

PART 3

AUTECOLOGY OF CTENOTUS TAENIOLATUS

3.0 GENERAL HABITAT DESCRIPTION

3.1 INTRODUCTION

For a discussion of the ecology of an animal to be relevant it is first necessary to describe the habitat, microhabitat and associated microclimate of that animal. Microhabitat and microclimate have both been shown to be important factors on which habitat selection is based (review by Heatwole 1977). The first aim of this chapter is to make such descriptions.

Further, as C.taeniolatus constructs burrows and as it is known that lizards often adjust the structure of burrows seasonally (Heatwole 1970, 1976) and for sex-related reasons, the second aim of this chapter is to investigate burrowing.

3.2 METHODS

When lizards were collected (Section 2.2) burrow and rock dimensions were taken at the site of capture. Burrow length, depth and width were measured with string, which was then compared against a graduated rule ($\pm 0.5\text{cm}$). Maximum rock length, depth and width were measured similarly. Rock size was estimated as rock volume by multiplying together length, depth and width and assuming the rock to be a rectangular prism. Substrate temperature under the rock, and lizard body temperatures were taken immediately after capture with a Comark single channel electronic thermometer ($\pm 0.1\text{ C}$). The presence of other animals under the rock was noted.

Continuous burrow temperatures were recorded using a Mersteel Temperature Recorder (± 1 C) at the Moonbi site. Probes were located in burrows under two rocks: one 4 cm deep, the other 40 cm. Other Meteorological data were collected from the Laureldale Meteorological Station.

Soil moisture levels were determined by collecting a known weight of soil from around a lizard burrow and then drying it at 100 C in an oven until the weight stabilized. Moisture content was expressed as a percentage of dry weight.

3.3 RESULTS

3.3.1 Microhabitat

In the New England Region C.taeniolatus were distributed throughout a number of different habitats from cleared grazing land to eucalypt woodland, usually in patches of suitable rocks, although logs were used if no rocks were present. Lizards used these rocks as refuges in their inactive periods and as ovipositional sites.

Rock size selected was independent of lizard size and sex. In a one-way analysis of variance comparing rock size for males, females and juveniles, no significant differences were found (Table 1). Similarly, no significant differences were found between rock sizes used by adults caught in summer and those caught in winter (Table 1). In fact rock size used by Ctenotus was very variable and followed no discernible pattern. Mean rock size was 4273.6 cm³ (SD=4803.4).

Lizards always selected rocks with soil underneath, as it was in soil that they constructed their burrows (Fig. 7), the entrances of which were often visible from the outside. Burrow structure, like rock size, was variable and followed no discernible pattern. Mean (SD) burrow length, width and depth were 22.5 (19.16), 12.8 (16.40) and 2.3 (1.89) cm respectively, and were not significantly different for males, females and juveniles, nor for adults captured in summer and those caught in winter (one-way analysis of variance, Table 2). Also, the sum of burrow and rock depth showed no significant difference for adults between summer and winter (Table 2).

Other animals were often found under the same rock as lizards, but not usually in the same burrow. These animals included lizards of the same and different species (Lampropholis delicata and L. quichenoti), centipedes, snails, termites and a number of ants of both carnivorous and granivorous species.

3.3.2 Microclimate

Burrow temperatures showed considerable daily and annual variation, which corresponded to fluctuations in ambient temperatures (Section 2.1). Figure 8 details some examples of the diel fluctuations found throughout the year in burrows under rocks 4 cm and 40 cm deep located in the Moonbi Ranges. Note that the mean and range of the temperatures, and the times of maxima and minima change throughout the year, especially for the shallower burrows. These fluctuations can be modelled monthly by assuming that daily fluctuation follows the pattern of two half sine waves, one simulating the steep section of the curve the other the gentler section. These sine waves have amplitudes of maximum minus minimum temperatures and periods equal to the time between maxima and minima (see section 8.1.2 for detailed explanation). Burrow

depth, as can be seen in figure 8, played an important role in determining burrow temperatures, as did position of the burrow in relation to the sun. Both of these were very variable (Section 3.3.1) and hence it was not possible to establish a predictive relationship between burrow temperature and these other parameters. Soil temperatures are easily measured during routine Meteorological monitoring programs and provide an estimate of the average burrow temperatures. Figure 9 details the soil temperatures at 5 cm and 10 cm respectively, recorded from the Laureldale weather station between 1979 and 1982. In all cases body temperatures of inactive lizards reflected the surrounding burrow temperatures. Mean soil moisture levels were 8.3% (SD=9.3).

Table 1: One-way analysis of variance comparing the effects of sex of lizard and season of capture on the rock size and burrow depth used by Ctenotus taeniolatus.

Source	Rock size			Burrow + rock depth		
	DF	MS	P	DF	MS	P
Season	1	18045777	NS	1	38.533	NS
Error	24	37619511		28	22.2976	
Total	25			29		
Sex	2	49283662	NS			
Error	36	21616368				
Total	38					

Table 2 : One-way analysis of variance comparing the effects of sex of lizard and season of capture on length, width and depth of burrows used by Ctenotus taeniolatus.

Source	Burrow length			Burrow width			Burrow depth		
	DF	MS	P	DF	MS	P	DF	MS	P
Sex	2	306.34	NS	2	13.13	NS	2	4.67	NS
Error	37	370.46		38	6.38		36	3.56	
Total	39			40			38		
Season	1	4.8	NS	1	1.88	NS	1	1.41	NS
Error	28	53.54		30	1.50		32	1.66	
Total	29			31			33		

Figure 7: Inactive Ctenotus taeniolatus in burrow (upper) and typical burrow (lower).

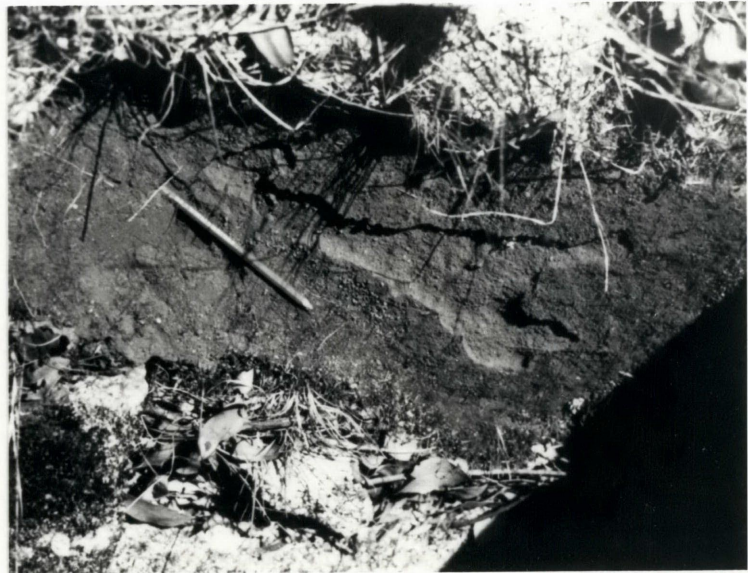
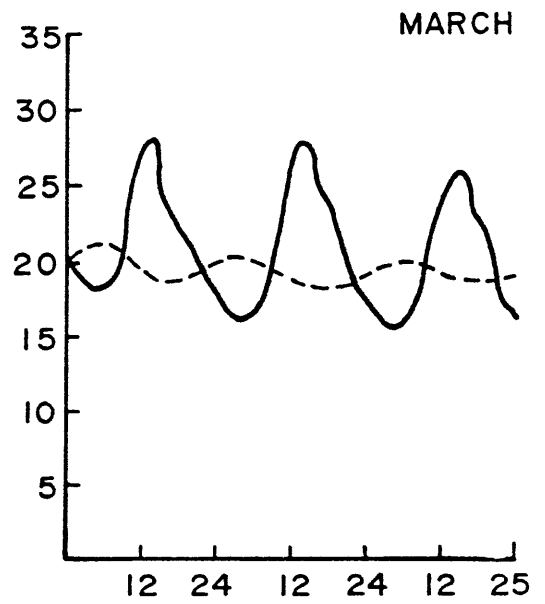
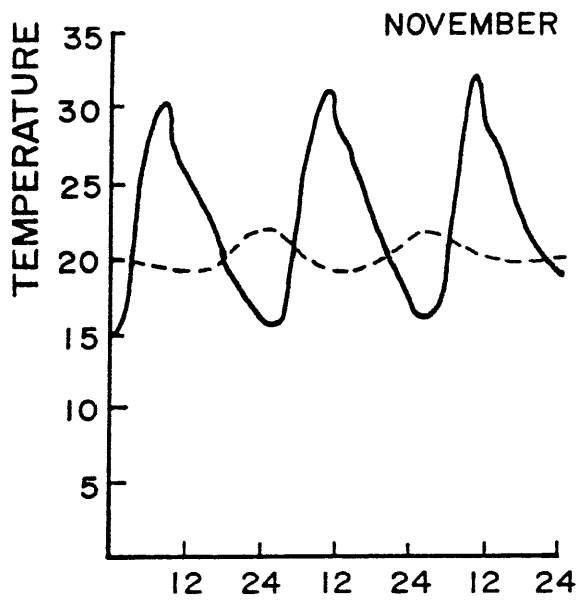
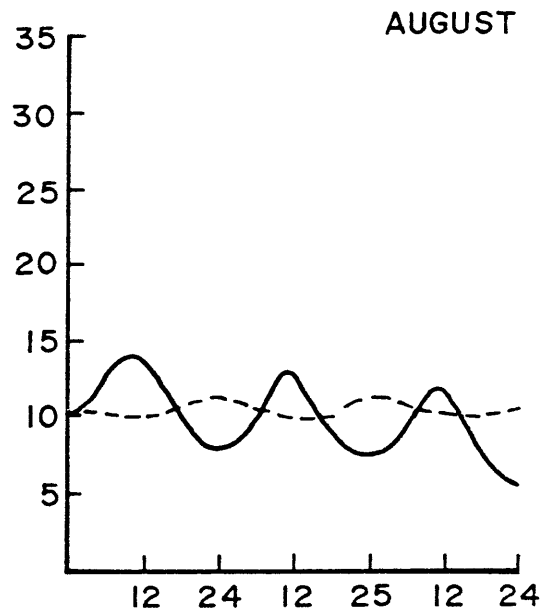
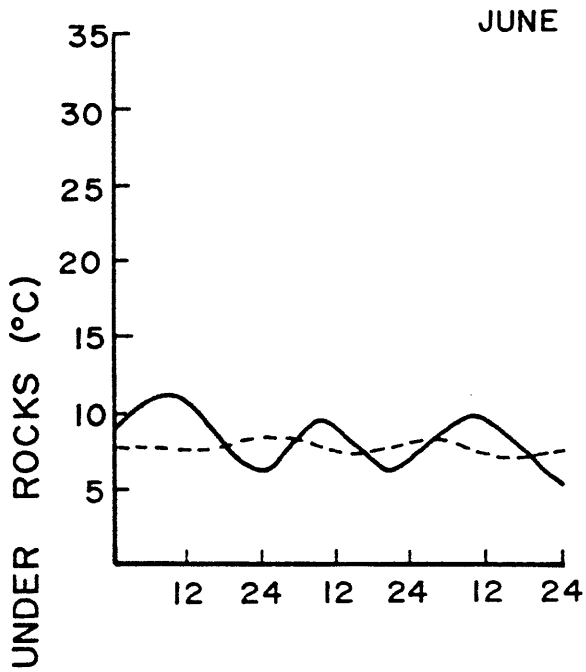


