PART 4

SIGNIFICANCE OF AUTOTOMY

RATIONALE

Soon after the commencement of the present study and later after detailed analysis of the results presented in Part 3 of this thesis it was obvious that C.taeniolatus was not like other temperate lizards in that it possessed no abdominal fat bodies and stored the majority of its energy reserves as lipids within the tail, which circumstantial evidence suggested it used for reproduction and maintenance over winter. Further, personal observations and communications with other herpetologists suggested that C.taeniolatus exhibited high levels of tail autotomy in nature. Taken together these results indicate that there exists a conflict of interests between the requirements of a lizard for reproduction and overwintering, and the necessities that induce a lizard to autotomise its tail. The aims of Part 4 of this thesis are to investigate this conflict and consequently to determine what trade-offs, if any, a lizard in this situation would have to undertake. In order to fulfil these aims (i) the actual costs of overwintering and reproduction were determined to see if the tail was necessary for these activities, (ii) experiments were conducted to test hypotheses generated from these observations, (iii) the frequency and position of autotomy was determined and related to the distribution of lipid in the tail, so that the relevance of the above results could be evaluated, and (iv) all three were taken to determine the overall significance of autotomy to C.taeniolatus.

8.0 COSTS OF OVERWINTERING AND REPRODUCTION

8.1 METHODS

8.1.1 Determination of metabolic rate

Metabolic rate was estimated for C.taeniolatus using a constant pressure volumetric system (McDonald 1976) (Fig. 49). Ten grams each of soda lime ('Carbosorb') and silica gel were added to each chamber to act as CO_2 and H_2O absorbers respectively. During each experiment the chambers were submerged in a water bath containing ethylene glycol as an antifreeze, and maintained within 0.5 C of set temperatures. Five respirometers were in operation during each run; a sixth respirometer acted as a thermobarometer (a control containing carbosorb and silica gel but no lizard) to account for changes in atmospheric pressure.

Each experiment was run at night for 1 to 3 hours after an initial 10 hour equilibration period. Measurements were in general made at 5 minute intervals although at higher temperatures this interval was shortened to 1 minute. Lizards were all captured within 10 km of Armidale in midwinter (22 July - 10 August 1981) and immediately returned to the laboratory where they were housed in a constant temperature cabinet which, in an effort to simulate winter conditions, was set to give 14 hours of light at 10 C and 10 hours of dark at 5 C. Lizards were kept at these conditions until used in an experiment 2 - 5 days later.

Six separate experimental temperatures were used: 0, 5, 10, 15, 20 and 30 C. Either five or 10 different lizards were run at each temperature with body weight (g) of each lizard being measured prior to an experiment. Results were discarded if a respirometer leaked or if

lizards were unduly disturbed during the experiment and, in all 38 readings were finally used. Measurements were expressed as metabolic rate (MR), O_2 ml/hr at STP.

It is known that both temperature and body weight affect metabolic rate in reptiles (Bennett and Dawson 1976). Metabolic rate (MR) is related to body weight (W) by a power function model $MR = aW^b$, where a and b are constants (Bennett and Dawson 1976), and to temperature by an exponential model, $MR = Ae^{BT+CT^2+\dots}$, where A, B, C are constants, as used in the calculation of Q_{10} values (Prosser and Brown 1961). To determine a model that could be used to predict metabolic rate from both temperature and body weight a stepwise multiple regression analysis was completed with $\log_e(MR)$ as the dependent variable, and temperature T, T^2, T^3, body weight W, $\log_e(W)$ and $T.\log_e(W)$ as possible independent variables. Only those variables that contributed significantly to the regression sum of squares were used in the final model.

8.1.2 Determination of overwintering temperatures and costs of overwintering

As metabolic rate, measured as O_2 consumption, is related to temperature (Bennett and Dawson 1976), in order to determine total O_2 consumption during the overwintering period, temperatures have to be known accurately over the entire interval. Accordingly continuous temperatures from a deep and a shallow burrow were monitored throughout the overwintering period (Section 3.3.2). Also, daily maximum and minimum soil temperatures (5 cm deep) were recorded routinely at the Laureldale Meteorological Station (Section 3.3.2). From these data a function was determined whereby burrow temperatures could be calculated for each hour of the overwintering period. Consequently, total O_2 consumption for this period was calculated using relationships between

metabolic rate, temperature and body weight, and between temperature and time. Total O_2 consumption for the overwintering period was multiplied by 19.646 to convert it from ml of O_2 to its energy equivalent in kJoules (Kleiber 1975). This conversion assumed that during the overwintering period lizards metabolised lipids only and thus ingested no food.

8.1.3 <u>Determination of reproductive costs</u>

Two methods were used to estimate the cost of reproduction in <u>C.taeniolatus</u>. Because of the difficulties in quantifying the metabolic costs of spermatogenesis, finding a mate, mating and other activities associated with reproduction, these costs were restricted to estimates of the potential energy in a completed clutch.

The first estimate, determination of lipid content in an egg, was measured using the lipid extraction technique of Thomson (1981). Lipid extractions were made on oviducal eggs, with embryos primarily at the cleavage plate stage (Stage 1-2; Defaure and Hubert 1961). At this stage in oviparous lizards the lipid content of the eggs should be complete.

The second estimate, a direct estimation of the energy content of an entire clutch, was determined using a formula derived by Vitt (1978), relating clutch wet weight (W_w;g) to energy content (kJ):

Total clutch energy content = $(0.2562.W_w + 0.0794)(27.324)$

Further relationships between clutch weight, clutch size and body size were determined previously in section 6.3.5, and are used in the final calculation of costs of a mean clutch.

8.2 RESULTS

8.2.1 Metabolic rate

Metabolic rates of C.taeniolatus at each experimental temperature are presented in table 25. The model (Fig. 50), determined by stepwise multiple regression procedures, predicting metabolic rate (MR) from temperature (T) and body weight (W) was:

$$\log_e(MR) = -4.5468^{***} + 0.0826^{***}T + 0.0511^{***}T.\log_e(W)$$

$$R^2 = 0.9394, \ P < 0.0001, \ n = 38$$

Table 25 : Metabolic rates of C.taeniolatus in mid-winter. Body weight is measured in g.

Temperature (C)	n	Mean body weight (SD)	Mean metabolic rates (SD)	
			mlO_2h^{-1}	$mlO_2g^{-1}h^{-1}$
5	5	2.9 (1.8)	0.037 (0.018)	0.010 (0.004)
10	10	2.9 (0.5)	0.044 (0.020)	0.018 (0.009)
15	4	2.9 (0.6)	0.060 (0.019)	0.022 (0.010)
20	9	3.3 (1.1)	0.263 (0.096)	0.062 (0.019)
30	10	2.9 (0.6)	0.444 (0.220)	0.164 (0.087)

8.2.2 Costs of overwintering

Deep and shallow burrow temperatures were found to follow a sinusoidal pattern which can be estimated by a combination of two sine waves, one with a half wavelength of 7 hours and the other with a half wavelength of 17 hours (as burrow temperatures reached a daily maximum more slowly than they acquired a nightly minimum (Section 3.3.2)). However, as deep and shallow burrows showed a large variation in magnitude of temperature change, maximum and minimum soil temperatures (5 cm deep) were used to estimate the average lizard burrow temperature (Section 3.3.2). Two estimates, a maxiumum and a minimum, of the overwintering period were made from field activity of lizards. The maximum lasted for 140 days, from early May to mid-September, the minimum 90 days, from mid May to mid-August. The real overwintering period would be somewhere between these two, and would vary from year to year and from site to site. Burrow temperatures were thus calculated for each hour of each day using the equation:

Temperature (T) = A + B.sin(t)

where $A = (T_{max} + T_{min})/2$, $B = (T_{max} - T_{min})/2$, t = time, ranging from 1 to 7 hours or 1 to 17 hours depending on the time of day.

