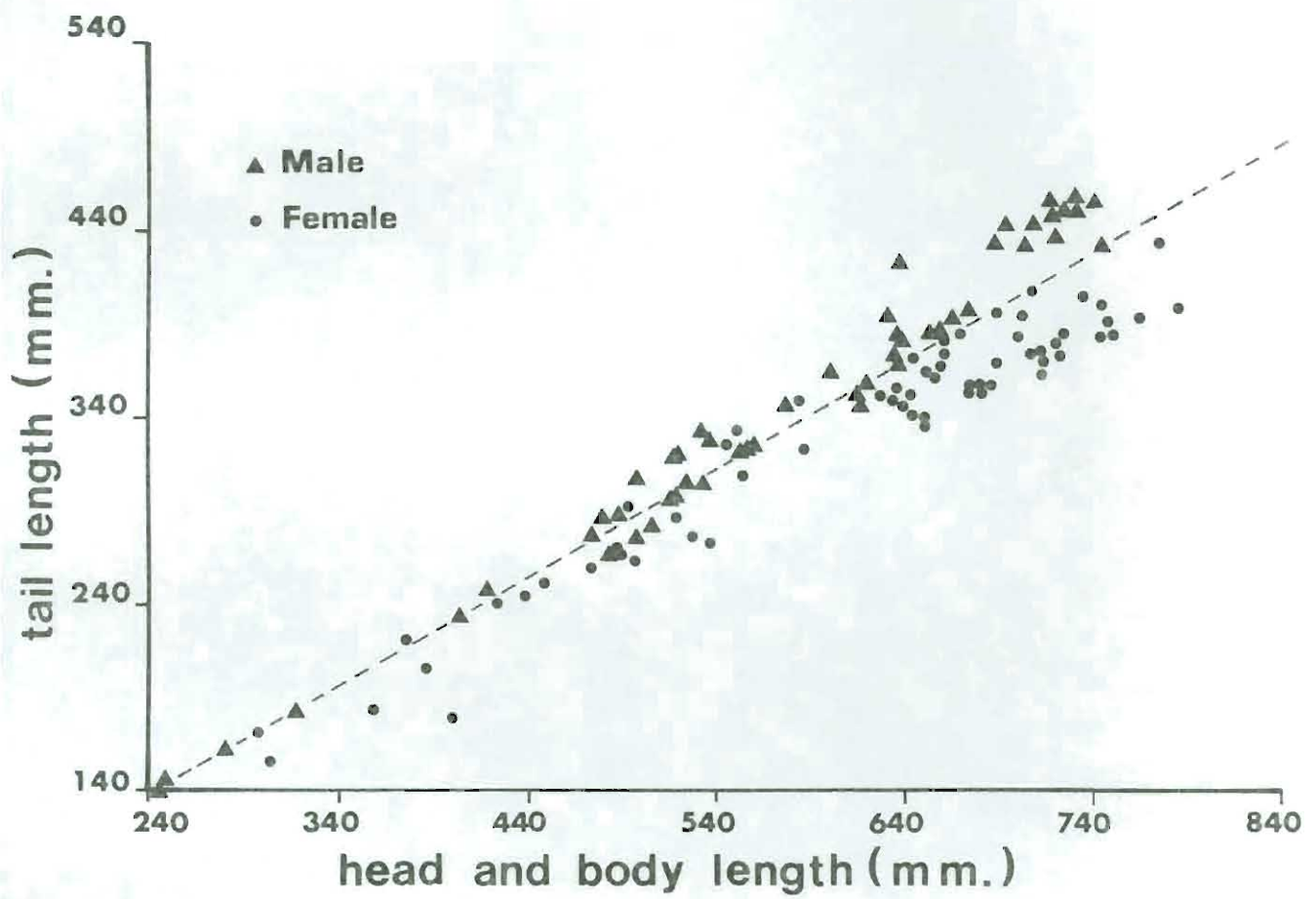


Figure 45. Sexual dimorphism in Thelotornis capensis in the Burkea africana - Eragrostis pallens Study Area.

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				
<u>Python sebae</u>	3	all males		
<u>Boaedon fuliginosus</u>	2	"		
<u>Lycophidion capense</u>	18	7	11	1:1,57
<u>Mehelya nyassae</u>	20	19	1	1:0,05
<u>Mehelya capensis</u>	3	all males		
<u>Philothamnus semi-variegatus</u>	22	18	4	1:0,22
<u>Philothamnus hoplogaster</u>	1	male		
<u>Prosymna sundevallii</u>	12	10	2	1:0,20
<u>Dasypeltis scabra</u>	20	15	5	1:0,33
<u>Telescopus semiannulatus</u>	4	3	1	1:0,33
<u>Dispholidus typus</u>	23	12	11	1:0,92
<u>Thelotornis capensis</u>	205	118	87	1:0,73
<u>Crotaphopeltis hotamboeia</u>	52	34	18	1:0,53
<u>Psammophylax tritaeniatus</u>	6	4	2	1:0,50
<u>Psammophis s. brevirostris</u>	130	90	40	1:0,44
<u>Psammophis jallae</u>	4	male		
<u>Amblyodipsas polylepis</u>	1	male		
<u>Xenocalamus bicolor australis</u>	2	male		
<u>Aparallactus capensis</u>	23	10	13	1:1,30
<u>Naje haje annulifera</u>	29	27	2	1:0,07
<u>Naje mossambica</u>	7	male		
<u>Dendroaspis polylepis</u>	4	male		
<u>Bitis arietans</u>	10	5	5	1:1

Table 25 (continued)

Species	Number in sample	Sex		Ratio Male:Female
		Male	Female	
Lizards				
<u>Lygodactylus capensis</u>	883	562	321	1:0,57
<u>Pachydactylus capensis</u>	4	2	2	1:1
<u>Pachydactylus bibroni</u>	6	3	3	1:1
<u>Agama atricollis</u>	13	7	6	1:0,86
<u>Chamaeleo dilepis</u>	2	1	1	1:1
<u>Lygosoma sundevallii</u>	30	19	11	1:0,58
<u>Mabuya capensis</u>	1	male	-	-
<u>Mabuya s. punctatissimus</u>	1	male	-	-
<u>Mabuya varia</u>	672	470	202	1:0,43
<u>Panaspis wahlbergi</u>	311	110	201	1:1,83
<u>Ichnotropis capensis</u>	1118	669	449	1:0,67
<u>Ichnotropis squamulosa</u>	1	male	-	-
<u>Nucras intertexta</u>	9	6	3	1:0,50
<u>Gerrhosaurus flavigularis</u>	9	4	5	1:1,25
<u>Varanus e. albigularis</u>	21	20	1	1:0,05
Amphibians				
<u>Bufo garmani</u>	320	131	189	1:1,44
<u>Bufo gutturalis</u>	30	7	23	1:3,29
<u>Bufo carens</u>	11	2	9	1:4,50
<u>Breviceps adsperus</u>	200	117	83	1:0,71
<u>Phrynomerus bifasciatus</u>	41	7	34	1:4,96
<u>Tomopterna cryptotis</u>	37	4	33	1:8,25
<u>Phrynobatrachus natalensis</u>	14	4	10	1:2,50
<u>Cacosternum boettgeri</u>	13	1	12	1:12,00
<u>Kassina senegalensis</u>	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 mm 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 semi-variegatus 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. semi-annulatus 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 brevirostris 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 $\frac{+}{-}$ 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 $\frac{+}{-}$ 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 brevirostris 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) 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 52 period	10	16	(3G) 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 Crotaphopeltis hotamboeia in the Burkea africana 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 1M	(1G) 6

1M = Mating female.