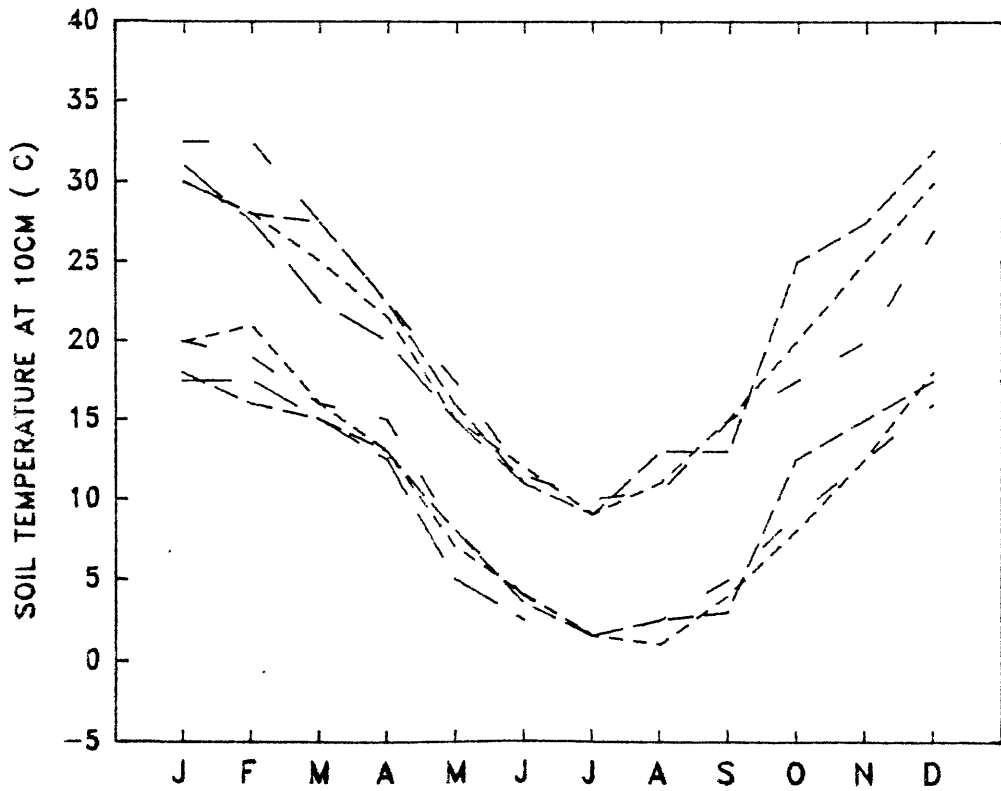
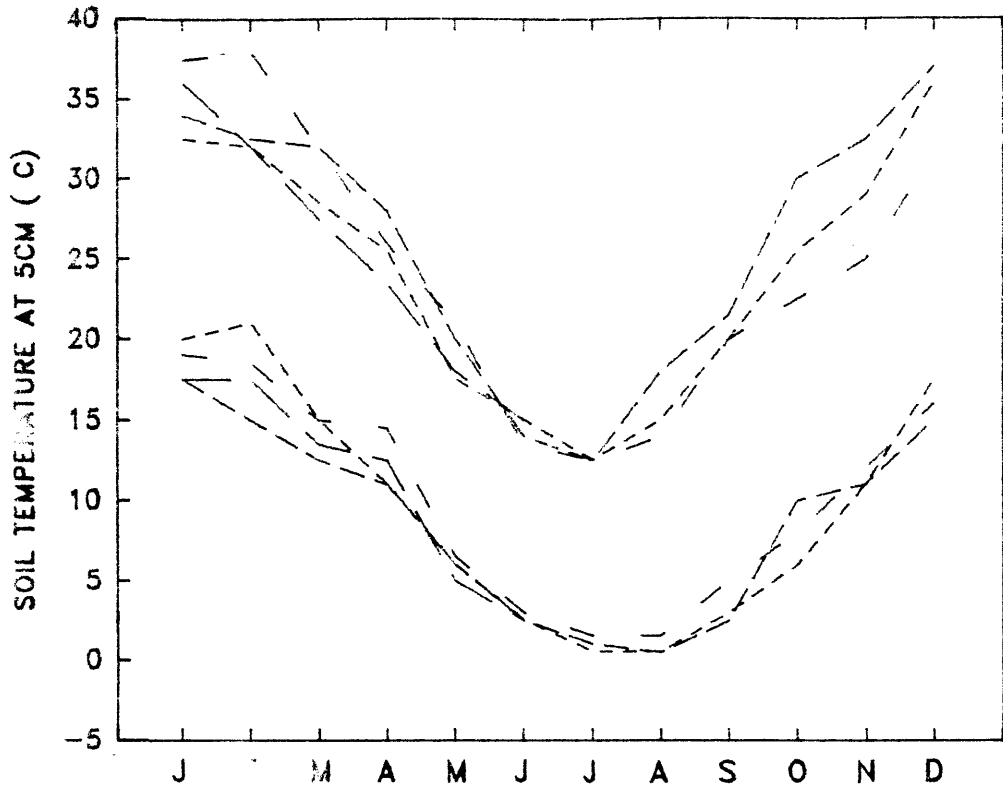
Figure 8: Daily temperature fluctuations under rocks 4 cm (—) and 40 cm (----) deep. Examples only are presented.



HOURS

TEMPERATURE UNDER ROCKS (°C)

Figure 9 : Mean monthly maximum and minimum soil temperatures from Laureldale Meteorological Station, taken at depths of 5 cm and 10 cm. Temperatures for 1979 are represented by -----, 1980 by ----, 1981 by --- and 1982 by ——. Months are represented by their first initial.



3.4 DISCUSSION

The aim of this chapter is to discuss variation within a microhabitat of Ctenotus taeniolatus rather than the variation among habitats over the entire range of Ctenotus. It is enough to say that Ctenotus does occur in a variety of habitats from coastal heathlands to dry sclerophyll forest and wetter montane forest but that in these areas it is usually associated with rocky situations (Cogger 1979, Jenkins and Bartell 1980, present study).

However, within the rocky habitats of New England Ctenotus is not very selective. It shelters under rocks of any size (or logs in some cases), with an amount of soil suitable for burrow construction. Also the morphology of the burrows is determined primarily by the depth, and presumably the type of soil available and does not vary consistently with lizard sex or size, or time of year. Thus, in the cold of winter or the heat of summer, with temperatures ranging from 0 to 35 C under shallow rocks, lizards do not dig significantly different or deeper burrows. Other animals that occurred under the rocks with lizards, were not found within the same burrows but in other excavations and they may not have come in direct contact with this aggressive carnivore.

4.0 FOOD AND FEEDING BEHAVIOUR

4.1 INTRODUCTION

Although C.taeniolatus, like many other members of the genus Ctenotus, is thought to be a widely foraging insectivore, which occasionally preys on small lizards (Jenkins and Bartell 1980, Pianka 1969), no comprehensive study of either its diet or foraging behaviour has been completed. Therefore the aims of the following chapter are to describe the foods of C.taeniolatus and to determine the type and seasonality of foraging behaviours employed.

4.2 METHODS

4.2.1 Analysis of gut contents

After discarding the oesophagus, the preserved alimentary canal of each lizard was divided into stomach and lower gut (small and large intestines, rectum). The contents of these two sections were analysed by making the following three measurements:

(i) numbers of each taxon of prey,

(ii) total volume of food (volume was measured by estimating the amount of water (ml) displaced by the stomach or lower gut and food, and then subtracting the volume displaced by the stomach or lower gut alone),

(iii) volume of each prey item. Volumes were estimated by measuring prey length, width and depth to the nearest 0.01 mm (using an ocular micrometer) and treating prey items as rectangular prisms. Appendages, such as wings and legs, were not included in these

estimates. It was assumed that prey were eaten whole.

4.2.2 Foraging Behaviour

Duration and mode of foraging, and durations of other behaviours were recorded by observing a large number of individuals for times ranging from 1 to 86 minutes (mean 15.9 mins) between 0900 and 1300 hr in spring/summer 1980/81 at the Moonbi site (Section 2.3). Observations were terminated when the lizards disappeared into long grass or retired under shelter for at least 20 min. Overall, because of the fast, alert nature of these lizards (even though a large number of lizards were observed) only 32 adults and 17 hatchlings were observed long enough to be included in the time budget analysis. All observations were made using binoculars, stop watch and tape recorder.

4.3 RESULTS

4.3.1 Type of food

The diet of C.taeniolatus was determined by combining information collected from 261 lizards sampled approximately monthly for a 3 year period (Section 2.2).

Tables 3, 4 and 5 indicate the foods found in the stomach and lower gut of C.taeniolatus over this period. Three estimates were used to determine the contributions of the different foods to the diet, (i) the percentages of lizards with food in the gut containing a particular kind of food, (ii) the percentage of the total prey volume that each type of food contributed, and (iii) the numbers of prey animals eaten.

C.taeniolatus is principally an insectivore. The most common food, lepidopteran larvae occurred in 30.5% of stomachs, followed by coleopteran adults and larvae, in 22.9%, orthopterans in 19.0% and formicids in 14.3%. Lepidopteran larvae also contributed the greatest volume of food in the stomach (49.1%), followed by orthopterans (21.3%) and coleopterans (12.8%). The remainder of invertebrates, although found in 39.5% of stomachs collectively contributed only 15.3% of the total volume.

The stomach and lower gut depicted a similar diet (Table 6) except in the cases of lepidopterans and formicids. These differences can probably be accounted for by differences in rate of passage and/or digestion between these vastly different types of animal.

Of all the lizards sampled, 59.8% had empty stomachs (23.4% had empty lower guts), 11.3% had stomachs which contained non-food items (49.8% of lower guts) and 0.8% had stomachs with nematode parasites of the genus Maxvachonia (4.6% of lower guts).

4.3.2 Diet and Season

The seasonality in the diet of C.taeniolatus was examined in three ways: by examining (i) the number of empty stomachs over a year, (ii) the volume of food in the stomach over a year and (iii) the major food types present at different times of year. Values for all three years were pooled. Lower guts were not examined for the first two estimates because of problems caused by variation in digestion rate and feeding time. The percentages of lizards with empty stomachs are depicted in figure 10. These percentages changed throughout the year, with the lizards captured over the inactive period between May and September having higher percentages of empty stomachs (85-100%) than those captured in the active period from October to March (30-70%). The

percentages of males and females with empty stomachs did not appear to differ from each other throughout the year. The very high percentages of empty stomachs present throughout the active periods were probably a result of the fact that all lizards were caught in the mornings, 1-4 hours after dawn. The small samples of juveniles caught at certain times made a seasonal comparison of that group invalid.

Figure 11 shows that the volume of food in the stomachs of lizards captured over winter was small, and in all cases these foods were in a very digested state.

The change in the four major food types (orthopterans, coleopterans, lepidopterans and formicids) over a year is shown in figure 12, along with months in which lizards were actively feeding. Over this period lepidopterans, coleopterans and formicids were found mainly in the stomachs taken from lizards caught in spring (September-October), while orthopterans predominated later (November-January). Similar patterns are found in the percentages of the lower guts with each food type, although lepidopterans were less common in the spring and formicids were more common overall, probably a result of the different digestibility of ants and caterpillars. Only formicids were present in the inactive winter periods, occurring in three stomachs and 16 lower guts. Again this result may reflect the relative indigestibility of ants as they were often found intact in the lower gut.

4.3.3 Diet and Size

Figure 13 details the relationship between snout-vent length (SVL) of a lizard and the maximum volume of each prey item (V) found in that lizard. After fitting a number of different transformations of the data, a linear relationship of the form $V = -170.1^{**} + 6.47^{**}.SVL$ ($R^2 =$

0.04, $n = 158$, $P < 0.05$; V in mls, SVL in mm) was found to account for a significant proportion of the total variation. However, even though this equation significantly described the above relationship, because of the large number of lizards that ingested very small prey items, it severely underestimated the maximum size of prey a lizard could eat. A more realistic estimate of maximum prey size was determined by regressing the maximum prey volume in each size class against the SVL of the lizard. The resultant equation ($V = -1742n^* + 61.9 \cdot \text{SVL}$, $R^2 = 0.97$, $n = 4$, $P < 0.05$) indicated that there was a rapid increase in prey sizes from hatchlings to large adults. That is, adults were capable of eating and did eat a greater diversity of prey sizes than hatchlings, even though the prey types differed little (Tables 3, 4, 5). Small prey such as ants and small beetles occurred in adult stomachs and small examples of larger prey types such as lepidopterans and orthopterans sometimes occurred in hatchlings, a trend which was apparent even though the sample of hatchlings examined was small (14).

4.3.4 Foraging Behaviour

Table 7 details a time-budget of daytime activities. Foraging was the most time consuming behaviour, comprising 78.3 and 79.8% total time in adults and hatchlings respectively. Foraging behaviour was subdivided into two types - active searching and sit-and-wait. Active searching was characterised by a moderately paced movement interspersed by an occasional quick dash over exposed rock. During such searching, lizards poked and dug with their fore feet and snout into holes, lichens on rocks and leaf litter, and also examined the substrate with tongue flicks. Occasionally a nervous twitching of the tip of the tail was observed. Active searching was interspersed with the sit-and-wait strategy, the position of which was changed frequently. Sit-and-wait behaviour was characterised by a stationary alert position with the body

or head elevated a few centimetres above ground level, usually on a rock or log. The head, held above the height of the limb girdles, was moved, frequently scanning the surrounds, or the lizard shuffled around at the same site in order to view throughout 360 degrees. Adults and hatchlings participated in both types of foraging behaviours, although hatchlings spent more time actively searching (45.4%) than adults (20.0%). Feeding successes/hr during sit-and-wait were similar for adults and hatchlings. However, hatchlings showed a greater number of feeding successes/hr overall, a result of the greater number of successes/hr when actively foraging, than when in the sit-and-wait position. This estimate of course did not take into account the volume or energy content of each food eaten.

Other activities occupied a total of 21.7 and 20.3% of the total time in adults and hatchlings, respectively. Basking behaviour was very distinctive and was characterised by a positional orientation to the sun, accompanied by the adpression of the abdomen to the substrate and the extension of the fore and/or hind limbs to the side or back of the lizard with the digits expanded and directed towards the sun.

As expected social interactions occupied more time in adults than hatchlings.

Table 3 : Foods found in the stomach of Ctenotus taeniolatus (volume in ml).

SPECIES	NO. OF STOMACHS		VOLUME		FOOD ITEMS
	Total	% of 105	Total	% of 316.2	
INSECTA					
Blattodea	8	7.6	30.37	9.60	8
Blaberidea	1	1.0	2.50	0.80	1
Undet.	7	6.7	27.87	8.80	7
Coleoptera	24	22.9	40.43	12.80	21
Scarabidae	3	2.9	3.54	1.10	4
Undet.adult	16	15.2	28.83	9.10	12
Undet.larvae	5	4.8	8.06	2.50	5
Diptera	1	1.0	0.4	0.10	2
Hemiptera	2	1.9	0.05	0.02	1
Heteroptera	1	1.0	0.02	= 0	1
Undet.	1	1.0	0.03	= 0	1
Hymenoptera	15	14.3	2.16	0.70	46
Formicidae					
Ponerinae	1	1.0	0.04	0.01	1
<u>Solenopsis</u> sp	2	1.9	0.20	0.06	5
Undet.Form.	12	11.4	1.92	0.60	40
Isoptera	3	2.9	0.15	0.05	6
Lepidoptera					
larvae	32	30.5	155.19	49.10	35
Odonata	2	1.9	0.52	0.16	2
Orthoptera	20	19.0	67.39	21.30	22
Tetrigidae	1	1.0	0.32	0.01	1
Acrididae	1	1.0	0.90	0.30	1
Undet.adults	17	16.2	62.42	19.60	19
Undet.nymphs	1	1.0	3.75	1.20	1
CHILOPODA	1	1.0	3.00	0.50	1
DIPLODA	2	1.9	8.20	0.50	1
ARACHNIDA					
Araneae	12	11.4	7.29	2.30	12
Lygosidae	5	4.8	1.50	0.50	5
Salticidae	1	1.0	1.00	0.31	1
Undet.	6	5.7	4.79	1.50	6
VERTEBRATA					
Lizard bones	1	1.0			
Tail- <u>Ctenotus taeniolatus</u>	1	1.0			
UNKNOWN	2	4.6	% of 261		
SHED SKIN	12	4.6			
PLANT MATTER	1	0.2			
SAND/DIRT	5	1.9			
PARASITE	2	0.8			
<u>Maxvachonia</u> sp					
EMPTY	156	59.8			

Table 4 : Foods found in the lower gut of Ctenotus taeniolatus (volume in ml).