The derived temperatures were then incorporated into the equation relating metabolic rate to temperature and body weight (Section 8.2.1), mls O_2 per hour were calculated, then summed for each overwintering period. This method is a modification of one used by van Beurden (1980) and was completed with the aid of a Fortran program.

Table 26 shows the mls of O_2 consumed and its energy equivalent during maximum and minimum overwintering periods for lizards between 1 and 7 g.

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Table 26 : Costs of overwintering of _Ctenotus taeniolatus_ for 90 and 140 days.

Body weight (g)	mlO_2		kJ	
	90 days	140 days	90 days	140 days
1	47.80	83.29	0.94	1.64
2	65.58	125.68	1.29	2.47
3	83.42	162.04	1.64	3.18
4	97.22	195.25	1.91	3.84
5	109.70	226.15	2.16	4.44
6	121.25	256.15	2.38	5.03
7	132.09	284.76	2.60	5.59

Table 27 : Wet weight (g) and energy content (kJ) of clutches of eggs of _Ctenotus taeniolatus_ of different sizes.

Body weight (g)	Wet weight of clutch (g)	Energy content of clutch (kJ)
2	0.6051	6.4055
3	0.7256	7.2490
4	0.8224	7.9212
5	0.9045	8.5014
6	0.9766	9.0060
7	1.0414	9.4598

8.2.3 Costs of reproduction

Mean lipid content of a clutch of eggs was found to be 25.2% (25.0-26.8%, n = 5) of the dry weight of a clutch.

Table 27 shows the average wet weight of a clutch and its energy content. As clutch weight was related to body size of the female by the equation: clutch wet weight = -0.17 + 0.016 SVL (Section 6.3.5), where wet body weight = $e^{-10.1929}.SVL^{2.80}$ (Section 6.3.1), values have been calculated for a range of lizard body sizes, using the following solution of the above two equations:

Clutch wet weight = $-0.17 + 0.609.(\text{wet body weight})^{0.357}$.

Figure 49 : Constant pressure volumetric system used to measure
metabolic rate in Ctenotus taeniolatus.

TO AIR

FLUID
TRAP

CALIBRATED
VOLUMETER
TUBE

LEVELLED
WIRE
SUPPORTING
CAGE

250 mm

30 mm

CO2 and H2O
ABSORBERS

WIRE SEPARATER
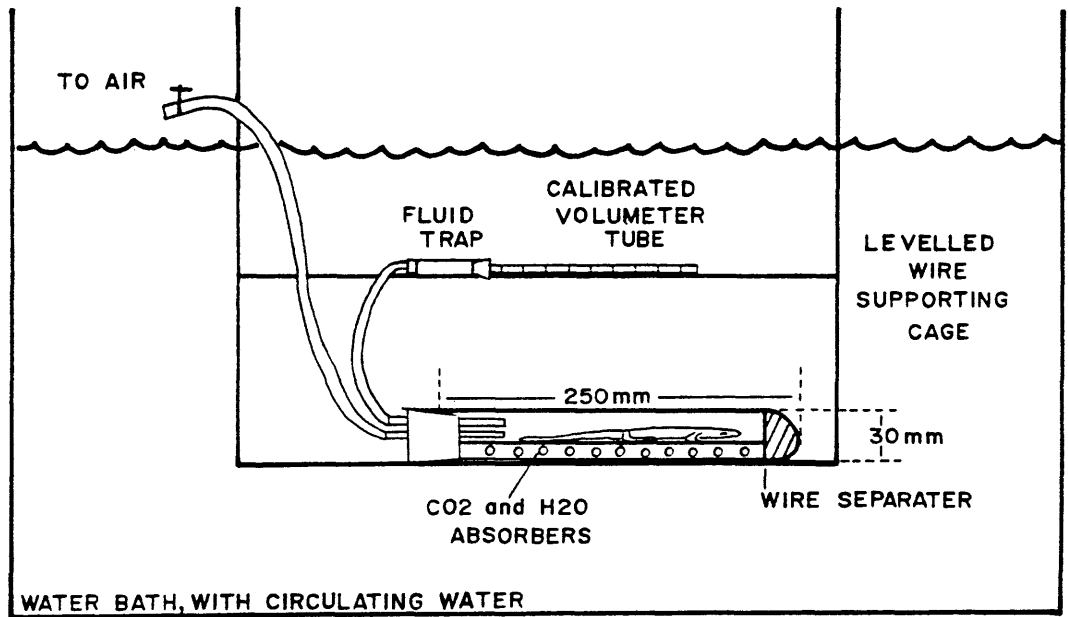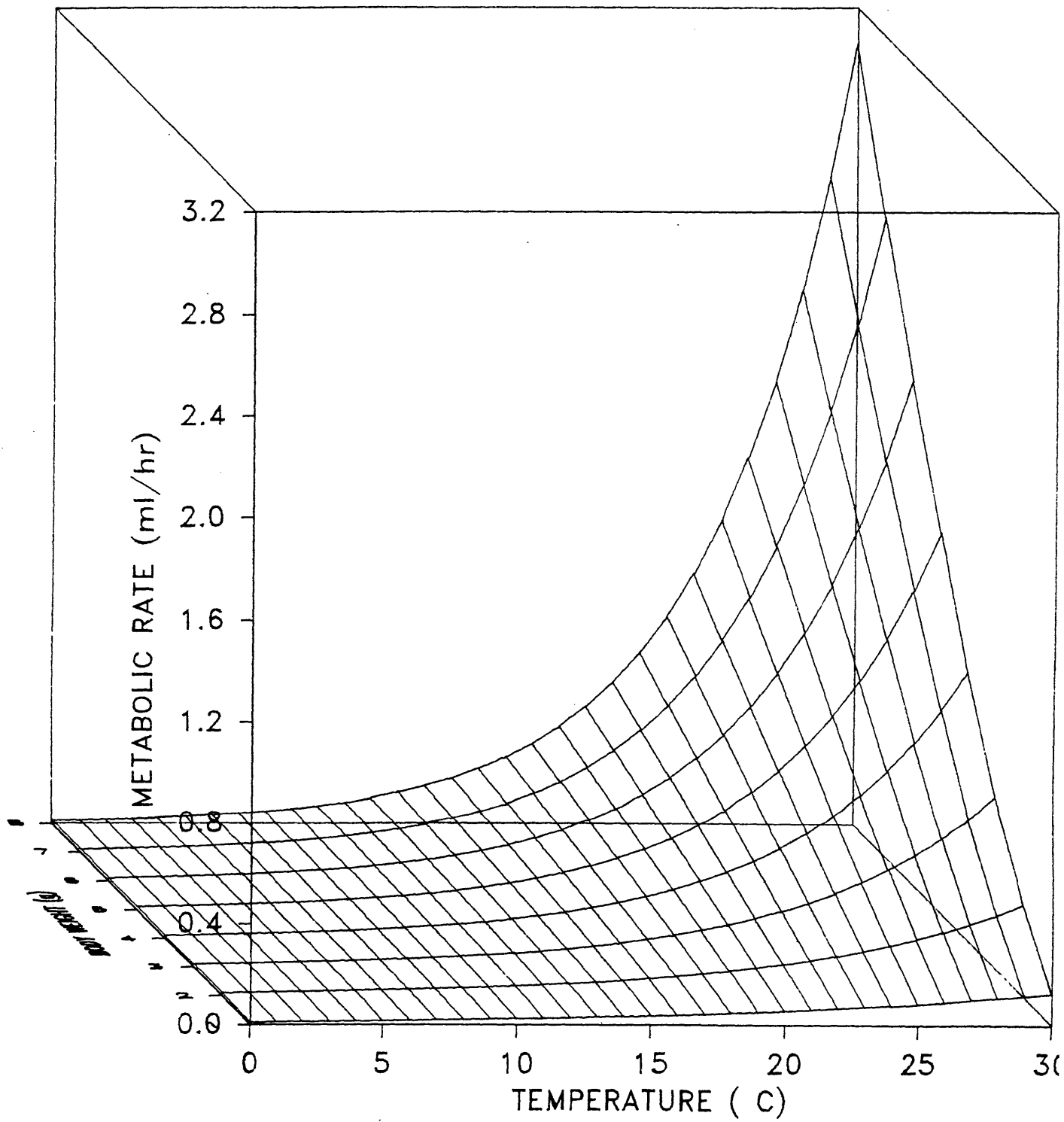
WATER BATH, WITH CIRCULATING WATER