Table 31. Distribution of the three age classes of Naja haje annulifera in the Burkea africana 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 3(2G)		5

1G = Gravid female.

Table 32. Distribution of the three age classes of Lycophidion capense 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	?	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) 3	2	2	1	1			1	3	3	5	(1G) 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 desiccate 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 desiccation 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 skaapstekker, 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

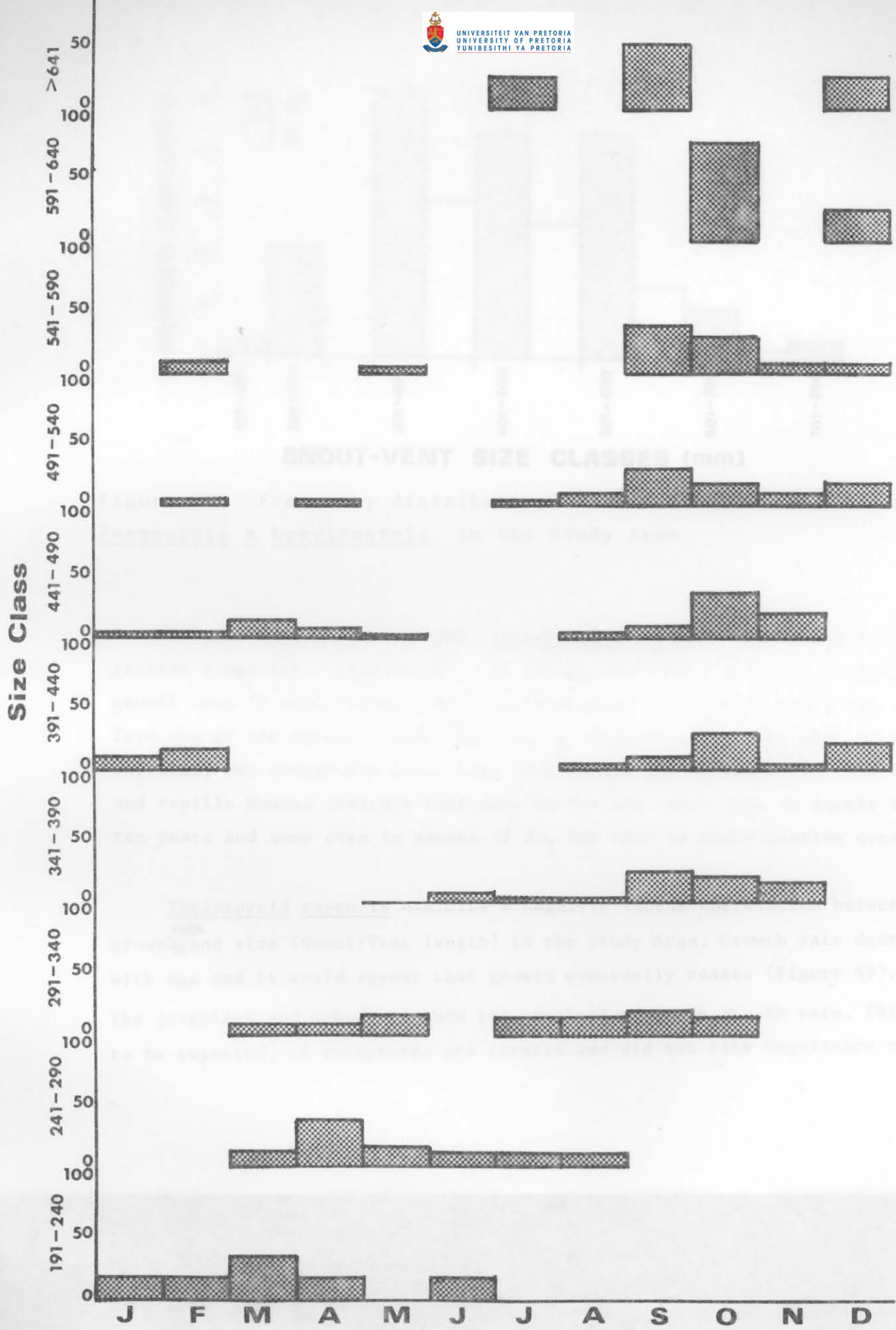


Figure 46. Monthly distribution of size classes of *Psammophis s. brevisrostris* in the Study Area.

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.

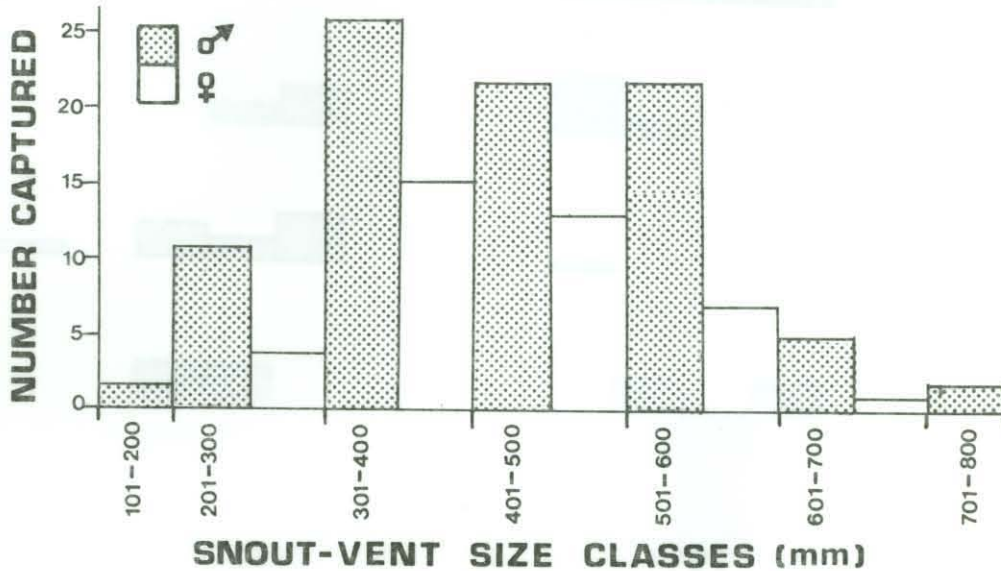


Figure 47. Frequency distribution of size classes and sex of Psammophis s. brevirostris in the Study Area.