SPECIES	NO. OF LOWER GUTS		VOLUME		FOOD ITEMS
	Total	% of 200	Total	% of 238.80	
INSECTA					
Blattodea	7	3.5	26.59	11.10	7
Coleoptera	40	20.0	25.58	10.70	41
Carabidae	4	2.0	2.72	1.10	4
Scarabidae	10	5.0	4.68	2.00	11
Undet.adults	25	12.5	17.94	7.50	25
Undet.larvae	1	0.5	0.24	0.10	1
Diptera	3	1.5	0.10	0.04	6
adults	2	1.0	0.06	0.03	2
eggs	1	0.5	0.04	0.02	4
Hemiptera	4	2.0	0.70	0.30	8
Heteroptera	1	0.5	0.02	= 0	4
Homoptera	1	0.5	= 0	= 0	1
Undet.	2	1.0	0.68	0.28	3
Hymenoptera	59	29.5	2.53	1.10	170
Formicidae					
Myrmicinae	2	1.0	0.01	= 0	11
<u>Solenopsis</u> sp	22	11.0	0.04	0.02	68
Ponerinae	1	0.5	0.02	= 0	4
Undet.adults	33	16.5	2.45	1.00	83
Undet.larvae	1	0.5	0.01	= 0	4
Isoptera	2	1.0	0.24	0.10	8
Lepidoptera					
larvae	23	11.5	116.50	48.8	24
Neuroptera	1	0.5	0.07	0.03	1
Odonata	1	0.5	0.01	= 0	1
Orthoptera	21	10.5	45.44	19.00	21
Tetrigidae	1	0.5	0.32	0.13	1
Undet.	20	10.0	45.12	18.90	20
CHILOPODA	1	0.5	3.00	1.30	1
DIPLODA	2	1.0	5.00	2.10	3
ARACHNIDA					
Araneae	16	8.0	11.11	4.70	16
Lygosidae	1	2.0	1.09	0.50	4
Salticidae	1	0.5	1.00	0.40	1
Undet.	11	5.5	9.02	3.80	11
Acarina	1	0.5	= 0	= 0	4
VERTEBRATA	2	1.0			
feather	1	0.5			
egg shell	1	0.5			
UNKNOWN	30	11.5	% of 261		
SHED SKIN	35	13.4			
PLANT MATTER	13	5.0			
SAND/DIRT	52	19.9			
PARASITES	11	4.2			
<u>Maxvachonia</u> sp					
EMPTY	61	23.4			

Table 5 : Foods found in the stomach of hatchling Ctenotus taeniolatus (volume measured in ml).

SPECIES	NO. OF STOMACHS		VOLUME		FOOD ITEMS
	Total	% of 14	Total	% of 14.8	
INSECTA					
Blattodea	1	7.1	2.50	16.9	1
Coleoptera	2	14.3	0.44	3.0	2
Hemiptera	2	14.3	0.05	0.3	2
Isoptera	1	7.1	0.03	0.2	1
Lepidoptera	2	14.3	5.80	33.2	2
Orthoptera	3	21.4	4.13	27.9	3
ARACHNIDA					
Araneae	5	35.7	1.83	12.4	5
SHED SKIN					
EMPTY	1	3.2	% of 261		
	17	45.2			

Table 6 : Representation of major food items in the stomach and lower gut of Ctenotus taeniolatus.

	% of lizards		% of volume	
	Stomach	Lower gut	Stomach	Lower gut
Blattodea	7.6	3.5	9.60	11.10
Coleoptera	22.9	20.0	12.80	10.70
Diptera	1.0	1.5	0.10	0.04
Hemiptera	1.9	2.0	0.02	0.30
Hymenoptera	14.3	29.5	0.68	1.10
Isoptera	2.9	1.0	0.05	0.10
Lepidoptera	30.5	11.5	49.10	48.80
Neuroptera	0	0.5	0	0.03
Odonata	1.9	0.5	0.16	= 0
Orthoptera	19.0	10.5	21.30	19.00
Chilopoda	1.0	0.5	0.50	1.30
Diploda	1.9	1.0	2.60	2.10
Araneae	11.4	8.0	2.30	4.70
Acarina	0	0.5	0	= 0
UNKNOWN	4.6	11.5		
SHED SKIN	4.6	13.4		
PLANT MATTER	0.2	5.0		
SAND/DIRT	1.9	19.9		
PARASITES	0.8	4.2		
EMPTY	59.8	23.4		

Table 7 : Time budget summary of daytime behaviour of Ctenotus taeniolatus. Figures in brackets are percentages of total observation time.

	Adults	Hatchlings
Individuals observed	32	17
Observation time (min)	583.39	231.96
Total foraging	456.66 (78.3)	185.32 (79.8)
Active search	116.38 (20.0)	105.32 (45.4)
Sit-and-wait	340.28 (58.3)	79.70 (34.4)
Basking	47.35 (8.1)	20.76 (9.0)
Social interaction	28.80 (4.9)	0.68 (0.3)
Shelter	50.58 (8.7)	25.50 (11.0)
Total feeding successes/hr, during total obs. time	1.2	4.4
Feeding successes/hr, during active search	3.1	8.5
Feeding successes/hr, during sit-and-wait search	1.1	1.5

Figure 10 : Percentages of empty stomachs of Ctenotus taeniolatus at different times of the year. Months are represented by their first initial (March and April as well as the winter months are combined), female, male and juvenile by F, M and J respectively. The number at the top of histogram is the sample size.

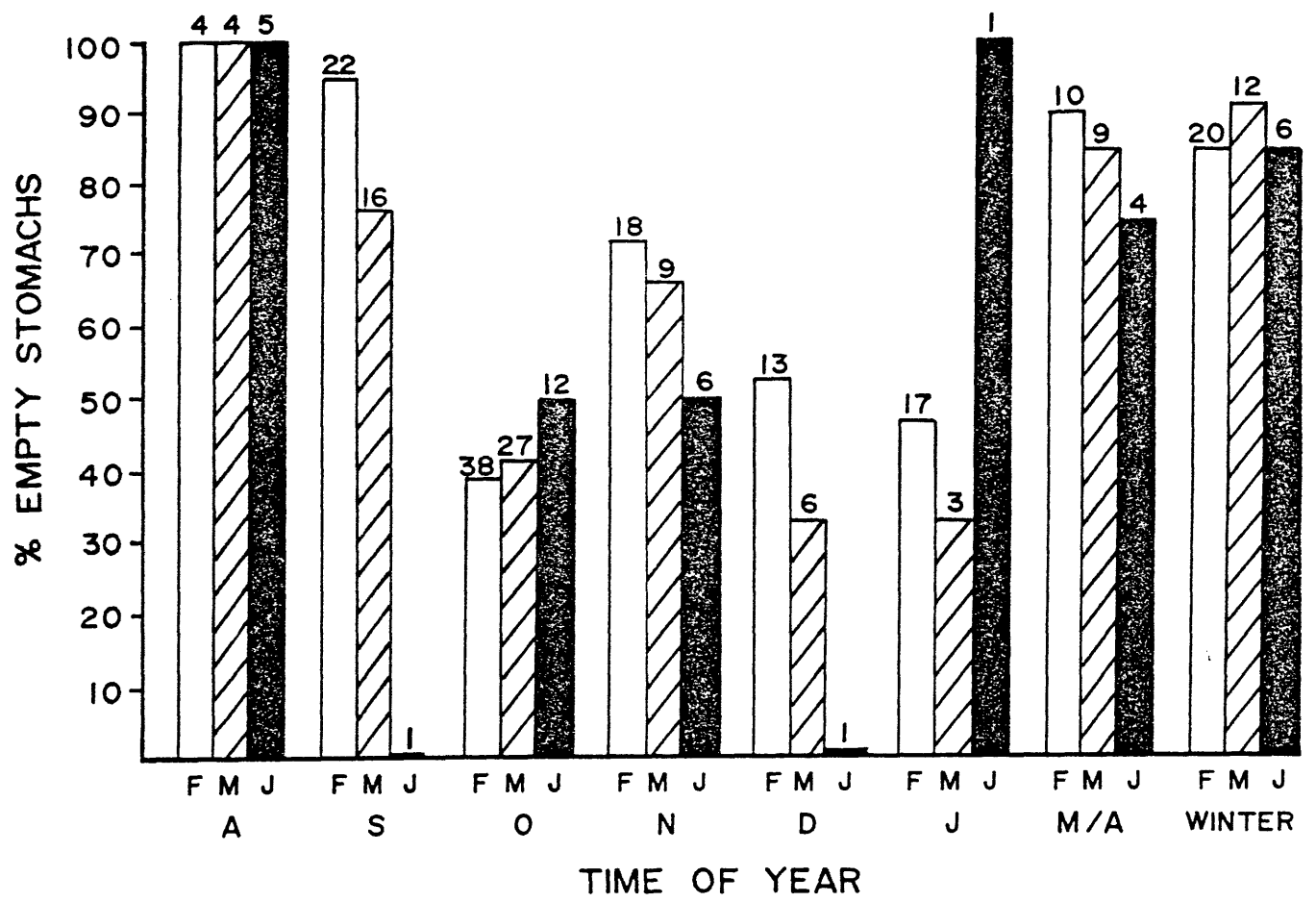


Figure 11 : Volume (mls) of food in the stomachs of Ctenotus taeniolatus at different times of the year. Months are represented by their first initial.

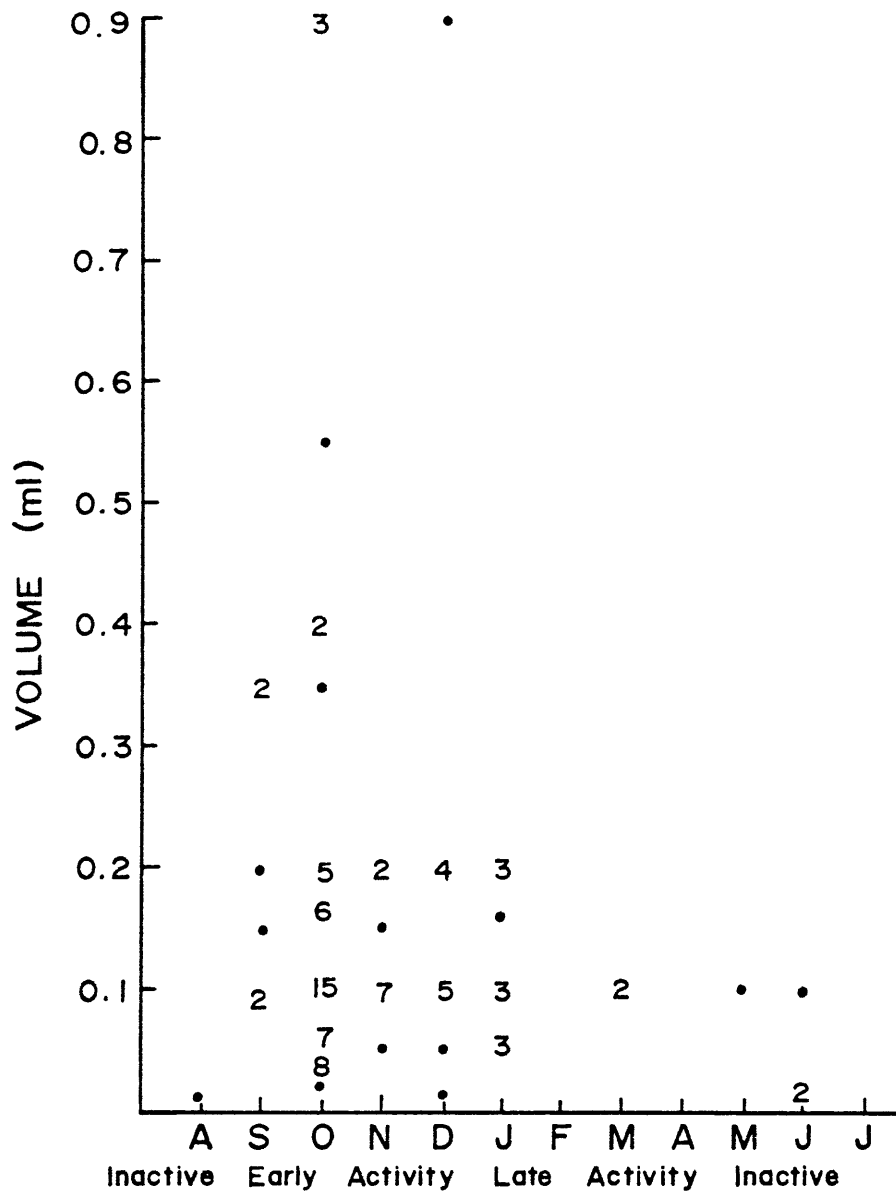


Figure 12 : Major groups of food from stomachs and lower guts of Ctenotus taeniolatus from August to January. Months are represented by their first initial.