Figure 50 : Relationship between metabolic rate, body weight and temperature for Ctenotus taeniolatus (see section 8.2.1 for details).

8.3 DISCUSSION

8.3.1 Cost of overwintering

Complete ecological energy budgets are rare among reptilian studies; many investigators have estimated various components of total energy budgets (Congdon et al. 1982, review). The present study fits into this category, as the aim was to investigate the energy utilised during the overwintering period, rather than to determine a complete energy budget. Such partial energy budget studies in the past have used a variety of techniques to determine costs. These have been reviewed by Congdon et al. (1982). However many of the problems often associated with estimating such costs were not encountered in the present study of overwintering in C.taeniolatus, as this species is inactive within burrows (Section 3.0) and does not reproduce (Section 6.0), grow (Section 5.0) or feed (Section 4.0) over most of the overwintering period. Minimal growth and feeding could occur at the beginning and end of the overwintering period when temperatures are warmer; however, this would vary from year to year and site to site, and was taken into account by estimating costs for a minimum and a maximum overwintering period. Consequently, although the doubly labelled water technique and its variations have been most recently used to determine the respiratory component of energy budgets (Congdon et al. 1979, Bennett and Nagy 1979, Congdon et al. 1982), in the present study the method of deriving the standard metabolic rate and extrapolating this to energy utilisation was thought to be appropriate. The metabolic rates determined for C.taeniolatus agree favourably with those reported for lizards of similar size (Table 28) as do the estimates of overwintering costs (Table 29).

To fine tune this extrapolation process further, oxygen consumption was related to both body weight and laboratory temperatures, rather than to laboratory temperatures alone, and hourly burrow temperatures over the entire overwintering period were used to predict O_2 consumption for each hour at each temperature rather than using mean temperatures or other generalised estimates of environmental temperatures (Shine 1971, Bartlett 1976, Mueller 1969). Also, laboratory temperatures were selected so that they extended over a range similar to that of environmental ones.

Despite these refinements, problems still existed that made for some variations in the final estimate of overwintering costs. These problems are involved with the use of constant laboratory temperatures to estimate daily energy costs. Respiration rates in reptiles have been found to vary during the diel cycle, independently of temperature and photoperiod, with daytime O_2 consumption rates being up to 5 times greater than those determined at night under otherwise similar conditions (Brownlie and Loveridge 1983, Hughes et al. 1982, Heusner and Jameson 1981, Mautz 1979). The apodous burrowing skinks, Typhlosaurus cregoi bicolor and Acontias meleagris meleagris (Brownlie and Loveridge 1983) and the cave dwelling xantusiid, Lepidophyma gaigeae (Mautz 1979), constituted exceptions in that no diel cycle was observed. The associated problem of circadian rhythms in seasonal respiration rates (Heusner and Jameson 1981, Bennett and Dawson 1976) was alleviated by using winter acclimatised lizards only. Further, Humphreys (1975, 1977) found in the spider, Geolycosa godeffroyi, that cyclical temperatures increased the respiration rate above the resting level calculated at constant temperatures. Although this effect has not as yet been examined in reptiles, the possibility of it occurring must be considered.

Taken together these influences suggest that the estimated costs of overwintering discussed above may underestimate actual costs. However, none of these effects have been investigated at the low temperatures present during winter, and it may be that at such low temperatures the effects of cyclical temperatures and diurnal rhythms are greatly reduced, as Halpern and Lowe (1968) and Patterson and Davies (1978) found for Uta stansburiana and Lacerta vivipara respectively. Further, the estimated energy required for metabolism and the estimated change in tail lipid over inactive periods of 90 and 140 days show reasonable agreement (Table 30), especially considering that the second estimate may significantly overestimate metabolic costs if only a few days elapse between the time of capture and the onset or end of winter inactivity (Bartlett 1976).

If one allows for the above and for limitations that result from other generalisations in the present estimate of overwinter costs in C.taeniolatus, some conclusions and hypotheses concerning the relationship between tail autotomy and overwintering ability can be proposed.

As one would expect, even over a very long winter of 140 days, Ctenotus has ample amounts of lipid within the tail alone to provide enough energy for maintenance (Table 31). This result and those of other studies (Avery 1970, 1974, Moberly 1963, Presst 1971, Brown et al. 1974) suggest that depletion of fat reserves during the overwintering period is an improbable cause of death (Bauwens 1981). However, if a lizard loses its tail this conclusion may be invalid, as death may result from either freezing (Lowe et al. 1971, Vitt 1974), a response exacerbated by the presence of an open wound (Lowe et al. 1971), or by reduction of the fat deposits necessary for maintenance over winter. Bauwens (1981) reported higher mortality rates over winter

in juvenile _Lacerta vivipara_ with partially regenerated tails, and suggested that the reduced tail fat deposits were associated with death. However, if C.taeniolatus loses its entire tail at the beginning of the overwintering period, in most cases lizards would still have adequate amounts of lipid in the carcass for maintenance, assuming that a lizard without a tail has the same metabolic expenditure as one with a tail (the most extreme case), although juveniles and males would be at risk especially if the winter were long (Table 31). Although carcass lipid is ether-soluble and therefore classically a depot lipid, its lack of mobility (suggested in section 7.4), may mean that it is unavailable, or if availiable cannot be utilised without disturbing the physiological condition of the lizard. These problems are examined further in section 9.1.1.