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

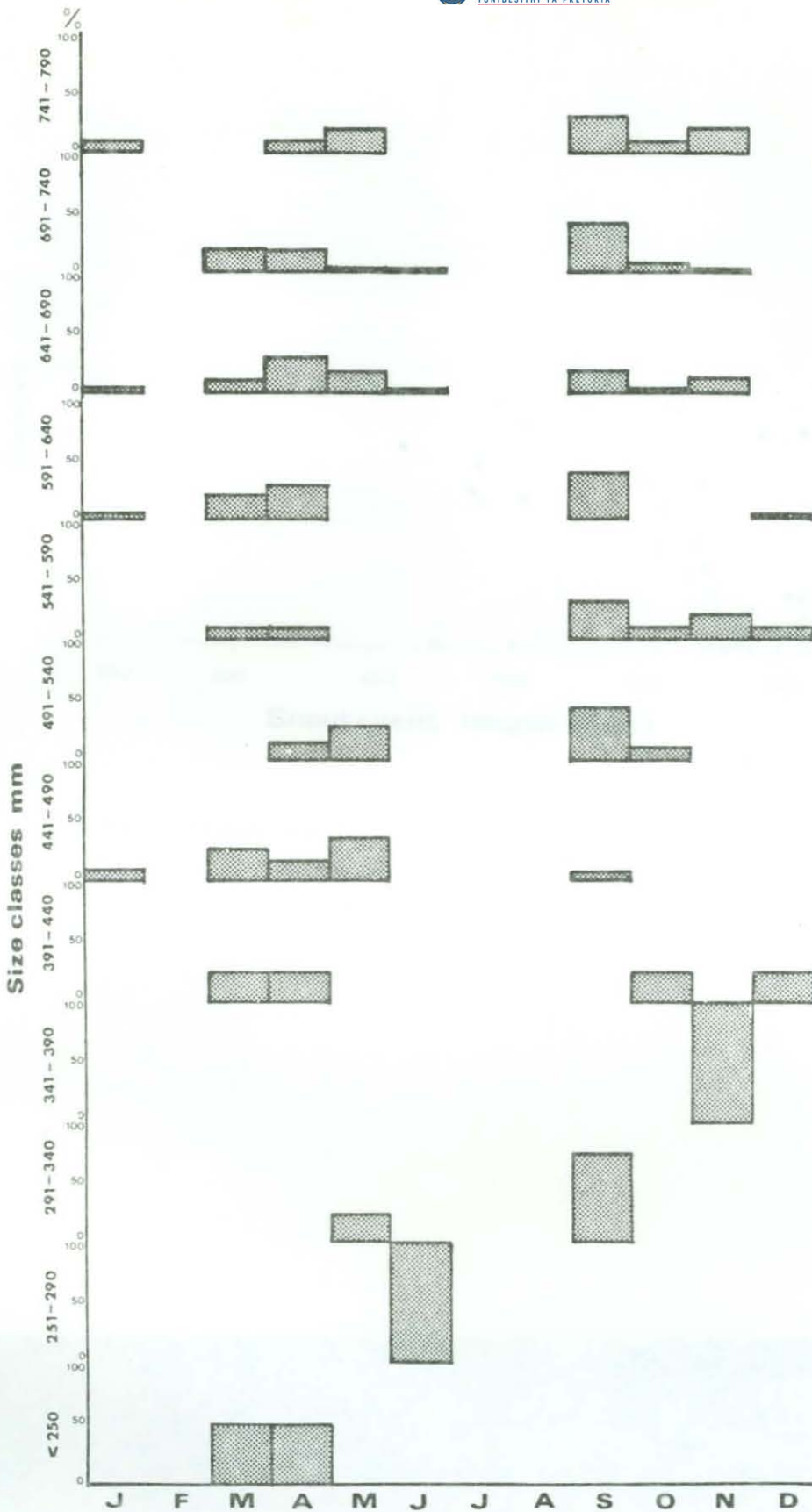


Figure 48. Monthly distribution of size classes of Thelotornis capensis in the Study Area.