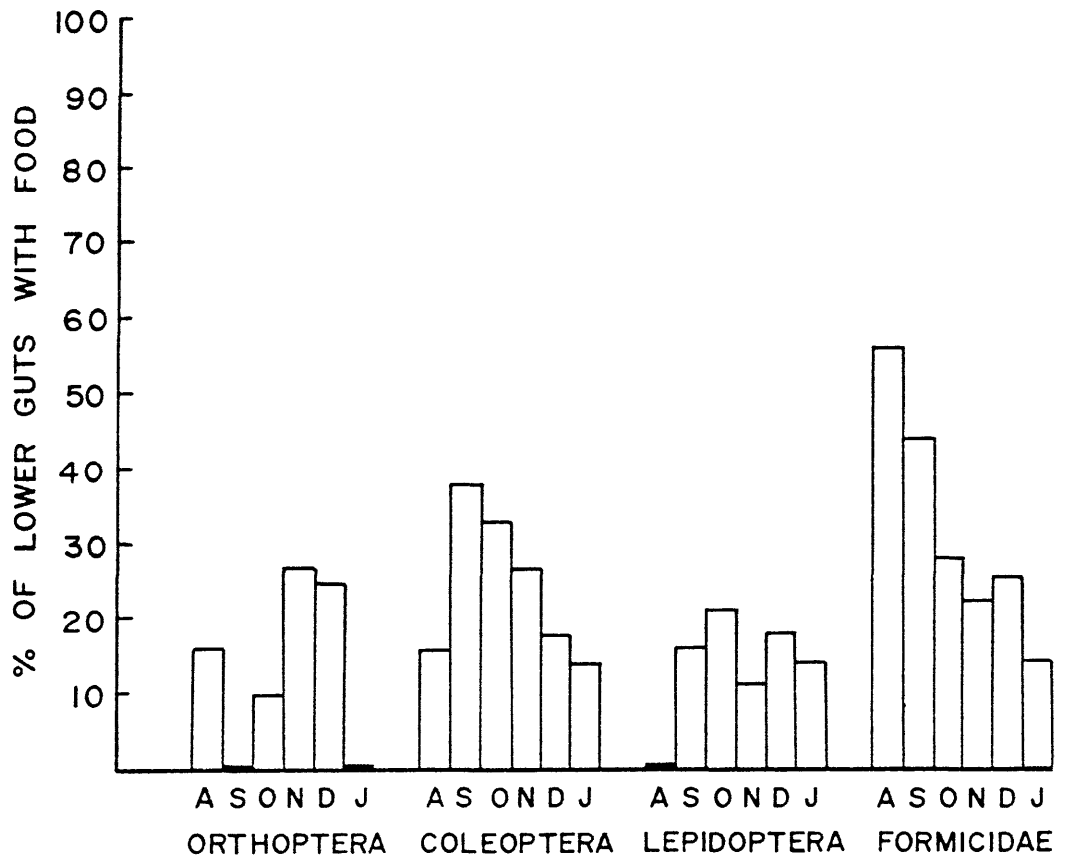
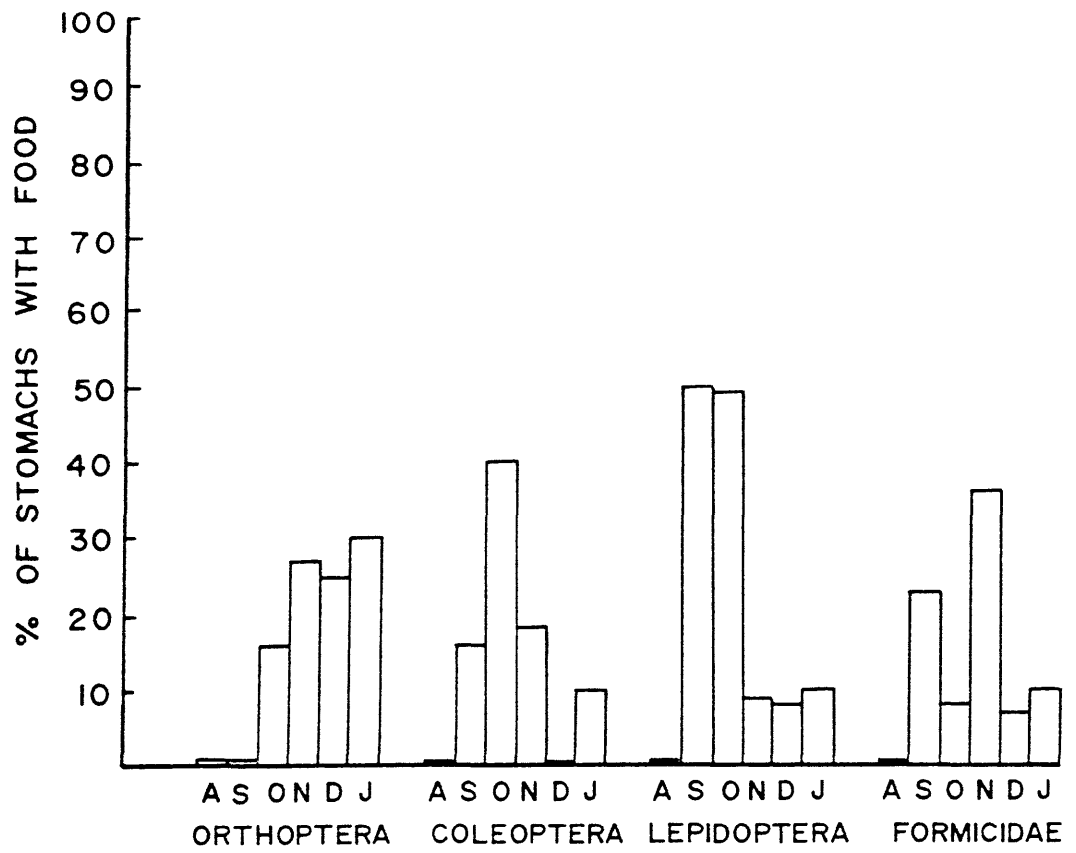
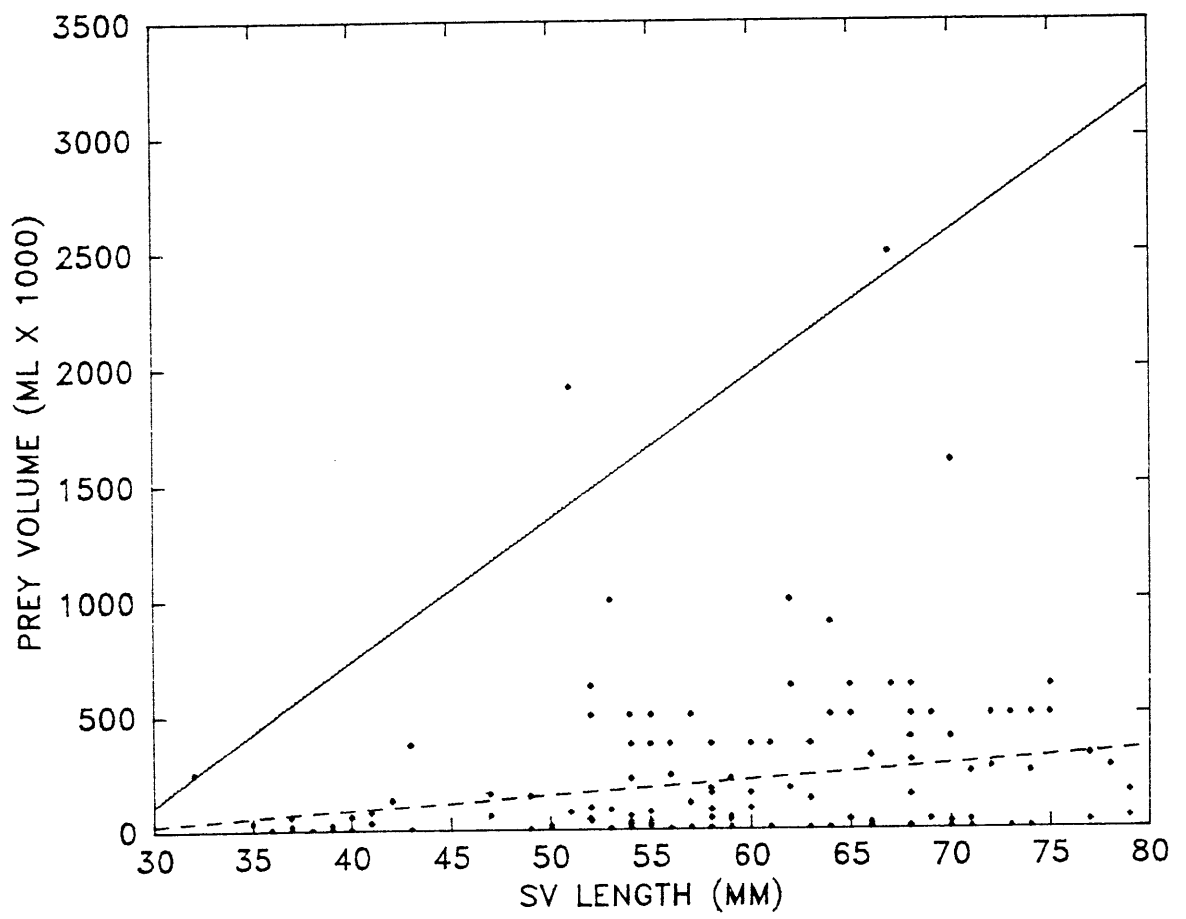


Figure 13 : Relationship between snout-vent length (SVL; mm) of Ctenotus taeniolatus and prey volume (mls). Dashed line represents the regression of snout-vent length against prey volume and intact line represents the regression of snout-vent length against maximum prey volume (Section 4.3.3).



4.4 DISCUSSION

Reptiles display a range of trophic levels which in lizards are often size related with the larger animals being herbivores and the smaller ones being carnivores or insectivores (Pough 1973, Stamps 1977). Many studies detail the specifics of lizard diets and although it is not possible to catalogue all of these here, those on Australian skinks are summarised in Table 8. One of the main disadvantages of many studies is that only one estimate of food importance is used, usually the number of stomachs containing a food item, an approach which often gives a biased interpretation. Brown (1958) pointed out the difficulties in interpreting feeding data from only one type of estimate and Hyslop (1980), in a review of stomach contents analysis for fish, indicated the advantages and disadvantages of different techniques. These comments were equally applicable to reptilian feeding studies.

C.taeniolatus fits into the category of a small carnivore, as it feeds predominantly on insects, with an occasional attack on small lizards (conspecifics and others). Of the species of Ctenotus, the diet of C.taeniolatus is most like that of C.robustus (Way 1979), C.lesueuri (Davidge 1979, Murray 1980) and C.fallens (Murray 1980), which are coastal or tableland species. Other species of Ctenotus examined (Pianka 1969) are predominantly desert forms and consequently have high levels of termites and ants in their diets, although this may also be linked to behavioural differences. In the present study plant matter and sand found in the stomach was in very small amounts and was undoubtedly consumed along with prey and shed skin. Undigested plant material was also found in the lower gut, particularly the rectum, suggesting further that it was not used as a food. However, in Ctenotus leae (Pianka 1969), C.lesueuri (Davidge 1979) and C.fallens (Murray 1980) plant material occurred more commonly than one would expect if it

were eaten accidentally. Large amounts of shed skin were also found in the stomach and lower gut which is consistent with reports from other reptiles (Groves and Groves 1972, Bustard and Maderson 1965, Barwick 1965). Shine (1971) claims that for an adult female Egernia cunninghami shed skin represented 5% of the energy ingested in a year. It would be interesting to ascertain how much of that energy is recycled, as it may be quite high if the skin were eaten when it first became loose and still retained its essential oils. Note that Ctenotus, like other skinks, does not shed its skin in a continuous sheet but in small patches.

The presence of seasonal differences in the diet of C.taeniolatus is a common occurrence with opportunistic feeders (Vitt and Ohmart 1974,77a,77b, Mitchell 1979), and is most likely a function of seasonal fluctuations in insect abundance (Ballinger and Ballinger 1979). This seasonality extends into winter, when lizards become inactive and feed little. Further, adult and juvenile diets do not differ qualitatively, although adults are capable of eating larger prey than hatchlings and hence have a greater diversity of sizes among their prey (Fig 13). These differences in prey size are related to differences in foraging strategy.

Lizards are reported to forage typically in one of three ways, either as sedentary, ambush predators (sit-and-wait), active, cruising predators (cruising or widely foraging) or as investigative, cruising predators (intensive foragers) (Schoener 1971, Regal 1978, Huey and Pianka 1981), although Regal (1978) proposes that these behaviours are points along a spectrum. In early studies of Ctenotus Pianka (1969) regarded this genus to consist of widely foraging predators; however C.taeniolatus does not fit into this category. Table 7 shows that C.taeniolatus divided time between of sit-and-wait and widely foraging

behaviours. Adults and hatchlings spent different amounts of time on each strategy, with adults spending more time waiting for prey than searching, even though the latter strategy was more successful per hour; hatchlings on the other hand spent approximately equal amounts of time waiting and searching, while their success rate when searching was 2.5 times greater than that of adults. This high success rate of hatchlings was probably due to their ability to search their habitat more extensively because of their small size rather than that they covered a larger area. Huey and Pianka (1981) state that foraging speed should influence the rate of encounters with prey, and hence it is expected that lizards would encounter more prey when actively foraging. These success rates of course do not take into account the type of prey caught or their energy content; they are only an account of the number of times a lizard is seen feeding. Further, Huey and Pianka (1981) and Vitt (1983) list a number of life history characteristics and tail morphologies postulated to be correlated with foraging mode, which when used to classify the behaviours of C.taeniolatus result in it being termed as both a widely foraging and a sit-and-wait predator. For example C.taeniolatus eat both mobile and sedentary, unpredictable prey, are preyed upon by both widely foraging (elapid snakes; Shine 1977a, 1980a) and sit-and-wait predators (raptors; Debus 1981) and use camouflage, speed and saltation as modes of escape from predators.

The question then arises as to why adults spend more time foraging using the sit-and-wait strategy, when it is the less successful, and according to Anderson and Karasov (1981) less efficient mode of foraging. Further, why adults and hatchling strategies differ. There are a number of possibilities which are probably not independent.