Table 28 : Oxygen consumption of small lizards

Species	Body weight (g)	O_2 consumption $mlg^{-1}h^{-1}$	Reference
5 C			
Lacerta vivipara	3.4	0.0119-0.0135 (winter) 0.0125 (summer)	Patterson and Davies 1978
Uta stansburiana	< 6.3	0.0178 (summer) 0.0169 (winter)	Halpern and Lowe 1968
Ctenotus taeniolatus	2.9	0.010 (winter)	this study
15 C			
Proscelotes arnoldi arnoldi	4.6	0.032	Brownlie and Loveridge 1983
Typhlosaurus creqoi	5.5	0.038	Brownlie and Loveridge 1983
Ctenotus taeniolatus	2.9	0.022	this study
20 C			
Anolis carolinensis	4.5	0.110	Maher and Levedahl 1959
Sceloporus undulatus garmani	4.1	0.059 (day) 0.038 (night)	Hughes et al. 1982
Sphenomorphus labillardieri	2.8	0.070	Dawson et al. 1966
Uta stansburiana	3.0	0.070	Roberts 1968
Ctenotus taeniolatus	3.3	0.062	this study
30 C			
Anolis carolinensis	4.5	0.190	Maher and Levedahl 1959
Sceloporus graciosus	5.0	0.164	Mueller 1969
S. undulatus	4.0	0.502 (day) 0.267 (night)	Hughes et al. 1982
Uta stansburiana	3.0	0.170	Roberts 1968
Ctenotus taeniolatus	2.9	0.164	this study

Table 29 : Energy requirements over winter for lizards (values converted from calories to joules by multiplying by 4.184).

Species	Body weight (g)	Energy requirement kJd^{-1}	Energy requirement $kJd^{-1}g^{-1}$	Method	Reference
Ctenotus taeniolatus	4	0.0212	0.0053	O_2 consumption in lab; over 90 days over 140 days	this study
Egernia cunninghami	240	1.504	0.0063	O_2 consumption in lab; over 124 days	Shine 1971
Dipsosaurus dorsalis	50	0.2357[1]	0.0047[1]	O_2 consumption in lab; over 150 days	Moberly 1963
Lacerta vivipara	3.4 / 3.4	0.034 (M) / 0.035 (F)	0.01 (M) / 0.01 (F)	O_2 consumption in lab; over 161 days	Patterson and Davies 1978
Sceloporus graciosus	5	0.0380-0.0583	0.0076-0.0106	O_2 consumption in lab and fat loss; over 220 days	Mueller 1969
S. jarrovi	13	0.4186[2]	0.0322[2]	O_2 in field with tritiated water; over 180 days	Congdon et al. 1979
S. occidentalis	13.8	0.05	0.0036	O_2 consumption in lab; over 100 days	Bartlett 1976

[1] calculated by multiplying O_2 consumption of $0.01ccg^{-1}hr^{-1}$ by 24 hours and the oxy-energy conversion factor, 19.646

[2] found to be active over winter

Table 30 : Comparison of overwintering costs determined from change in tail lipid of
Ctenotus taeniolatus over the overwintering period and energy required from metabolism.
F denotes female and M denotes male.

| Body weight (g) | | Overwinter 90 days | | Overwinter 140 days | |
		tail lipid (kJ)[1]	metabolism (kJ)	tail lipid (kJ)[1]	metabolism (kJ)
1	F	0.4651	0.94	0.5720	1.64
	M	0.3418		0.6757	
2	F	0.7950	1.29	1.8165	2.47
	M	1.0772		2.1265	
3	F	1.3435	1.64	3.0328	3.18
	M	1.8125		3.5773	
4	F	1.9000	1.91	4.2689	3.84
	M	2.5478		5.0281	
5	F	2.4286	2.16	5.4971	4.44
	M	3.2792		6.4789	
6	F	2.9732	2.38	6.7254	5.03
	M	4.0185		7.9258	
7	F	3.5137	2.60	7.9536	5.59

[1] calculated from Fourier series predicting lipid index for each month of the year, the
relationship between wet weight and FFDW and converted from g to kJ by multiplying by
the lipid combustion factor, 39.748 (Kleiber 1975).

Table 31 : Comparison of energy required for metabolism with that present in the lizard *Ctenotus taeniolatus* in the form of stored lipid at the beginning of the overwintering periods of 90 and 140 days. F denotes female and M denotes male.

90 DAYS

Body weight (g)	Energy required for metabolism (kJ)		Energy present in tail in lipid form (kJ)[1]	Energy present in carcass in lipid form (kJ)[1]
1	0.94	F	1.4150	0.6876
		M	1.1368	0.2671
2	1.29	F	4.4478	2.1661
		M	3.5694	0.8387
3	1.64	F	7.4845	3.6449
		M	6.0019	1.4111
4	1.91	F	10.5173	5.1235
		M	8.4345	1.9834
5	2.16	F	13.5500	6.5982
		M	10.8631	2.5558
6	2.38	F	16.5829	8.0768
		M	13.2997	3.1282
7	2.60	F	19.6156	9.5554

140 DAYS

Body weight (g)	Energy required for metabolism (kJ)		Energy present in tail in lipid form (kJ)[1]	Energy present in carcass in lipid form (kJ)[1]
1	1.64	F	1.5263	0.7115
		M	1.1646	0.2671
2	2.47	F	4.7976	2.2378
		M	3.6648	0.8387
3	3.18	F	8.0688	3.7649
		M	6.1649	1.4111
4	3.84	F	11.3441	5.2913
		M	8.6651	1.9834
5	4.44	F	14.6153	6.8168
		M	11.1652	2.5558
6	5.03	F	17.8866	8.3431
		M	13.6614	3.1282
7	5.59	F	21.1539	9.8694

[1] calculated from Fourier series predicting lipid index for each month of the year, the relationship between wet weight and FFDW and converted from g to kJ by multiplying by the lipid combustion factor, 39.748 (Kleiber 1975).

8.3.2 Costs of reproduction

The estimation of the cost of reproduction, although attempted by many researchers (Shine 1977b, Avery 1974, Congdon and Tinkle 1982, Dutton et al. 1975, Andrews and Asato 1977, Bennett and Nagy 1977, Congdon et al. 1979, Ballinger and Schrank 1972, Schwaner 1980, Congdon et al. 1978, Tinkle and Hadley 1975, Ballinger and Clark 1973, Andrews and Rand 1974, Vitt and Congdon 1978, Congdon et al. 1982, and others), is one of the more difficult determinations within a total energy budget as it involves not only the estimation of concrete parameters such as energy content of eggs, but also the estimation of less quantifiable ones such as costs of finding a mate and mating, costs of carrying eggs or young and costs of parental care. These costs are paid for by energy acquired directly by feeding and indirectly from stores (lipid in particular), the capacity of which is increased by energetic trade-offs such as reduced growth rates of the whole animal (Tinkle 1967, Tinkle and Ballinger 1972, Ballinger 1973a, Dunham 1978) or regenerated parts (Dial and Fitzpatrick 1981), or increased vulnerability to predation (Shine 1980b) during the breeding season. Shine (1980b) considers the latter trade-off to be the more costly.