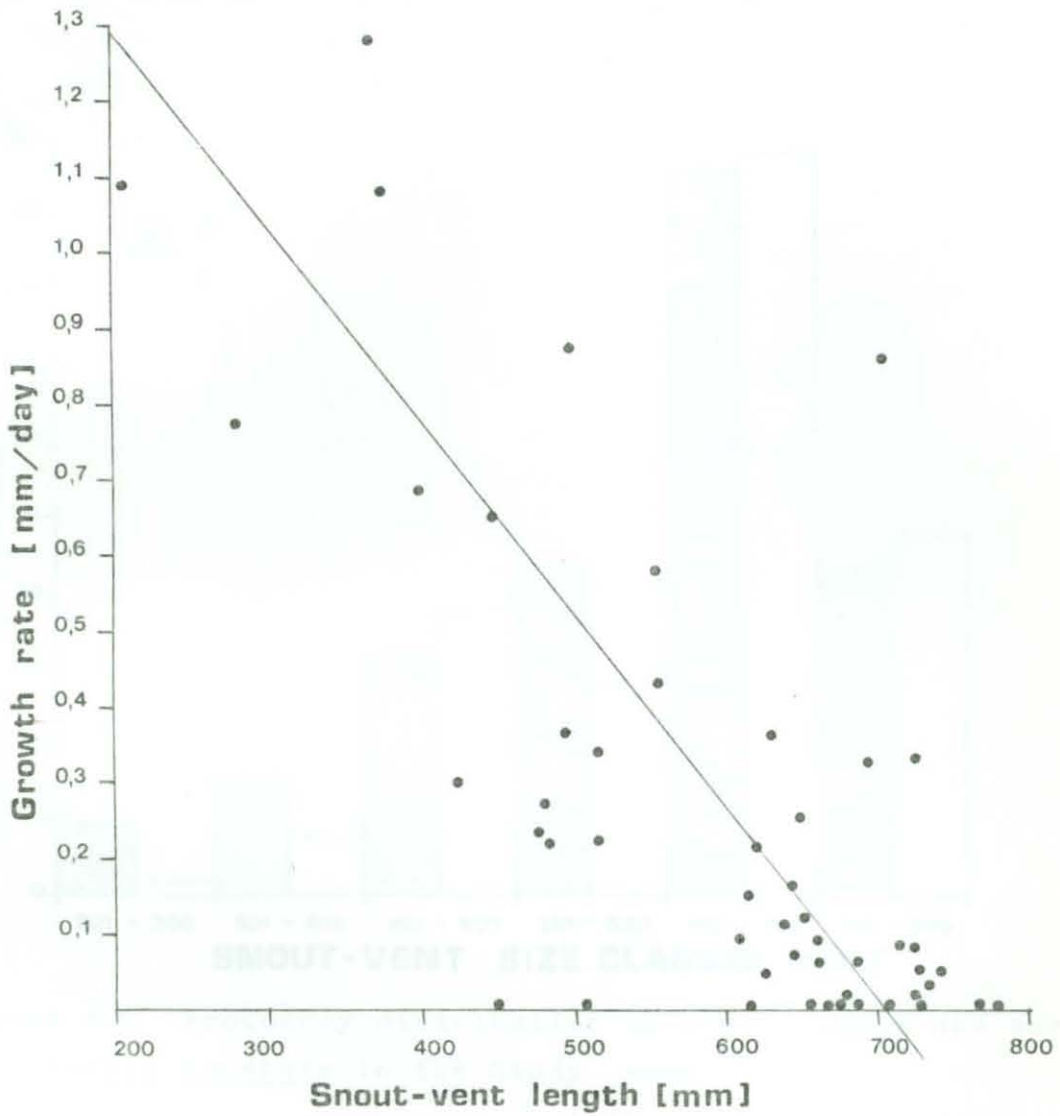


Figure 49. Negative linear correlation between size and growth rate in Thelotornis capensis in the Study Area.

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.

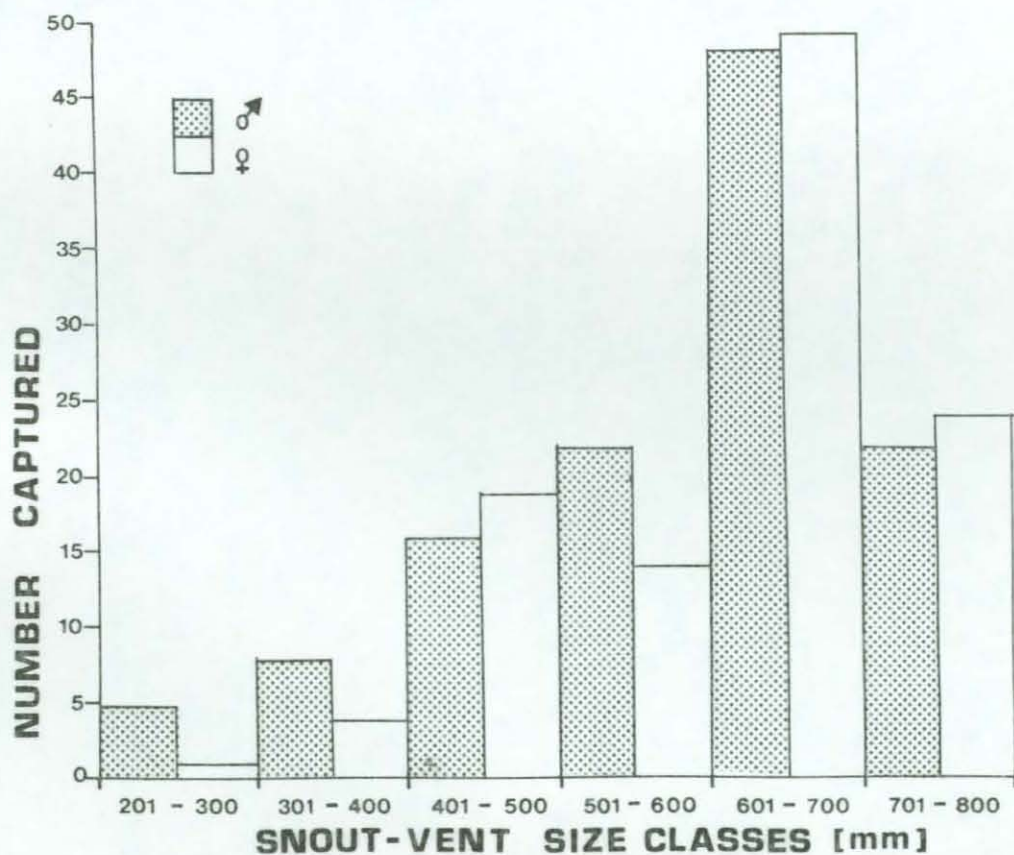


Figure 50. Frequency distribution of size classes and sex of *Thelotornis capensis* in the Study Area.

It is apparent that the population 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 $15,08 \times 10^3$ J/g dry weight. Therefore, for every 100 g of rodent consumed, a potential amount of $750,85 \times 10^3$ 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 $15,13 \times 10^3$ J/g. Therefore, of the original $750,85 \times 10^3$ J ingested, $75,33 \times 10^3$ 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)
<u>Psammophis sibilans brevirostris</u>					
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
<u>Philothamus s. semivariegatus</u>					
186	F	47	3,4	15	0,32
<u>Telescopus s. semiannulatus</u>					
44	M	33	- 0,85	0	0
44	M	47	-1,85	5	0,10
<u>Dasypeltis s. scabra</u>					
148	M	22	3,10	8	0,36
172	F	347	3,25	87	0,25
<u>Naja mossambica</u>					
21	M	164	?	76	0,46
73	M	152	140,0	20	0,13
<u>Aparallactus c. capensis</u>					
152	F	14	0,70	0	0
<u>Lycophidion capense</u>					
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)
<u>Naja haje annulifera</u>					
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
<u>Dispholidus t. typus</u>					
160	M	363	120,00	19	0,05
<u>Crotaphopeltis h. hotamboeia</u>					
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.