1. The type of prey caught using the sit-and-wait strategy may be larger or richer in energy than those caught by actively foraging, e.g. lepidopteran larvae or orthopterans.

2. Energetic cost of active searching may be higher for an adult than for a hatchling as adults would presumably need to search longer for prey than hatchlings, remembering that the diet of adults is made up predominantly of small prey (Fig. 13). Also, hatchlings would be able to search small crevices more thoroughly.

3. All behaviours reported in the results may not be independent. Lizards while in the sit-and-wait position could also be resting or basking, even though they are not in the described basking position. Hence, it may be that adults need longer to bask to optimum temperatures than hatchlings. Certainly surface area to volume ratios would suggest this is the case. If this argument is extended to its logical conclusion, then the ratio of sit-and-wait to active searching would be expected to change with time of day or season. It is known that the lacertid Aporosaura anchietae changes its foraging mode depending on wind conditions (Robinson and Cunningham 1978) and the gecko Ptenopus garrulus changes its strategy during termite swarms (Huey and Pianka 1981).

Table 8 : Summary of literature on Australian skinks: (1) = number or % of lizards, (2) = number or % of prey items, (3) = volume or weight (as total or %) of prey.

SPECIES	MAJOR FOODS	NUMBER LIZARDS	METHOD	SOURCE
<u>Anotis maccoyi</u>	spider, beetle larvae, isopods	90	2,3	Robertson 1976
<u>Carlia fusca</u>	beetles, termites, hemipterans	44	2	Belmont 1977
<u>Carlia novae-quinea</u>	Collembola, termites, hemipterans	59	2	Belmont 1977
<u>Ctenotus ariadnae</u>	termites	5	2,3	Pianka 1969
<u>Ctenotus atlas</u>	termites	26	2,3	Pianka 1969
<u>Ctenotus brooksi</u>	beetle, ants	62	2,3	Pianka 1969
<u>Ctenotus calurus</u>	termites	27	2,3	Pianka 1969
<u>Ctenotus colletti</u>	Homoptera-Hemiptera	5	2,3	Pianka 1969
<u>Ctenotus dux</u>	locusts, beetles	47	2,3	Pianka 1969
<u>Ctenotus grandis</u>	termites	61	2,3	Pianka 1969
<u>Ctenotus helenae</u>	termites	72	2,3	Pianka 1969
<u>Ctenotus leae</u>	Hemiptera-Homoptera, plants	16	2,3	Pianka 1969
<u>Ctenotus leonhardii</u>	termites, larvae	104	2,3	Pianka 1969
<u>Ctenotus pantherinus</u>	termites	61	2,3	Pianka 1969
<u>Ctenotus piankae</u>	Thysanura, spiders	10	2,3	Pianka 1969
<u>Ctenotus quattuordecimlineatus</u>	larvae, termites	93	2,3	Pianka 1969

Table 8 (continued)

SPECIES	MAJOR FOODS	NUMBER LIZARDS	METHOD	SOURCE
<u>Ctenotus schomburghii</u>	termites	79	2,3	Pianka 1969
<u>Ctenotus fallens</u>	orthopterans, plants	76	3	Murray 1980
<u>Ctenotus impar</u>	termites	11	3	Murray 1980
<u>Ctenotus lesueuri</u>	beetles, orthopterans	6	2	Murray 1980
	orthopterans, beetles	47	1,3	Davidge 1979
	spiders			
<u>Ctenotus robustus</u>	orthopterans, beetles, ants	42	1,2	Way 1979
<u>Ctenotus spaldingi</u>	termites, cockroaches	5	2	Belmont 1977
	spiders			
<u>Egernia cumminhami</u>	clover, beetles, orthopterans	92	1,2,3	Barwick 1965
<u>Egernia striolata</u>	ants, dictyopterans, orthopterans, ants	35	1,2	Bustard 1970
<u>Egernia whitii</u>	ants, beetles, spiders	187	1	Hickman 1960
	hemipterans			
<u>Hemiergis decrensiensis</u>	ants, beetles, larvae, hemipterans	83	2,3	Robertson 1976
	ants, beetles, spiders	57	1,2	Crome 1981
<u>Hemiergis peronii</u>	beetles, mites, snails, cockroaches			Smyth 1968
<u>Lampropholis delicata</u>	Collembola, ants, flies	99	2	Belmont 1977
	larvae			
	spiders, ants, beetles	8	1,2	Crome 1981
<u>L. quichenoti</u>	Collembola, ants, flies, spiders, larvae	104	2	Belmont 1977
	spiders, beetles, ants	131	1,2	Crome, 1981
<u>Lerista bougainvillii</u>	beetles, cockroaches, hemipterans	19	2	Smyth and Smith 1974
<u>Lerista christinae</u>	spiders, cockroaches, Thysanura	14	3	Murray 1980
<u>Lerista elegans</u>	spiders, beetles, wasps	204	1,3	Davidge 1979

Table 8 (continued)

SPECIES	MAJOR FOODS	NUMBER LIZARDS	METHOD	SOURCE
<u>Lerista</u> <u>lineata</u>	spiders, beetles, woodlice	121	1,3	Davidge 1979
<u>Menetia</u> <u>greyii</u>	termites, hemipterans, ants	44	2	Smyth and Smith 1974
<u>Menetia</u> sp.	spiders, beetles, termites	35	1,3	Davidge 1979
<u>Morethia</u> <u>boulengeri</u>	moths, cockroaches, spiders, ants	80	2	Smyth and Smith 1974
<u>Morethia</u> <u>obscura</u>	orthopterans, spiders hemipterans	59	2	Murray 1980
<u>Spheno-</u> <u>morphus</u> <u>quovii</u>	ants, orthopterans, damselflies, beetles	59	1,2	Veron 1969a

5.0 GROWTH

5.1 INTRODUCTION

Although many studies of growth of lizards are available in the literature, only two such studies have been completed for Australian skinks (Barwick 1965, Pengilley 1972). The aim of this chapter is to present data on growth rates of C.taeniolatus, to discuss these in relation to equations of size and age that have been used to model growth in other lizards and thus to present the growth history of C.taeniolatus.

5.2 METHODS

Analysis of growth of C.taeniolatus was approached using the analysis of size classes in a population, and the analysis of individual growth rates with growth models.

5.2.1 Analysis of size classes

Two methods were used in the analysis of size classes over time: frequency histograms of size classes and cluster analysis of the length - weight relationship. In both cases only two time periods were examined because in many months only small numbers of lizards were caught. The periods selected were January-February, the time when hatchlings emerge, and November-December, the time prior to hatching of young. Only lizards caught in the mark-recapture study were incorporated in these analyses as other methods of capture were often biased towards adults.

Cluster analysis was employed in addition to the analysis of size-frequency histograms as this method utilised changes in weight as well as snout-vent length, thus allowing for detection of growth patterns in which weight and snout-vent length did not increase isometrically. The cluster analysis was carried out using the Clustan computer package (Wishart 1982) in which Ward's method of calculating the incremental sum of squares of the Euclidean distances was used as the clustering criterion with the process being continued until the residual sum of squares within a cluster was less than 5% of the total sum of squares.

5.2.2 Individual growth

Linear growth of C.taeniolatus was determined from changes in snout-vent length (SVL) monitored during the mark-recapture program described in section 2.3. Twenty four size changes were recorded for males and 24 for females. Thirty-five lizards could not be classified as either male or female and were therefore not included in any of the following analyses. Changes in weight with time were not considered as body weight is dependent on reproductive condition, season, and in lizards in particular, the amount of tail lost or regrown.

Fitting a growth model.

There are several models available to describe the relationship between size and age. Ricker (1979) detailed many of these as they have been applied to fish growth, and Andrews (1982) summarised those used for reptiles. In this study the procedure of Schoener and Schoener (1978) was followed and the fit of the three following growth curves was compared. Schoener and Schoener (1978) described the derivation of these models in detail.

1. Von Bertalanffy Model

$$dL/dt = a_1 \cdot r (1 - L/a_1)$$

where variable L is SVL and t is growth time, and parameter a_1 is maximum or asymptotic length and r is the characteristic growth rate

$$\text{or } L_2 = a_1 - (a_1 - L_1) \cdot e^{-r \cdot D}$$

where L_1 and L_2 are the SVL at the beginning and end of a time interval respectively, and D is the duration of that time interval.

2. Logistic-by-length Model

$$dL/dt = L \cdot r \cdot (1 - L/a_1)$$

$$\text{or } L_2 = a_1 \cdot L_1 / (L_1 + (a_1 - L_1) e^{-r \cdot D})$$

where parameters and variables are as defined in Model 1.

3. Logistic-by-weight Model

$$dL/dt = (r \cdot L/3) \cdot (1 - L^3/a_1^3)$$

$$\text{or } L_2 = a_1 \cdot L_1 / (L_1^3 + (a_1^3 - L_1^3) e^{-r \cdot D})^{1/3}$$

where parameters and variables are as defined in Model 1.

All three models were fitted to male and female growth data using Derivative-free Nonlinear Regression (BMDPAR; Ralston 1979), a non-linear least squares program which estimates the parameters of a function by selecting those parameters producing the minimum sum of squares of the residuals. An important part of the program is the selection of the initial values of the parameters. The initial parameters used here (male $a_1 = 0.0836$, $r = 56.8591$; female $a_1 = 0.0037$, $r = 68.2256$) were determined by a similar program listed by

Fabens (1965), which did not require precise initial values.

Also confidence intervals for the parameters were computed from

$$b - (t_{1-\alpha/2}(n-k))s < B < b + (t_{1-\alpha/2}(n-k))s$$

where s was the asymptotic standard deviation of the parameter B , b the estimate of B , $t_{1-\alpha/2}(n-k)$ the two-tailed value of t at significance level α with $n-k$ degrees of freedom, n the sample size and k the number of parameters (Schoener and Schoener 1978).

The same non-linear regression procedures were used to obtain equations predicting size from age. These equations are integrals of the previous differential equations with the constant of integration (b) being calculated from known age-size data.

Finally it is commonly accepted that lizards from temperate zones which are inactive and feed little over winter (see section 4.3.2) show no appreciable growth over this time. To account for this, 90 days were subtracted from each time interval that spanned or intruded into the winter no-growth period. Consequently all times and ages represented are estimates of growth times and not actual time.

5.3 RESULTS

5.3.1 Size classes

Figure 14 shows the size-frequency histograms for females and males from the January-February and the November-December periods. These clearly showed at least two size groups of females and males from January-February, the first group represented the hatchlings of the year (30-45 mm SVL), the second group older individuals. In females the second group was further subdivided into two groups: those lizards

between 50 and 60 mm and those between 65 and 80 mm SVL. In November-December the groups were not defined, the smallest individuals of males and females were greater than 35 mm SVL, with the largest number of lizards appearing at 45-50 mm SVL.

Figures 15 and 16 show graphs of snout-vent length versus weight for the lizards described above. Clusters of like-sized individuals of both females and males in January-February indicated the presence of 4 and 3 size classes respectively. In November-December there were 3 and 4 size classes for female and male lizards respectively.

In summary, it was easy to distinguish newly emerged hatchlings of both sexes from other individuals in January-February and also approximately one year later in November-December. Although, from this point it was not possible to determine the age accurately from size groups. In females it was possible to distinguish three other size groups which probably represented 1, 2 and 3+ year old individuals in both January-February and in November-December. Groups among males were less distinct with only two groups being found. These probably represented 1 and 2+ year old individuals. The variation present in the smallest size grouping in November-December for both females and males reflects variation in individual growth rates during the first year of life. In males the cluster analysis indicated that this group was made up of two distinct size groupings.

The above data reaffirm that females grow larger and heavier than males (Section 6.3.1). Further, it was not possible to distinguish between the ages of individuals on the basis of size after 3 years in females and 2 years in males, indicating that growth is reduced after this time.

5.3.2 Individual growth

C.taeniolatus begin to hatch in late January with a snout-vent length of 33 (SD = 1.7) mm . At this stage there were no apparent differences between males and females.

The changes in snout-vent length of marked individuals captured from 1979 to 1982 are shown in figures 17, 18 and 19. Data from the few lizards captured before and after winter (May - August) confirmed the fact that lizards grew little over this time.

Growth Model

A comparison of the goodness of fit of the three models is shown in Table 9. Using the criterion that the most satisfactory model was that which produced the least sum of squares of the residual (SSQR), the von Bertalanffy Model was the best fit to female growth data and the logistic-by-weight was the best for data from males (Fig. 21). However, the differences in the goodness of fit among the three models was not great. The observed and predicted growth rates according to each model for males and females are shown in figure 20 and a number of features are apparent from these graphs. Firstly, observed growth rates were quite variable, especially in lizards less than 55 mm SVL, and all 3 models systematically underestimated growth rates of these individuals. Secondly, as a consequence of this, and the small sample sizes, there was considerable overlap in the 95% confidence intervals of the estimates of a_1 and r for males and females in all three models (Table 9). Accordingly, the growth rates of males and females could not be shown to be significantly different even though it was apparent from the length-weight relationships detailed and compared in section 6.3.1 that females do grow larger and heavier than males (females to 75mm, males to 70mm SVL).

Table 9 : Parameters (asymptotic SVL, a_1 , and growth rate, r ,) and goodness of fit (residual sum of squares, SSQR, and coefficient of determination, R^2) for three growth models. Confidence intervals (95%) are in brackets. * indicates model selected as best fit.