Although there is currently no direct way of estimating the energetic costs of the above reproductive activities (more commonly expressed as a ratio and termed reproductive effort) Congdon et al. (1982) discuss three indirect methods in present use. These estimates of costs are determined by considering (i) reproductive production alone, or (ii) reproductive production and energy expended on reproductive activity as a proportion of the total energy budget including maintenance energy, and (iii) reproductive production plus reproductive energy as a proportion of the total energy budget excluding maintenance energy. However, such estimates use energy of respiration

associated with reproductive activity to determine the energy expended on reproductive activity and so are often dependent on the choice of maintenance scope which in itself can be highly variable (Congdon et al. 1982). Further, since there is some discussion about how respiration due to activity should be partitioned into that required for reproduction and that required for growth, the relative merits of different estimates of reproduction remain to be determined.

Although the analysis of a total energy budget, or the determination of the energy due to reproductive activities, was beyond the scope of the present study, the minimum cost of reproduction was determined by calculating the energy content of a clutch of eggs. Table 32 shows these values are of the same order as those reported for other small lizards (Vitt 1978). The lipid content of eggs, originally thought to be an estimate of energy content (Smyth 1974), was less than 30% of dry weight and consequently accounted for only a proportion of the energy content. Thompson (1981) presents similar results for other reptiles.

In a comparison of lipid reserves in the carcass and tail of C.taeniolatus with the energy content of a clutch of eggs (Table 32) it is apparent that there are ample amounts of lipid available at the beginning of the reproductive period, but that the change in total lipids over this period is often less than that required to produce the clutch, while the change in tail lipids alone, the most mobile depot, is much less than that required. In fact, depending on the size of the lizard, between 21.3% and 70.1% of the energy in a clutch of eggs can be accounted for by the change in tail lipids. Even though both tail and carcass lipids are low at the end of reproduction they are by no means depleted. Obviously lizards must be actively feeding over this period and using this food as a source of the raw material needed for egg

production. Shine (1980b) found no appreciable reduction in feeding during reproduction in a number of Australian skinks. Further, Licht (1974) found that supplementation of the diet of Anolis lizards during the breeding season reduced the rate of lipid depletion, indicating that under normal conditions when energy demands are high because of egg production, there is insufficient food for storage. Tail lipids of male C.taeniolatus are also used in significant amounts during the breeding season, but are much less so than those of females (Table 33).

Therefore, for females the possibility exists that during the reproductive period dietary energy is used first but that it is not enough to fill the quota for egg production and reserves are therefore called upon. However, if a lizard loses its tail it no longer has this 'back up' energy supply and the energy content of a clutch could be reduced. It is known that removal of the fat bodies in Uta stansburiana (Hahn and Tinkle 1965) and in Ameiva festiva and A.quadrilineata (Smith 1968), and removal of the tail in Hemiergis peroni (Smyth 1974) after vitellogenesis has begun, will reduce the number and quality of eggs ovulated. The relationship, however, between lipid stores and egg development is not a simple one, as fat mobilisation and vitellogenesis are mutually stimulated either directly or indirectly by oestrogens (Hahn 1967). Hahn and Tinkle (1965) found also, that if the fat body is removed prior to the initiation of follicular yolking, no yolking occurred. These last two facts suggest that there is a sophisticated hormonal feedback system in operation that results in the inhibition of vitellogenesis if depot fat and associated compounds are not present. This whole question is examined further in section 9.3.2.

Table 32 : Comparison of energy in lipid form used over the reproductive period of Ctenotus taeniolatus with that required by a clutch of eggs.

Body weight (g)	kJ in clutch	Lipid at start reproduction Tail(kJ)[1]	Carcass(kJ)[1]	Lipid at end reprodution Tail(kJ)[1]	Carcass(kJ)[1]	Change in total lipids (kJ)	Change in tail lipids (kJ)	% of clutch contributed by tail lipids
2	6.4055	3.3826	1.4429	2.0192	0.6280	2.1782	1.3634	21.3
3	7.2490	5.6960	2.4250	3.3945	1.0573	3.6687	2.3015	31.7
4	7.9212	8.0012	3.4064	4.4120	1.4866	5.5091	3.5892	45.3
5	8.5014	10.3107	4.3882	6.1450	1.9159	6.6380	4.1657	49.0
6	9.0060	12.6200	5.3700	7.5203	2.3451	8.1245	5.0997	56.6
7	9.4598	14.9293	6.3557	8.8956	2.7744	9.6150	6.0337	63.8

[1] calculated from Fourier series predicting lipid index for each month of the year, the relationship between wet weight of body and FFDW and converted from g to kJ by multipying by the lipid combustion factor, 39.748 (Kleiber 1975).

Table 33 : Change in tail lipid of male <u>Ctenotus</u> <u>taeniolatus</u> over the reproductive period. Note carcass lipid does not change significantly over this period so is not included in estimations.

Body weight (g)	Change in tail lipid (kJ)[1]
2	0.5231
3	0.8798
4	1.2363
5	1.5930
6	1.9496

[1] calculated fron Fourier series predicting lipid index for each month of the year, the relationship between wet weight of body and FFDW and converted from g to kJ by multiplying by the lipid combustion factor, 39.748 (Kleiber 1975).

9.0 EFFECTS AND RELEVANCE OF AUTOTOMY

9.1 METHODS

9.1.1 Experiment - effect of autotomy on overwintering

To investigate the effect of whole tail autotomy on survival overwinter and to determine the ability of C.taeniolatus to use carcass lipid stores when tail lipid stores are unavailable, two similar experiments were conducted between May and September of 1981 and 1982. In the first experiment 40 C.taeniolatus, half of which had their tails removed at the first break plane, were housed in cages within separate constant temperature cabinets set at 10 C for 14 hours and 5 C for 10 hours (photoperiod was set at 14L:10D), in an effort to simulate winter temperatures. Lizards were collected from the New England region 2 to 3 days prior to the experiment and were weighed, measured (snout-vent length and tail length, mm) and toe-clipped for identification. Those lizards with tails removed were housed for 3 days at room temperature to ensure that wounds healed before the commencement of the experiment, so that any deaths could not be attributed to the interaction between the presence of a fresh wound and low temperatures. Five lizards with tails (controls) were sampled monthly at which time body weight and snout-vent length, and lipid content of the carcass and tail were measured (Section 7.2.2). Treated lizards were left until either death or until the end of the overwintering period (90 days) occurred, when snout-vent length, carcass lipid and tail regrowth were measured. During the experiment lizards were watered but not fed.

In the second experiment the procedure of the first experiment was repeated with the exception that 44 treated and control C.taeniolatus (20 of which were juveniles) were housed in an outside enclosure designed to simulate the natural habitat. Lizards were not sampled sequentially throughout the experimental period, but were removed only at death or at the end of the winter period (15 September), when body weights, snout-vent length, tail regrowth and lipid content of tail and carcass were measured. Although lizards were not fed during the experiment, food was available in the form of naturally occurring insects and snails; water was supplied.