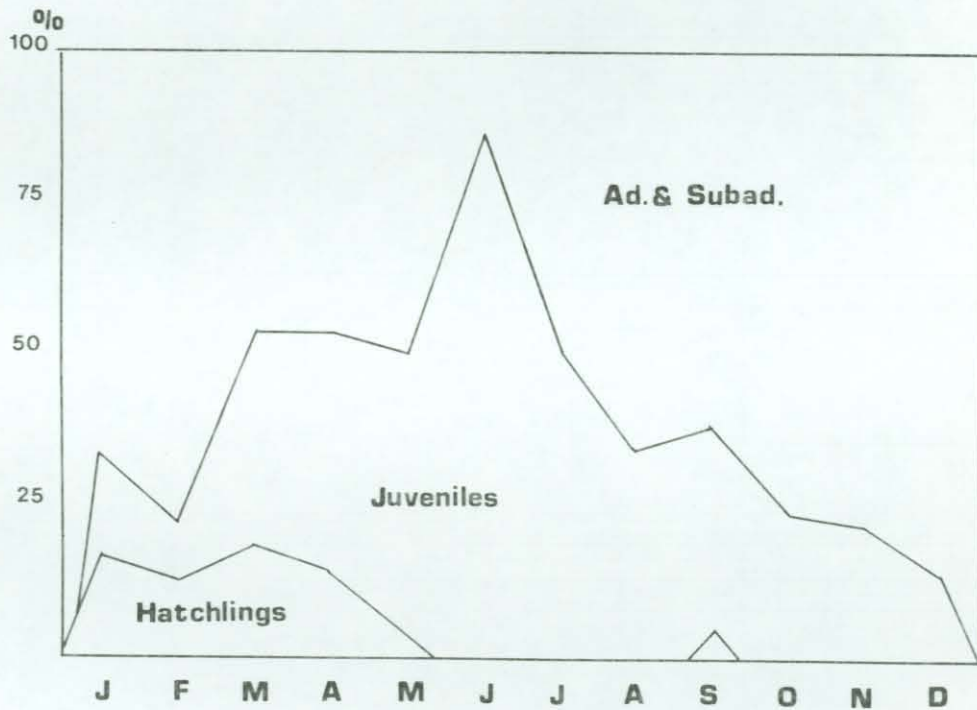
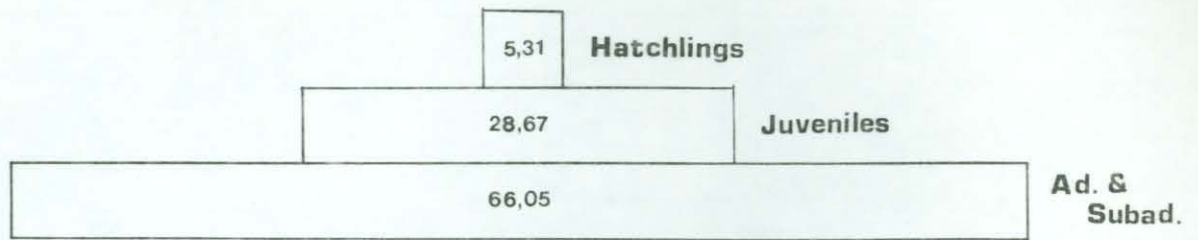


Figure 51. Relationship of three arbitrary age classes of snakes capture in the *Burkea africana* - *Eragrostis pallens* Study Area, May 1975 to May 1977.

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°) 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.

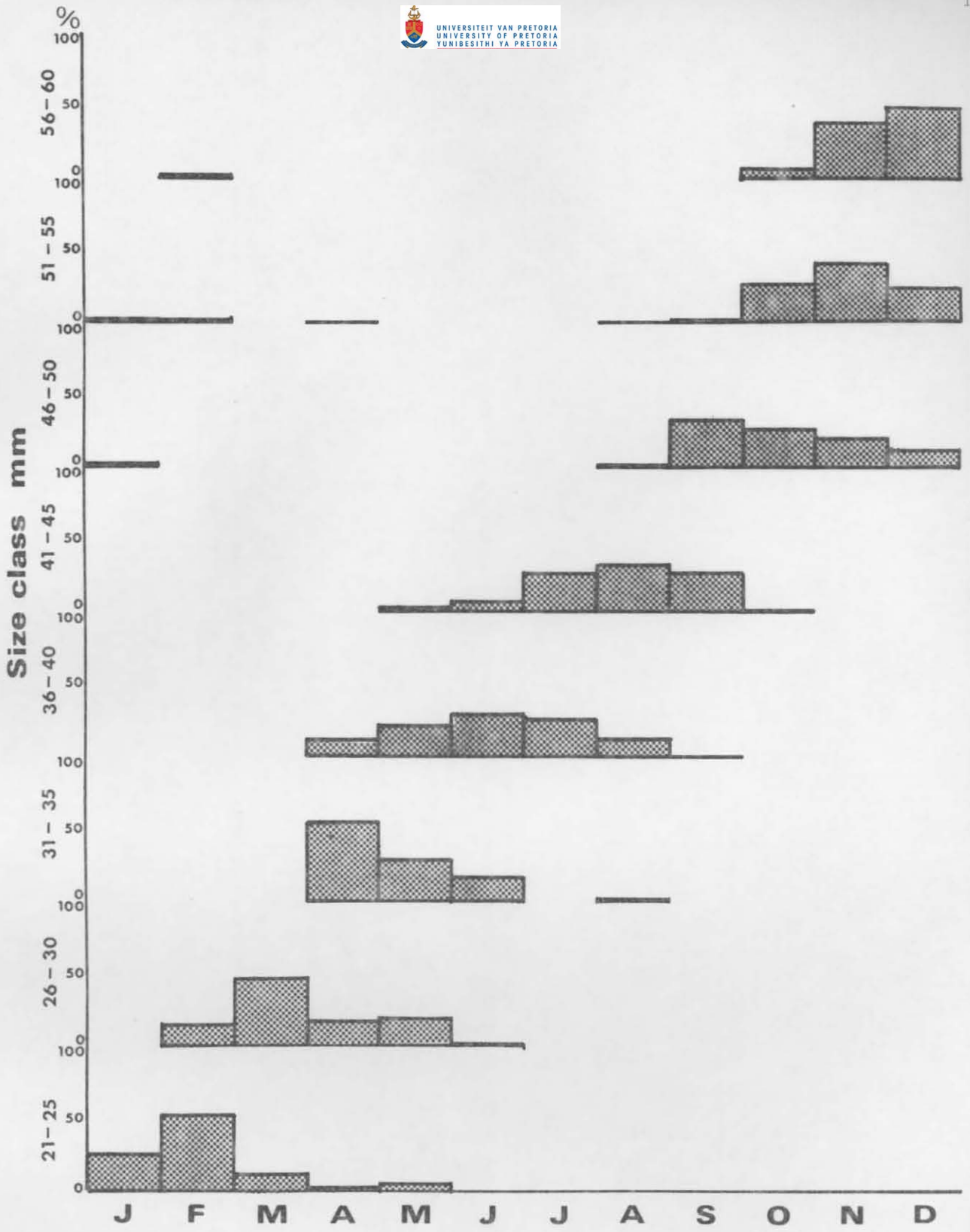


Figure 53. Monthly distribution of size classes of *Ichnotropis capensis* in the Study Area.