	Female	Male
Von Bertalanffy (n=24)		
SSQR	265.710*	414.895
a_1	69.37 (64.94-73.81)	67.14 (58.10-76.18)
r	0.0033 (0.0021-0.0046)	0.0037 (0.0011-0.0062)
R^2	0.7863	0.6715
Logistic-by-length (n=24)		
SSQR	314.145	378.640
a_1	68.79 (64.90-72.67)	65.11 (59.40-70.82)
r	0.0049 (0.0031-0.0063)	0.0059 (0.0031-0.0086)
R^2	0.7473	0.7002
Logistic-by-weight (n=24)		
SSQR	372.364	347.389*
a_1	67.87 (64.32-71.42)	63.64 (59.42-67.86)
r	0.0068 (0.0049-0.0086)	0.0083 (0.0052-0.0114)
R^2	0.7005	0.7249

Figure 14 : Frequency distribution of size classes (SV length) of male and female Ctenotus taeniolatus captured in January-February and November-December.

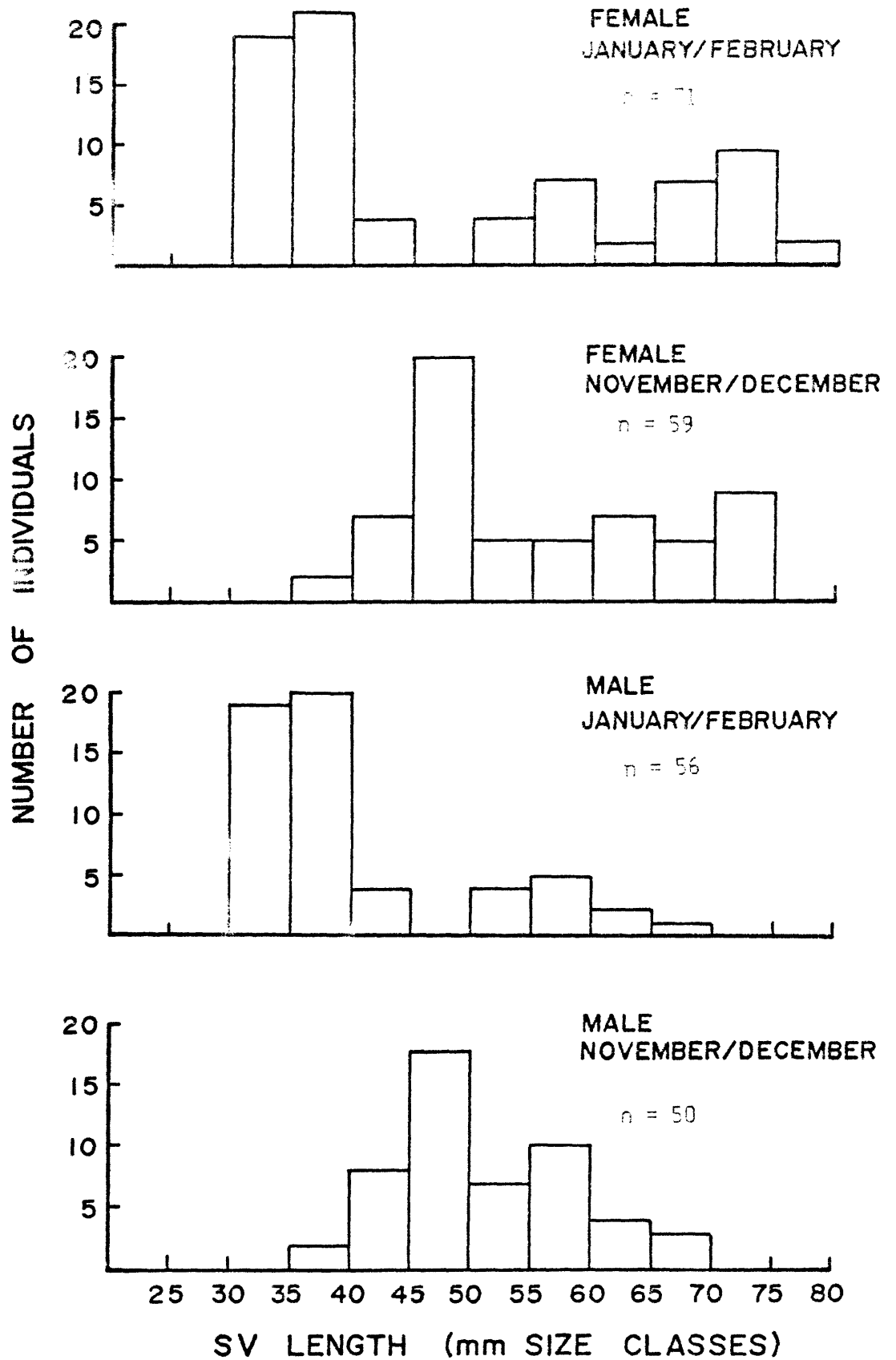


Figure 15 : Snout-vent length - body weight relationship for female Ctenotus taeniolatus captured in January-February and November-December. Circles represent size groups determined after cluster analysis (Section 5.3.1).

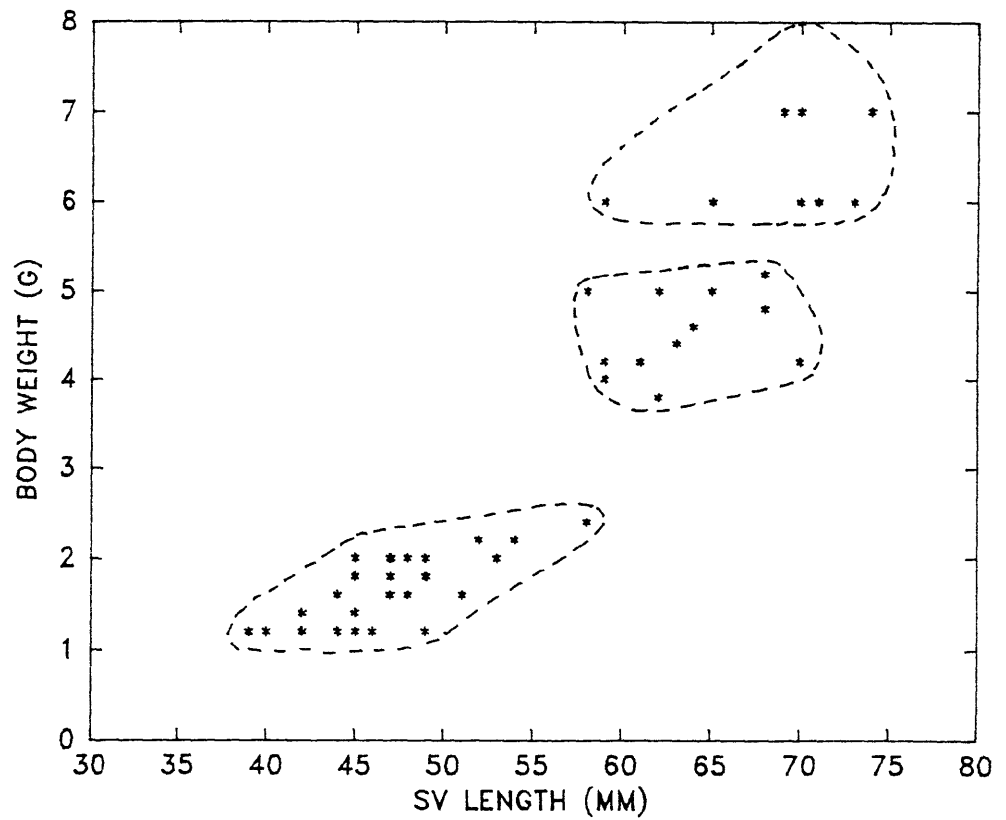
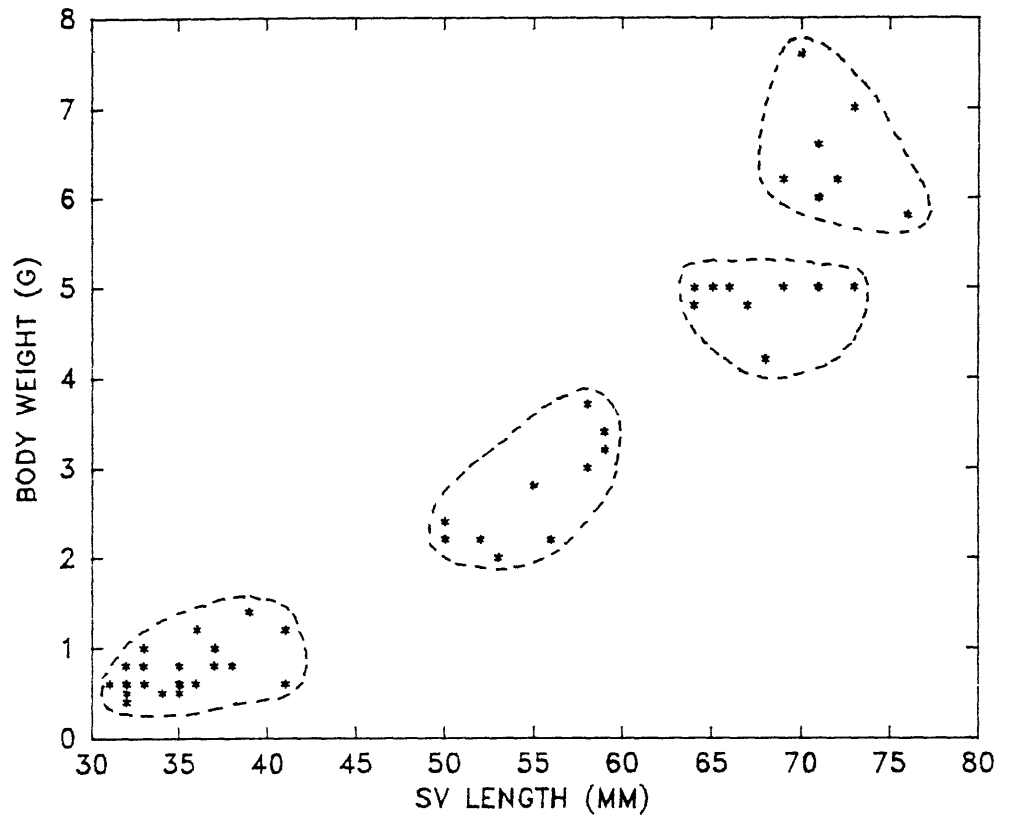


Figure 16 : Snout-vent length - body weight relationship for male Ctenotus taeniolatus captured in January-February and November-December. Circles represent size groups determined after cluster analysis (Section 5.3.1).

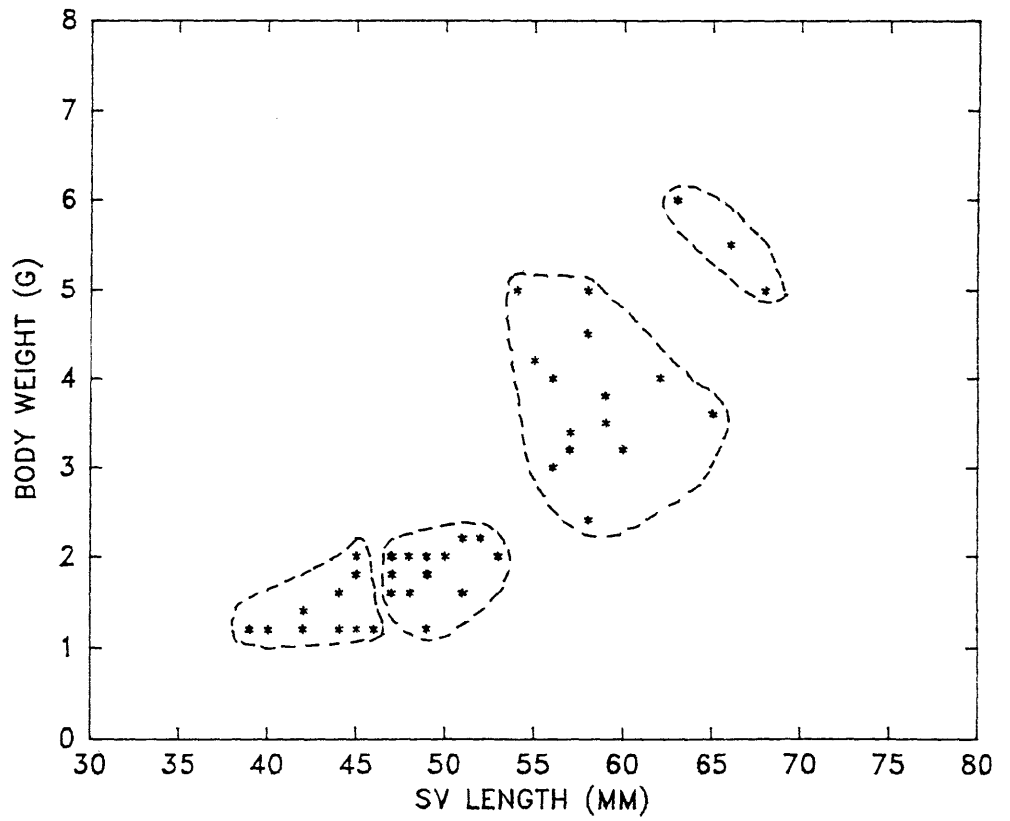
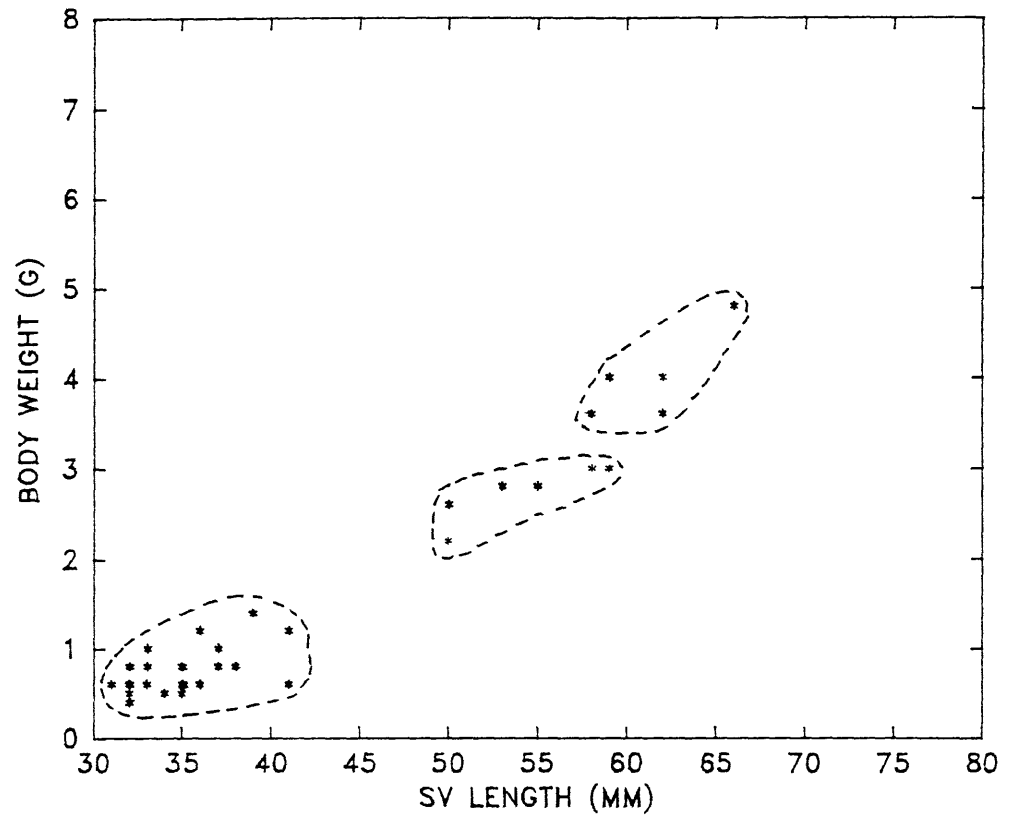


Figure 17 : Individual changes in snout-vent length of female Ctenotus taeniolaus captured between 1979 and 1982. Months are represented by their first initial.