9.1.2 Experiment - effect of autotomy on reproduction

To examine the effect of whole tail autotomy on the number and quality of eggs ovulated, two experiments were conducted between September and December of 1980 and 1982. In the first experiment 10 male and 10 female C.taeniolatus and 10 male and 10 female Lamprocholis guichenoti, half of which had their tails removed at the first break plane, were housed in adjacent outside enclosures, designed to simulate the natural habitat of each species. L.guichenoti, an oviparous skink which stores lipid in both abdominal fat bodies and in the tail, was included as a control so that any changes in reproductive parameters could be reliably attributed to the loss of lipid stores and associated compounds rather than to the loss of the tail per se. Male and female C.taeniolatus and L.guichenoti were caged together to facilitate mating; even though L.guichenoti had probably mated in the previous autumn, males were still included with this group as a safeguard. When it was apparent by the external appearance of females that ovulation had occurred, lizards were removed, measured (snout-vent length, tail regrowth), killed and the eggs removed, counted and weighed. Ovaries were then sectioned to determine the presence of atretic follicles and

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stomachs were examined to confirm that lizards had been feeding.

In the second experiment the procedure of the first experiment was duplicated using C.taeniolatus alone to determine the repeatability of the experiment. Lipid analysis was added to the procedure using the technique of Thomson (1981), so that lipid content of the carcass, tail, tail butt (non-autotomised section of the tail) and regenerated tail was measured in the treated lizards.

9.1.3 Lipid distribution within the tail

In the tail of C.taeniolatus lipid is stored in 4 circum-skeletal blocks associated with each fracture plane down the length of the tail. To determine a model whereby lipid content at any position in a tail could be predicted from its location, tails of 4 male and 4 female adult C.taeniolatus, collected in March and December, were partitioned into 10 similar sections; section 1 being closest to the vent. The length (mm) of each section was measured and the lipid content determined following the procedure of Thomson (1981). Both measurements were then expressed as proportions of the total tail length and total lipid content respectively, so that reliable comparisons among lizards of different sizes could be made. March and December were selected as representative times of the year as in these months tail lipid content was expected to be maximal and minimal respectively (Section 7.3.3.1). A preliminary comparison of lipid content in each section was carried out between males and females, and within and between time of year (March, December) using a 2-way analysis of variance, with 4 lizards per cell. As sections were not independent (the sum of sectional lipid content equalled 1) 10 separate analyses were completed.

Final models were determined by fitting the Misterlich or von Bertalanffy curves of the form $y = A - B.e^{-ax}$ to the observations of cumulative length of tail (x) and the cumulative lipid content (y), both expressed as proportions of the totals, using the BMDP3R non-linear regression package (Jennrich 1979). The coefficients of the four models were then compared using analysis of variance procedures, with the combination of the four models into a lesser number occurring if no significant differences were apparent.

9.1.4 Frequency and position of autotomy

The overall and within size class frequency of autotomy was determined from samples of C.taeniolatus collected during the present study from the New England region and from samples collected in other studies throughout NSW and Queensland, and housed at the Australian Museum, Sydney. The position of autotomy was determined from the patterns of occurrence of lizards with freshly autotomised tails, i.e., tails in which a cap of scar tissue covered the distal end, an indication that the tail was not lost during collection.

Position of autotomy was determined only in those lizards with freshly autotomised tails, captured between September and April, so that the possibility of a biased sample due to winter death induced by autotomy was eliminated. Position of autotomy was then estimated by measuring the length of the tail from the vent to the break and expressing this as a proportion of the predicted tail length, determined from the relationship between snout-vent length and tail length in male and female C.taeniolatus with original tails.

9.2 RESULTS

9.2.1 Experiment - effect of autotomy on overwintering

Removal of the tail had a detrimental effect on the overwintering ability of lizards. In experiment 1, in which lizards were subjected to controlled temperatures, tailless lizards survived a maximum of 66 days compared with 90 days in the control lizards (experiment terminated at 90 days), with 47% of treated lizards dying in 22 days (Fig. 51). No body growth or tail regeneration was observed over the experimental period.

Further the relationships between carcass lipid, expressed as a proportion of fat-free dry carcass weight (FFCW), and time from commencement of experiment for control and treated lizards (Fig. 51) were not significant (Table 34) indicating that there was not a significant decrease in carcass lipid in either the tailed or tailless lizards, i.e., carcass lipid was not used, and was possibly unavailable as an energy reserve for overwintering in C.taeniolatus.

Although experiment 2 did not proceed as expected, with all juveniles and 3 tailless adults disappearing (presumed dead), and the remaining lizards being unseasonably active at temperatures below 10 C for most of the experimental period, some conclusions can still be drawn. Firstly, all of the tailless adult lizards were dead within 37 days after the commencement of the experiment; tailed adults survived for 72 days (heavy rain of two weeks duration appeared related to the sudden death of all controls at this time). Secondly, none of the tailless lizards appeared starved and all contained lipids within the carcass (expressed as lipid/FFCW) equivalent to the mean levels determined in the initial control group of experiment 1 ($F_{2,11}$ = 0.5759, NS). These data reaffirm the results of experiment 1.

Table 34 : Summary of regression analyses for the relationship between carcass lipid/FFCW and time from commencement of experiment (days) of tailed and tailless Ctenotus taeniolatus in the overwintering experiment at controlled temperatures.

	Source	DF	MS	Probability	
With tails	Regression	1	0.00173	NS	Regression
	Dev^n from mean	2	0.00240	NS	using multiple
	Within cell var^n	14	0.00159		y values
	Total	17			
Without tails	Regression	1	0.00069	NS	Weighted
	Residual	20	0.00054	NS	regression
	Total	21			

9.2.2 Experiment - effect of autotomy on reproduction

The results (Table 35) of both experiments confirm that the removal of the tail had a detrimental effect on reproduction. Non-orthogonal two-way analysis of variance (Table 37), followed by multiple comparisons using Newman-Keuls' Studentised Range, showed that the number of eggs ovulated by L.quichenoti in 1980, with and without tails, were not significantly different. The number ovulated by C.taeniolatus without tails was significantly less (P < 0.005) than the number ovulated by C.taeniolatus with tails, indicating that the removal of the lipid stores, and not the tail per se, had a significant effect on the number of eggs ovulated, reducing the clutch size by 75%. Further, when the experiment was repeated in 1982, C.taeniolatus without tails did not ovulate, while the control animals ovulated numbers of eggs similar to the control C.taeniolatus in 1980. In both experiments the ovaries of tailless C.taeniolatus contained atretic follicles, which, when added to the number of eggs ovulated produced a clutch size usual for C.taeniolatus and similar to the control lizards. The presence of these atretic follicles indicated that ovarian eggs were resorbed, presumably before development was complete as many of them appeared to be at advanced stages of resorbtion. Also, although average wet weight of eggs ovulated did not differ significantly (Table 38) between tailed and tailless C.taeniolatus, because of the large difference between the number of eggs ovulated between treatments, tailed lizards produced heavier clutch weights than tailless lizards. Unfortunately, in L.quichenoti oviposition occurred before weights could be determined. All oviducal eggs of C.taeniolatus were opened and found to contain embryos.

All lizards were seen feeding and had food in their stomachs at the end of the experimental periods indicating that both species fed through all stages of reproductive development. Possible differences in feeding success of tailed and tailless lizards were not examined.