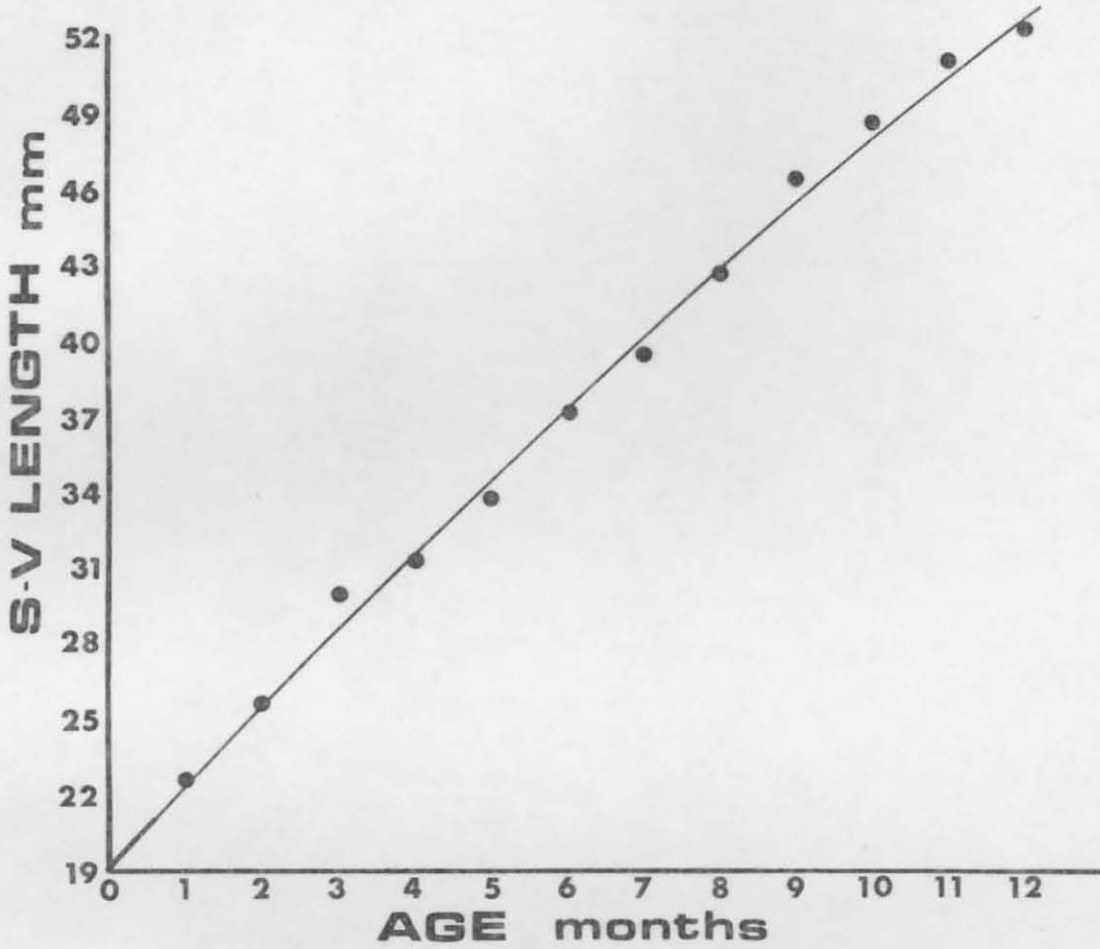


Figure 54. Mean growth rate of *Ichnotropis capensis* in the Study Area.

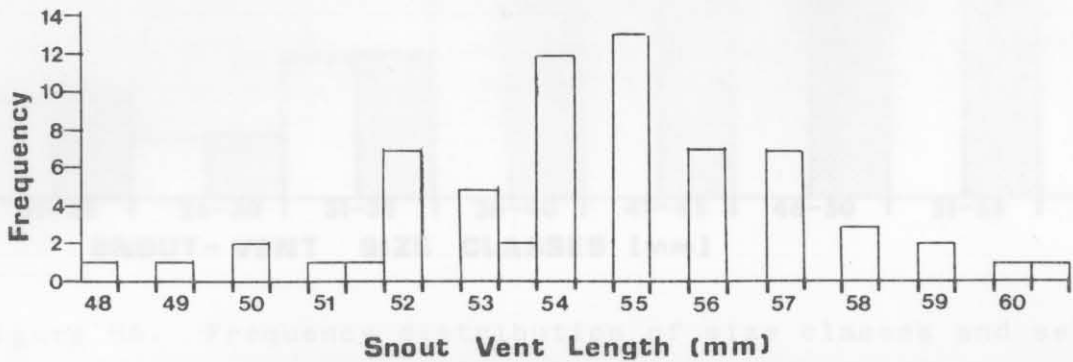


Figure 55. Size class frequency distribution of gravid Ichnotropis capensis in the Study Area.

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).