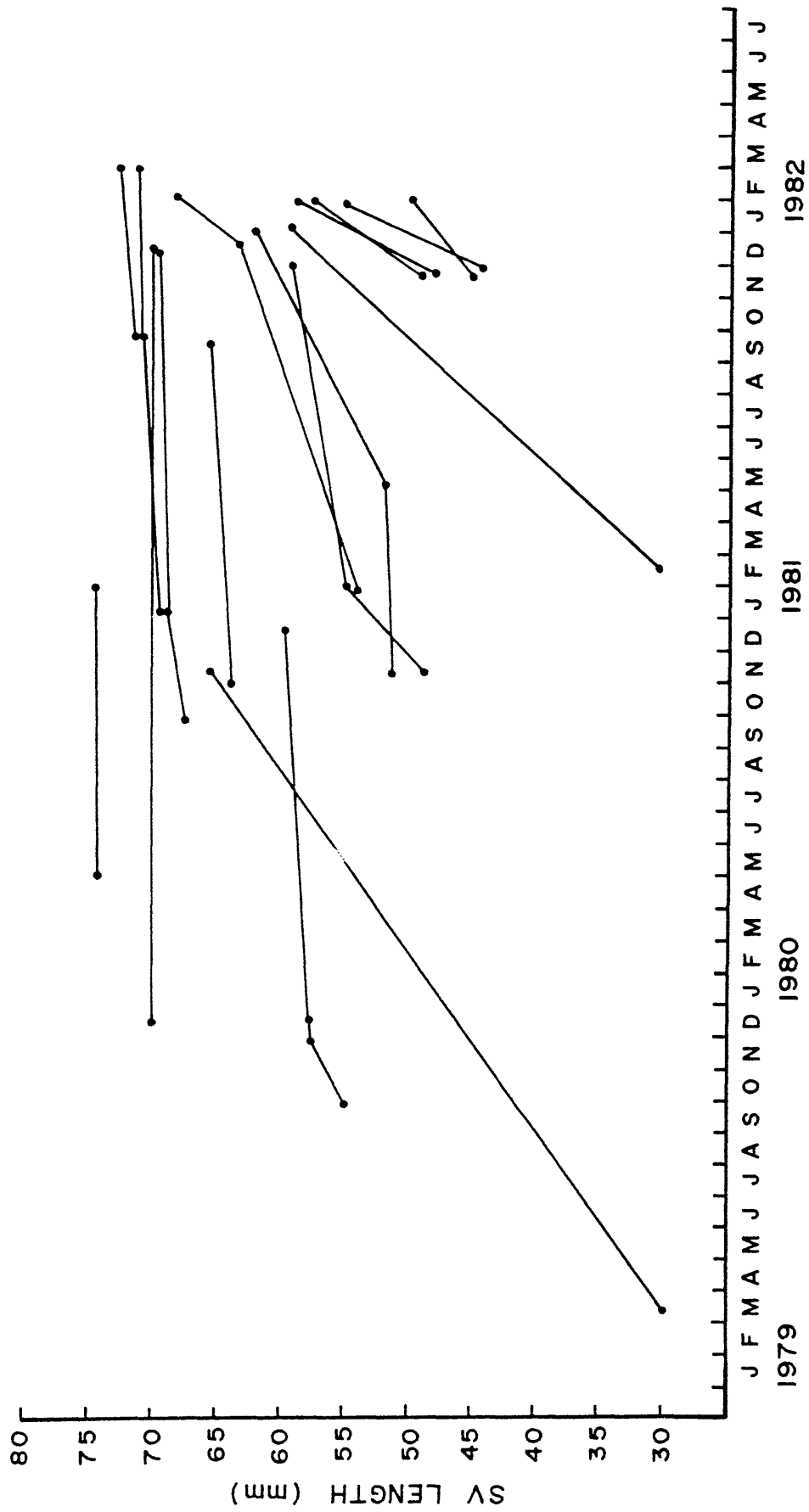


Figure 18 : Individual changes in snout-vent length of male Ctenotus taeniolatus captured between 1979 and 1982. Months are represented by their first initial.

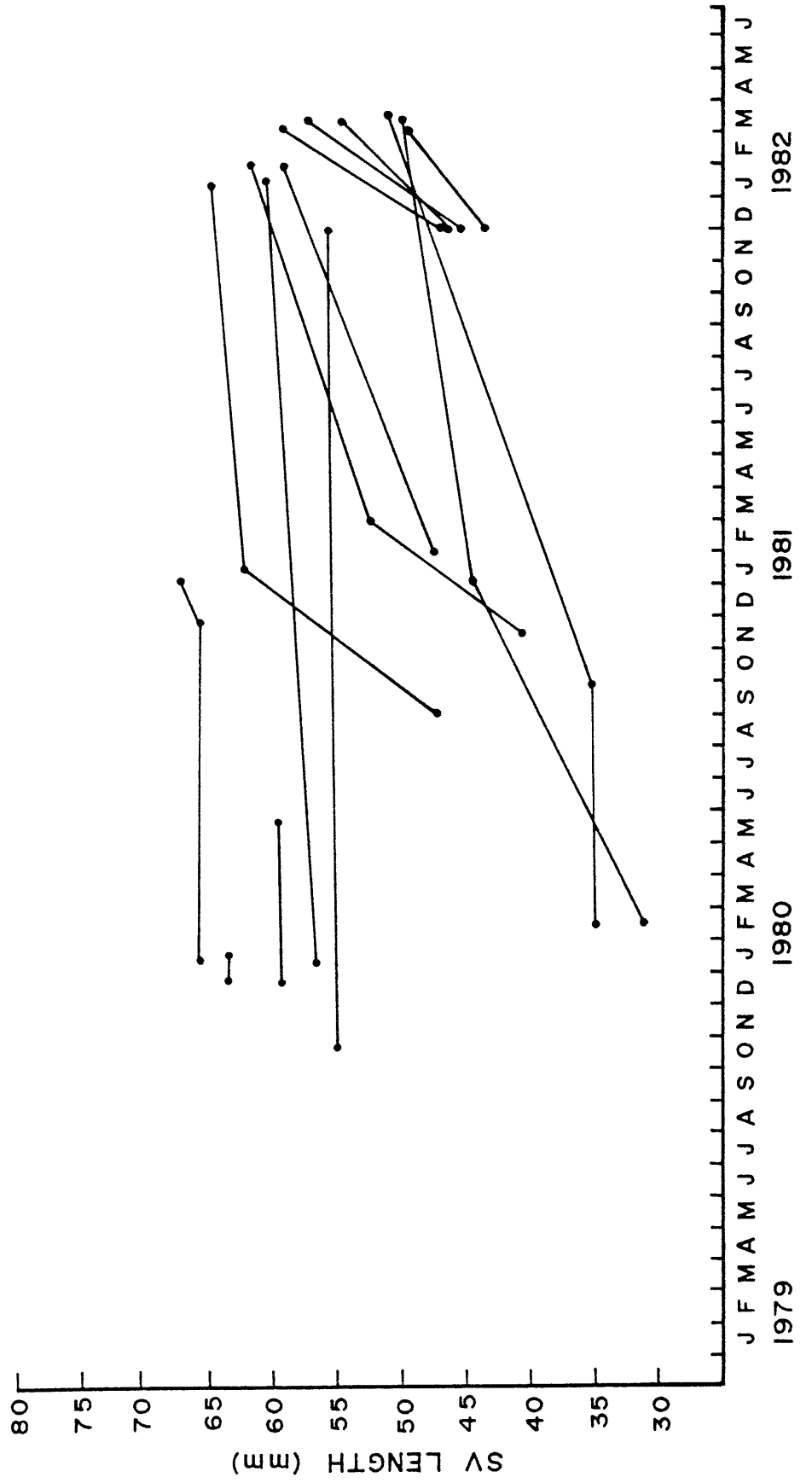


Figure 19 : Individual changes in snout-vent length of unsexed Ctenotus taeniolatus captured between 1979 and 1982. Months are represented by their first initial.

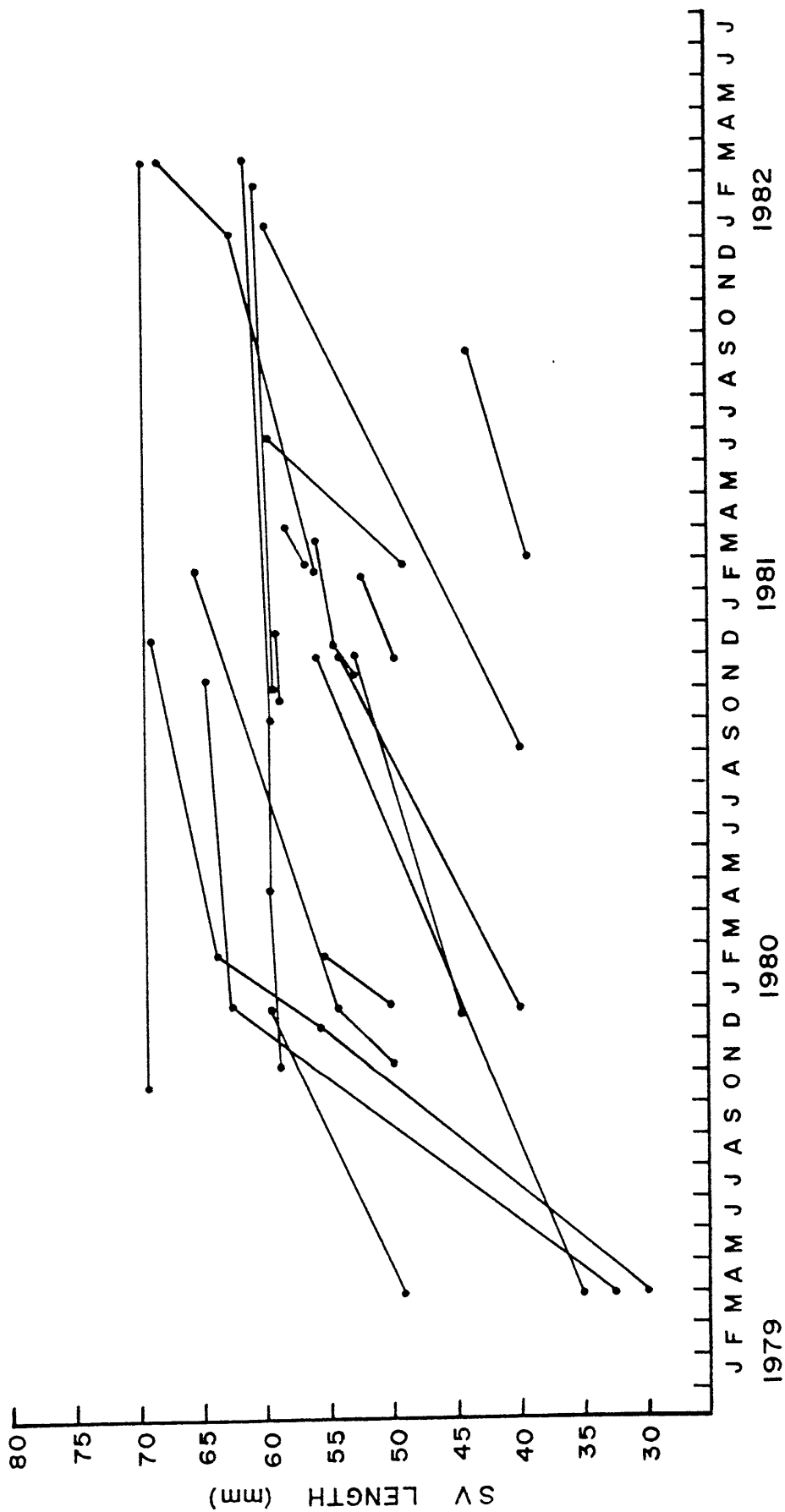


Figure 20 : Relationship between snout-vent length and growth rate in female and male Ctenotus taeniolatus. Lines represent lines of best fit of three growth models, von Bertalanffy (____), Logistic-by-length (-----) and Logistic-by weight (.....).