Due to the loss of a number of lizards during both experiments the original balanced designs presented in methods section 9.1.2 had to be replaced by unbalanced designs necessitating the use of non-orthogonal analyses of variance (BMDP2V computer package; Jennrich and Sampson 1979).

In these analyses (Table 39) tail regeneration rates (mm/day) (Table 36) were found not to be significantly different between species, nor between sexes in the summer of 1980, but were found in C.taeniolatus to be significantly greater (Table 40) in 1982 than in 1980, when averaged over sexes. Male and female tail regeneration rates in C.taeniolatus over both years were not significantly different. As the increases in tail regeneration rates were the same for male and female C.taeniolatus in 1982 these changes cannot be connected to the reduced ovulation rate for females in the same period.

At the end of experiment 1 the lipid content of the carcasses of tailless C.taeniolatus (Table 41) was not significantly different from the mean levels of carcass lipid occurring in the natural state (Section 7.3.3.2). The regenerated tail sections of all lizards contained some quantity of lipid (Table 41) which when combined with the amounts in the tail butt was 32.7% of that normally found in the tail of female C.taeniolatus, and 27.5% of that found in males.

Table 35 :   Effect of tail loss on ovulation in Ctenotus taeniolatus and Lampropholis guichenoti.

	Tails intact			Tails removed	
SVL (mm)	Number ovulated	Mean wet weight egg (g)	SVL (mm)	Number ovulated	Mean wet weight egg (g)
Ctenotus taeniolatus					
1980					
68	5	0.242	67	1 (3 atretic)	0.154
66	3	0.100	63	1 (2 atretic)	0.200
69	4	0.258	65	1 (2 atretic)	0.277
1982					
60	3	0.258	59	0 (2 atretic)	-
71	5	0.300	73	0 (4 atretic)	-
63	3	0.234	72	0 (3 atretic)	-
72	4	0.220	67	0 (3 atretic)	-
68	3	0.268	60	0 (3 atretic)	-
Lampropholis guichenoti 1980					
46	2		42	4	
40	3		40	3	
42	3		40	3	
43	4		43	3	

Table 36 : Regeneration rates (mm/day) of Ctenotus taeniolatus and Lampropholis quichenoti.

| | Female | | Male | |
	SVL (mm)	Regen. rate	SVL (mm)	Regen. rate
Ctenotus taeniolatus				
1980	67	0.073	57	0.067
	63	0.103	58	0.090
	65	0.980	52	0.140
1982	59	0.592	62	0.423
	73	0.915	54	0.549
	72	0.790	52	0.900
	67	0.605	55	0.321
	60	0.444	57	lost tail twice, no regrowth at time of recapture
Lampropholis quichenoti				
1980	42	0.148	43	0.333
	40	0.091	45	0.242
	40	0.248	42	0.100
	43	0.194	43	0.164
			36	0.106
			45	0.203

Table 37 : Non-orthogonal two-way analysis of variance comparing number of eggs ovulated by Ctenotus taeniolatus and Lampropholis quichenoti, with and without tails, in 1980.

Source	DF	MS	Probability
Species (S)	1	1.3393	NS
Treat (T)	1	6.4821	< 0.005
S x T	1	9.0536	< 0.005
Error	10	0.4750	
Total	13		

Table 38 : Non-orthogonal one-way analysis of variance comparing average weight of eggs ovulated by Ctenotus taeniolatus with and without tails in 1980 and 1982.

Source	DF	MS	Probability
Treat (T)	2	0.0037	NS
Error	8	0.0033	
Total	10		

Table 39 : Non-orthogonal two-way analysis of variance comparing regeneration rates (mm/day) of male and female Ctenotus taeniolatus in 1980 and 1982.

Source	DF	MS	Probability
Year (Y)	1	0.5046	< 0.05
Sex (S)	1	0.1361	NS
S x Y	1	0.0299	NS
Error	11	0.0757	
Total	14		

Table 40 : Non-orthogonal two-way analysis of variance comparing regeneration rates (mm/day) of male and female Ctenotus taeniolatus and male and female Lampropholis quichenoti in 1980.

Source	DF	MS	Probability
Species (Sp)	1	0.0139	NS
Sex (S)	1	0.0649	NS
Sp x S	1	0.0872	NS
Error	12	0.0488	
Total	15		

Table 41 : Lipid content (g) of carcass, tail butt and regenerated tails of male and female _Ctenotus_ _taeniolatus_ in 1982.

	Carcass	Tail butt	Regenerated tail	Total tail
Female	0.031	0.052	0.010	0.062
	0.040	0.090	0.087	0.177
	0.052	0.061	0.020	0.081
	0.074	0.032	0.020	0.052
	0.059	0.017	0.055	0.072
Mean	0.051			0.089
SD	0.017			0.051
Male	0.011	0.009	0.020	0.029
	0.012	0.018	0.010	0.028
	0.014	0.011	0.015	0.026
	0.117	0.009	0.030	0.039
Mean	0.039			0.031
SD	0.052			0.006

9.2.3 Lipid distribution within the tail

A comparison of lipid content in each tail section between sexes and times of year showed few significant differences in distribution of lipid down the tail (Table 42). In particular males had greater proportions of lipid than females in the section closest to the vent, a section which is not autotomised and contained only a small proportion of the total tail lipid (males 9%, females 3%). Similarly there were differences half way down the tail in sections 5 and 6, where females had a greater proportion of the total tail lipid than males, although in December when overall lipid levels were at a minimum, males had greater levels than females. Finally in section 10, females had greater proportions than males, while proportions in March were higher than those in December.

The significance of these differences becomes clear when the relationships between cumulative length of tail and cumulative lipid content (expressed as proportions) were compared for male and female lizards from March and December. Such comparisons revealed that there were no significant differences between the above models determined for males in March and for females in March and December, while the model determined for males in December differed significantly from all three (Table 43, Fig. 52). Accordingly, data from males in March and females in March and December were pooled and a single predictive model of the form $y = 1.09 - 1.37.e^{-3.24x}$ ($R^2 = 0.9550$), was determined, while the model for males in December remained as in Table 44.

Table 42 : Summary of results of analyses of variance comparing lipid content at different positions down the tail of male and female <u>Ctenotus taeniolatus</u> captured during different months (March, December). Numbers 1 to 10 refer to position on the tail, with number 1 being the section closest to the vent. Stars (*) represent significance levels as designated in section 2.4.

Source	1	2	3	4	5	6	7	8	9	10
Sex (S)	M>F*	NS	NS	NS	F>M*	NS	NS	NS	NS	F>M*
Month (M)	NS	NS	NS	NS	NS	**	NS	NS	NS	M>D**
S x M	NS	NS	NS	NS	NS	M:F>M D:M>F	NS	NS	NS	NS

Table 43 : Relationship between cumulative length of tail (x) and cumulative lipid content (y) (expressed as proportions) for male and female <u>Ctenotus</u> <u>taeniolatus</u> collected in March and December. Model fitted is of the form $y = A - B.e^{-ax}$, where A, B, and a are constants. Standard deviations of constants are presented in brackets.