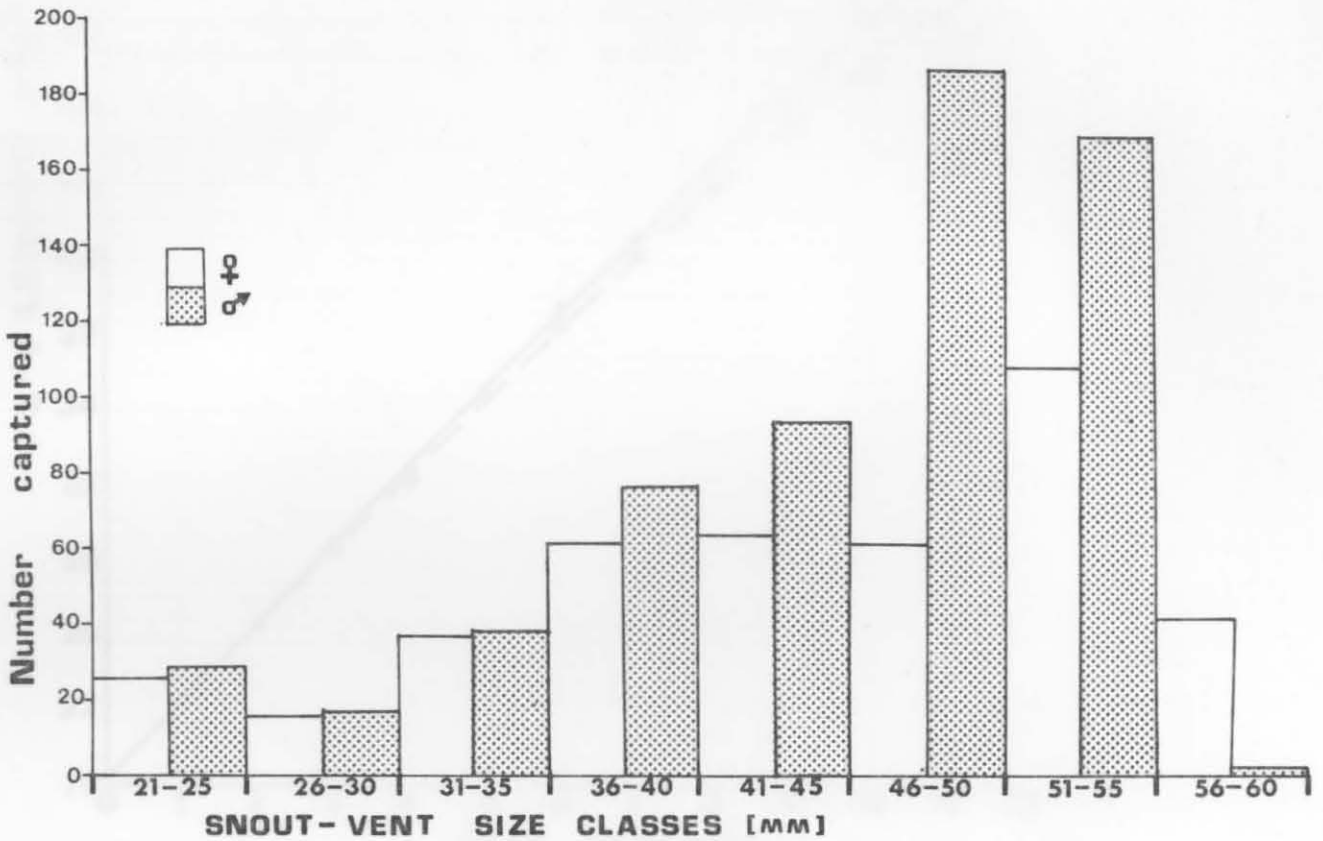


Figure 56. Frequency distribution of size classes and sex of Ichnotropis capensis in the Study Area.

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

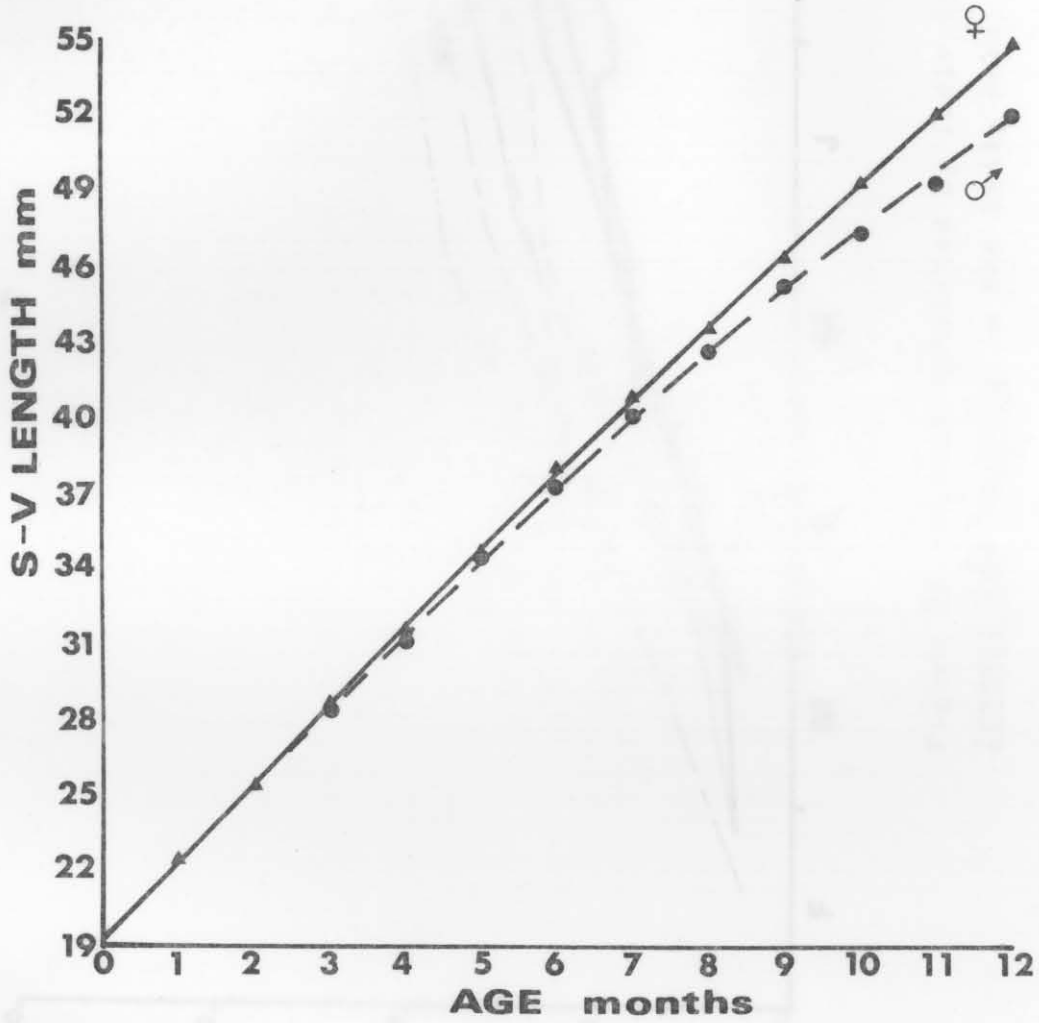


Figure 57. Differential mean growth of male and female Ichnotropis capensis in the Study Area.