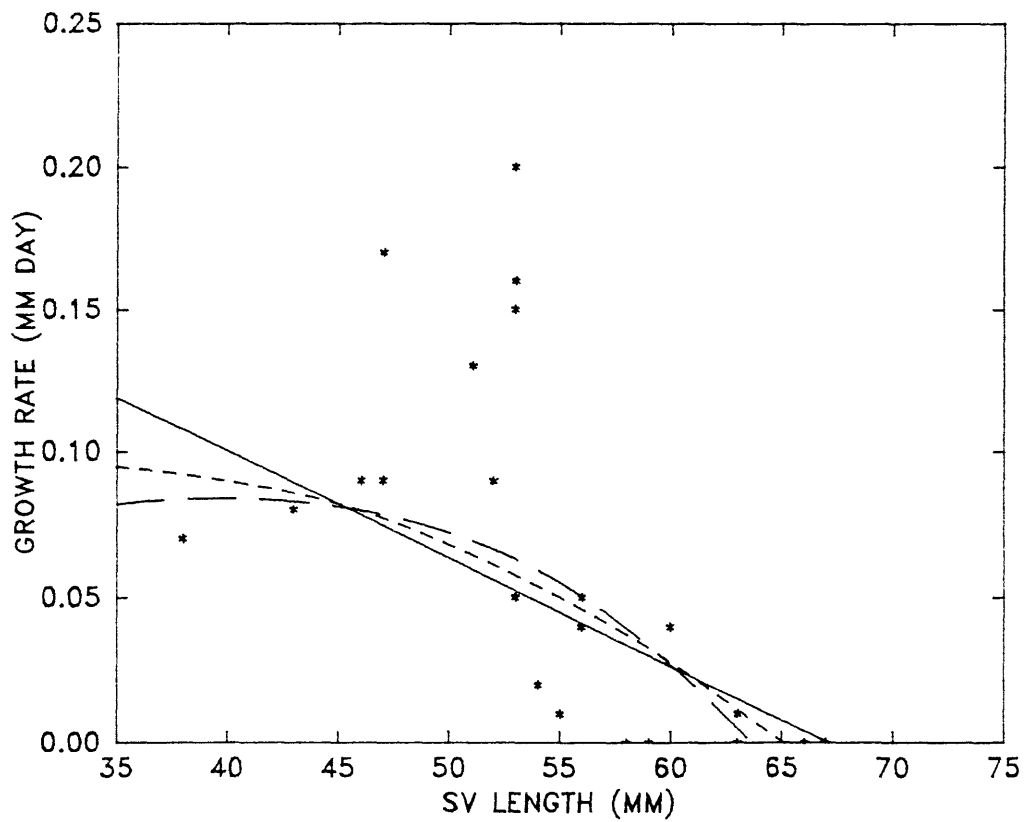
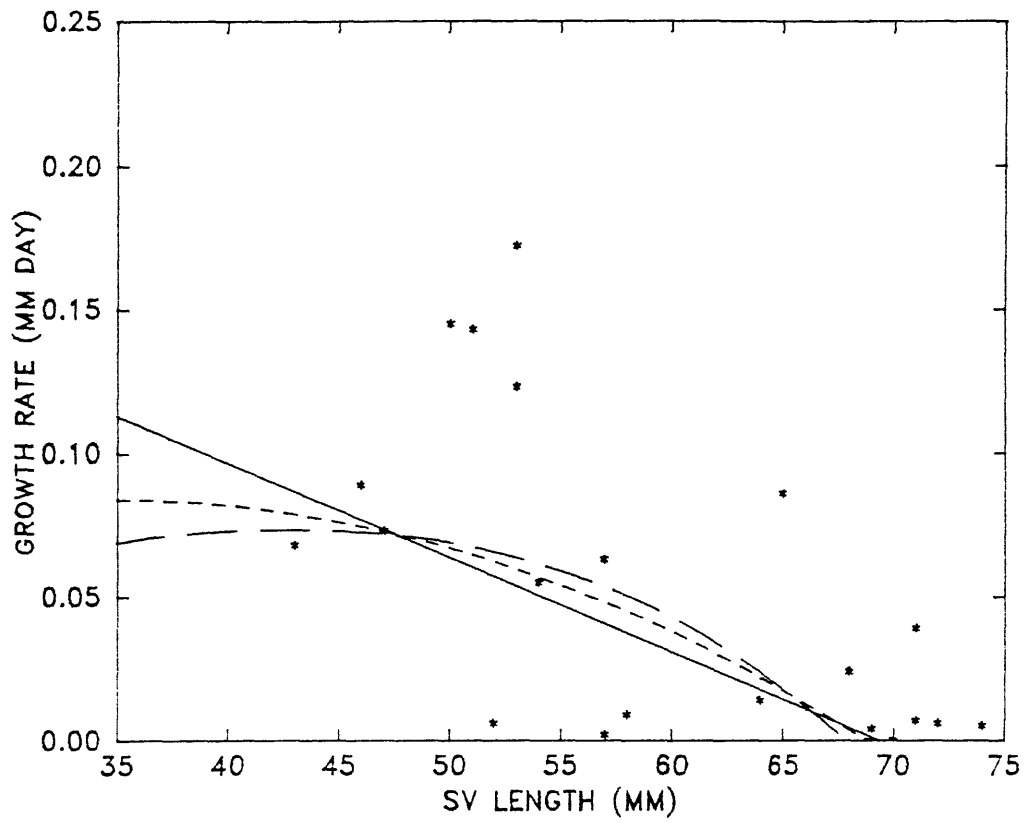
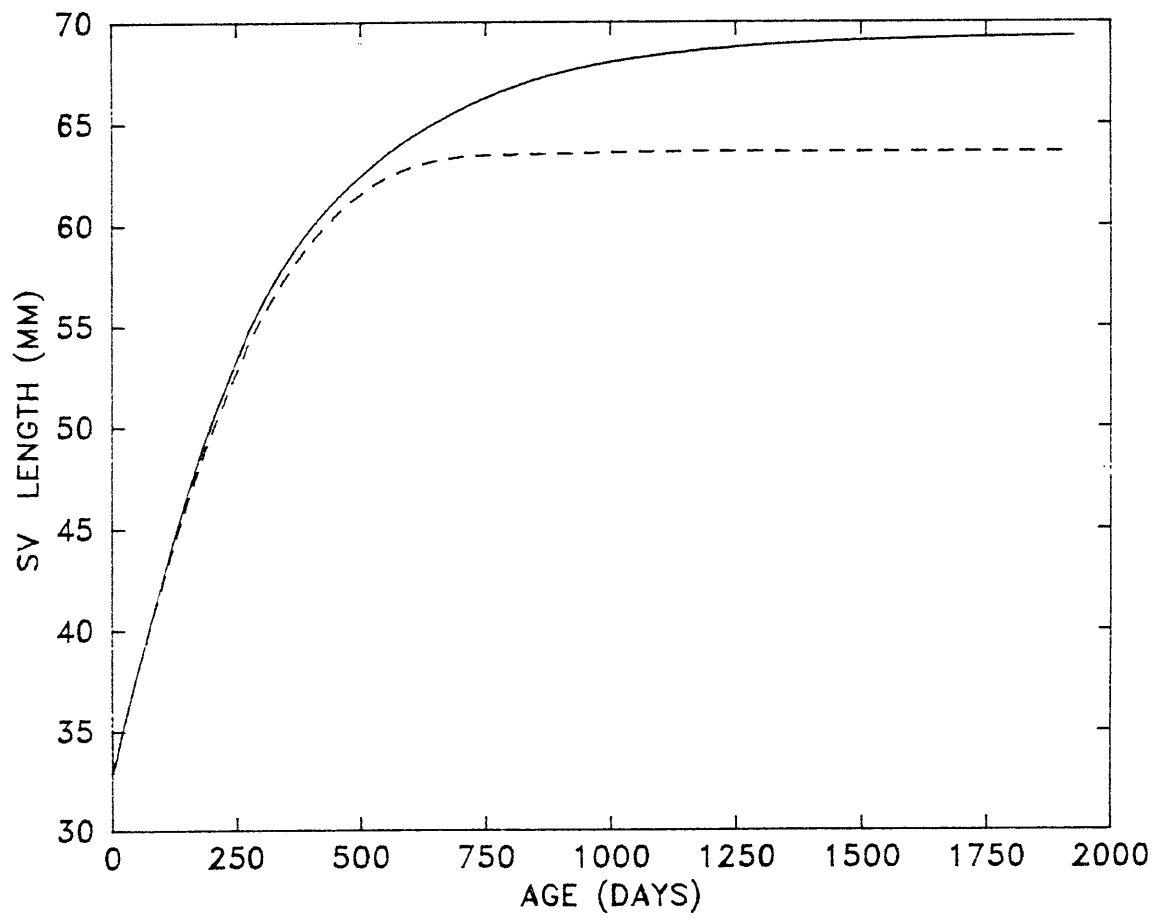


Figure 21 : Final growth models for female (—) and male
(-----) Ctenotus taeniolatus (see Table 9).



5.4 DISCUSSION

Most studies of post-natal growth in reptiles are limited, and often anecdotal or descriptive. Van Devender (1978) and Andrews (1982) summarised many of these. Further, Barwick (1965), Pengilley (1972), Bradshaw (1971) and Bustard (1970) have examined growth in Australian lizards. However, growth is a highly complex process and theoretical studies of optimisation ecology suggest that it is one of the three major life history categories used to maximise fitness (Gadgil and Bossert 1970). As a consequence recent studies have concentrated on approaches more conducive to quantification and statistical analysis and which invariably involve the development of growth models. Three models, von Bertalanffy, logistic-by-length and logistic-by-weight, are most commonly used (Schoener and Schoener 1978, Dunham 1978, present study), although, as with all models, these have limitations, and can therefore result in inaccurate predictions (Dunham 1978). Firstly, all of the above models are stationary and therefore parameters are assumed to be time-invariant over the recapture period. Dunham (1978) argued that the existence of seasonal variation in growth refutes this assumption and that unless recapture data are partitioned into periods where growth is similar (thus meeting the assumption of stationarity) better model fit is likely to be impossible. In the present study the no-growth period over winter, a phenomenon found in many lizards (Pengilley 1972, Bustard 1970, Barwick 1965), was subtracted from each recapture time interval. However, this still does not account for variation in growth rate between summer, autumn and spring, and could lead to errors in prediction.

A second limitation is a result of size distribution within the sample. In samples which fail to represent all size classes, particularly the smaller classes, it is impossible to determine which model would produce the best fit.

In an evaluation of growth models Andrews (1982) claims that the von Bertalanffy and logistic growth models make very different predictions about the shapes of growth curves. Theoretically, this is possible; however, in real terms the three models can make similar predictions. For example in C.taeniolatus the von Bertalanffy model predicts that growth is maximal in the smallest size class (30-36 mm SVL), while if growth in length is logistic the maximal rate of growth will be observed at 50% of the asymptotic length, estimated as 34 mm SVL in females and 32.5 mm SVL in males. Note that the average hatchling is approximately 50% of male maximum SVL and 46% of female maximum SVL. Figure 4 in Dunham (1973) shows the closeness of these three models in the iguanid, Sceloporus merriami, as does figure 21 in the present study, where female growth was found to follow a von Bertalanffy model and male growth a logistic-by-weight model. Overall it appears that all three models make similar predictions, at least for small, short-lived lizards in which hatchling size is large relative to maximum adult size.

However, even though all models used accounted for high percentages of the total variation in growth in C.taeniolatus, observed and predicted values did not correspond closely, especially for lizards below 55 mm SVL. This is in part due to the limitations of the models discussed above, but is also the result of the large variation in growth rates present in lizards of this size class. Variability in growth has been attributed to a number of causes, both intrinsic and extrinsic.

Bradshaw (1971) using Amphibolurus ornatus and Ferguson and Brockman (1980) using sceloporine lizards found that a genetic component attributed to such variation. Stamps and Tanaka (1981) and Nagy (1973) suggest that water stress alone decreased growth rates in Anolis aeneus and Sauromalus obesus respectively, while many authors suggest that food quality and food availability, often as a result of drought, can cause variation in growth rates within the same population of lizards (Andrews 1982). During the 3 years of the present study the New England region was in severe drought, so it is likely that both water stress and food availability had an effect on growth rates of some lizards during the early stages of their life when growth was greatest. In lizards over 55 mm SVL and approaching adulthood, growth and variation in growth was reduced indicating that growth was a less important component of the total energy budget, and consequently less affected by environmental conditions.

However, although there are some limitations on the ability of models to predict age from size of individuals, it is still possible to get an overall summary of growth in C.taeniolatus, if these data are used in conjunction with data from size class frequencies.

In summary (Fig. 22), females attain a greater maximum size than males, and also mature at a larger size (female 52 mm, male 43 mm SVL; Section 6.3.1). The amount of variation in growth rates in the small size classes makes it difficult to determine the age at sexual maturity, but it seems likely that most males and females begin breeding in their second year or third summer. The possibility that they breed before this, especially for males, cannot be excluded, as some individuals reach the minimum size for sexual maturity in the first year (second summer). However, this possibility is unlikely, for C.taeniolatus has a strict breeding season and males would have to reach 43 mm SVL and

females 52 mm SVL prior to September of that year, a rare event considering the lack of growth over winter. Pengilley (1972) found that of 12 species of small skink examined from the southern highlands of Australia, the majority also reached sexual maturity in their second year. The maximum age of small skinks is unknown; however, a number of male and female C.taeniolatus were captured repeatedly over 3 years, so assuming a period of 2 years to reach sexual maturity these lizards are capable of living at least 5 years.

Figure 22 : Important life history events and their relation to average growth pattern in female (-----) and male (——) Ctenotus taeniolatus.