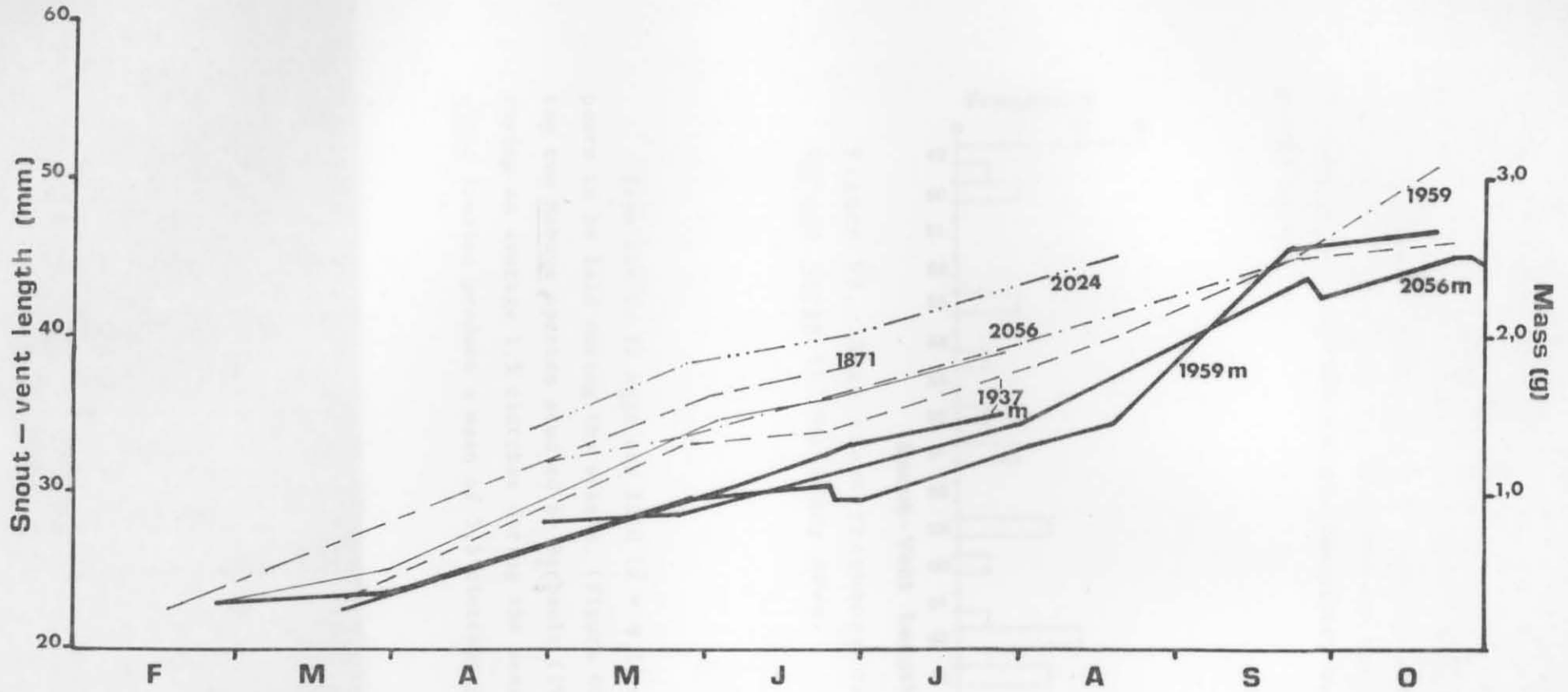


Figure 58. Growth exhibited by individual recaptured Ichnotropis capensis in the Study Area.

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 iridescent 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.

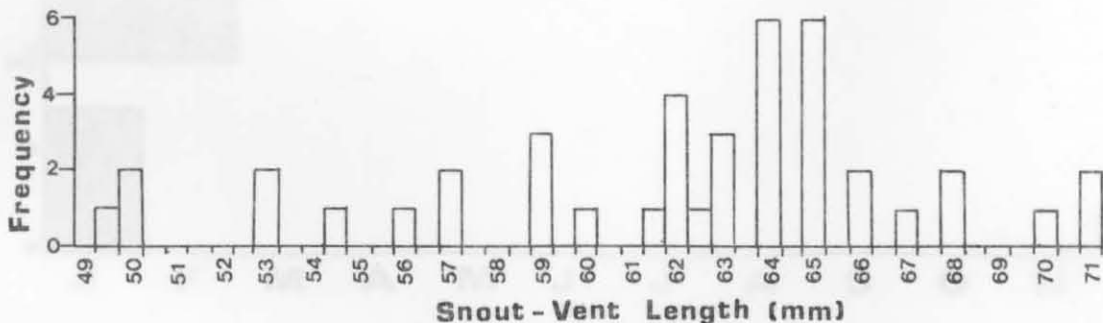


Figure 59. Size class frequency distribution of gravid Mabuya varia in the Study Area.

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.

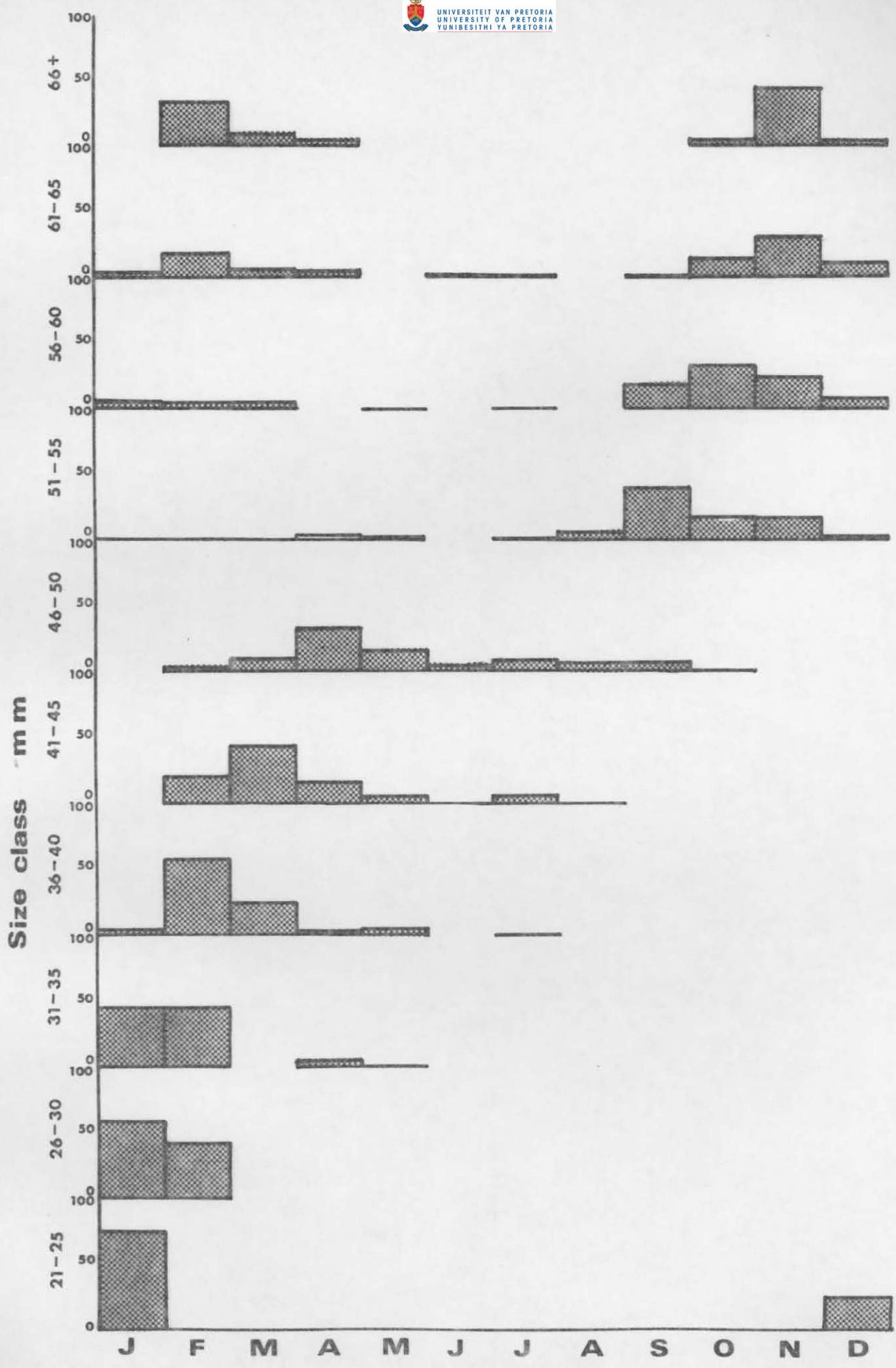


Figure 60. Monthly distribution of size classes of *Mabuya varia* in the Study Area.