	B	a	A	R^2
Males-March	1.3050 (0.0397)	3.3915 (0.2987)	1.0836 (0.0322)	0.9677
Females-March	1.3659 (0.0397)	3.2005 (0.2216)	1.1011 (0.0293)	0.9813
Males-Dec.	1.7274 (0.2845)	5.4803 (1.3044)	0.9837 (0.0670)	0.7207
Females-Dec.	1.4459 (0.0681)	3.2925 (0.4462)	1.0916 (0.0558)	0.9287

Table 44 : Comparison of the relationship between cumulative length of tail and cumulative lipid content (expressed as proportions) between male and female <u>Ctenotus</u> <u>taeniolatus</u> caught in March and December.

Comparison	DF	A		B		a	
		SS	P	SS	P	SS	P
Total variation	3	1.2493	NS	1.5711	NS	3.5978	NS
Male-Dec vs rest	1	3.7156	NS	4.2646	P < 0.05	3.5823	P < 0.01
Within rest	2	0.0314	NS	0.2250	NS	0.0183	NS
Pooled error	148	0.00237		0.02218		0.5097	

9.2.4 Frequency and position of autotomy

Frequency of autotomy in C.taeniolatus from New England and throughout NSW and parts of Queensland are presented in Table 45. Percentage of lizards with autotomised tails in the New England region was 10 to 20 % less than those in the rest of NSW. Contingency table analysis showed that within samples from New England and the rest of NSW there were significant differences in the numbers of male and female lizards with regenerated tails in each size class (Table 46); the occurrence of tail damage in juveniles was less than in adult males and females (Table 46).

C.taeniolatus have fracture planes in every vertebra except the one adjacent to the vent and those at the tip of the tail, and are thus capable of shedding their tail at almost any position. The position of autotomy for C.taeniolatus from New England and the rest of NSW is presented in figure 53, as proportion of the tail remaining versus proportion of lizards with freshly autotomised tails. The snout-vent length (SVL) to tail length (TL) relationship used to predict original tail length was

$$TL = 1.7632^{***}SVL - 2.6383^{ns}, \quad R^2 = 0.8849, \quad P < 0.0001, \quad n = 224.$$

Lines for males and females were found to be homogeneous (slope $F_{2,220} = 1.773$, NS; elevation $F_{2,220} = 0.148$, NS), and were thus pooled.

Table 45 : Frequency of autotomy expressed as percentages of total sample of _Ctenotus taeniolatus_ from the New England region and from NSW and parts of Queensland (Australian Museum collection).

SVL class (mm)	New England Female	New England Male	NSW Female	NSW Male
30-35	10.7	10.7	40.9	40.9
35-40	16.7	16.7	32.1	32.1
40-45	28.6	29.5	48.6	48.6
45-50	30.3	28.2	12.5	0
50-55	25.7	35.5	57.1	40.9
55-60	38.0	50.8	42.9	73.9
60-65	28.8	44.4	51.9	44.0
65-70	36.7	40.0	60.3	63.6
70-75	49.0	-	60.9	33.0
75-80	53.3	-	70.8	-
Overall adults	39.3	45.7	59.5	56.3
Overall juveniles	22.6		32.0	

Table 46 : Summary of contingency table analysis comparing proportions of _Ctenotus taeniolatus_ with regenerated tails in each 10 mm SVL size class. X^2_a refers to chi-squared distribution with a degrees of freedom.

	New England	NSW
All females	$X^2_9 = 24.111$, P < 0.05	$X^2_9 = 21.63$, P < 0.05
Female - juvenile	$X^2_6 = 11.82$, NS	$X^2_8 = 6.088$, NS
All males	$X^2_7 = 25.807$, P < 0.05	$X^2_8 = 24.05$, P < 0.05
Male - juvenile	$X^2_3 = 11.096$, P < 0.05	$X^2_5 = 6.366$, NS
Overall		
male,female,juv.	$X^2_2 = 42.06$, P < 0.001	$X^2_2 = 27.27$, P < 0.001
male,female	$X^2_1 = 1.61$, NS	$X^2_1 = 0.419$, NS

Figure 51 : Effects of autotomy on overwintering. (a) Number of Ctenotus taeniolatus dead at different times after commencement of experiment. Control lizards were removed after 90 days. (b) Relationship between carcass lipid/FFCW of Ctenotus taeniolatus and days after commencement of experiment. (o = tailed, x = tailless).
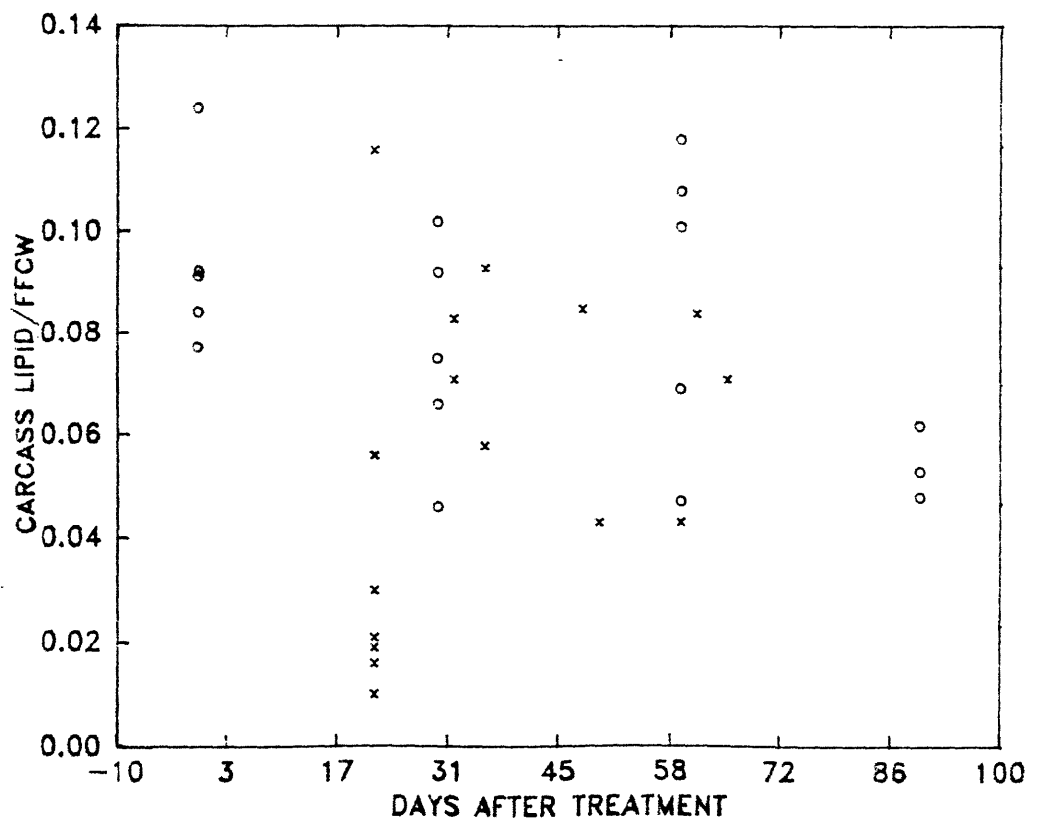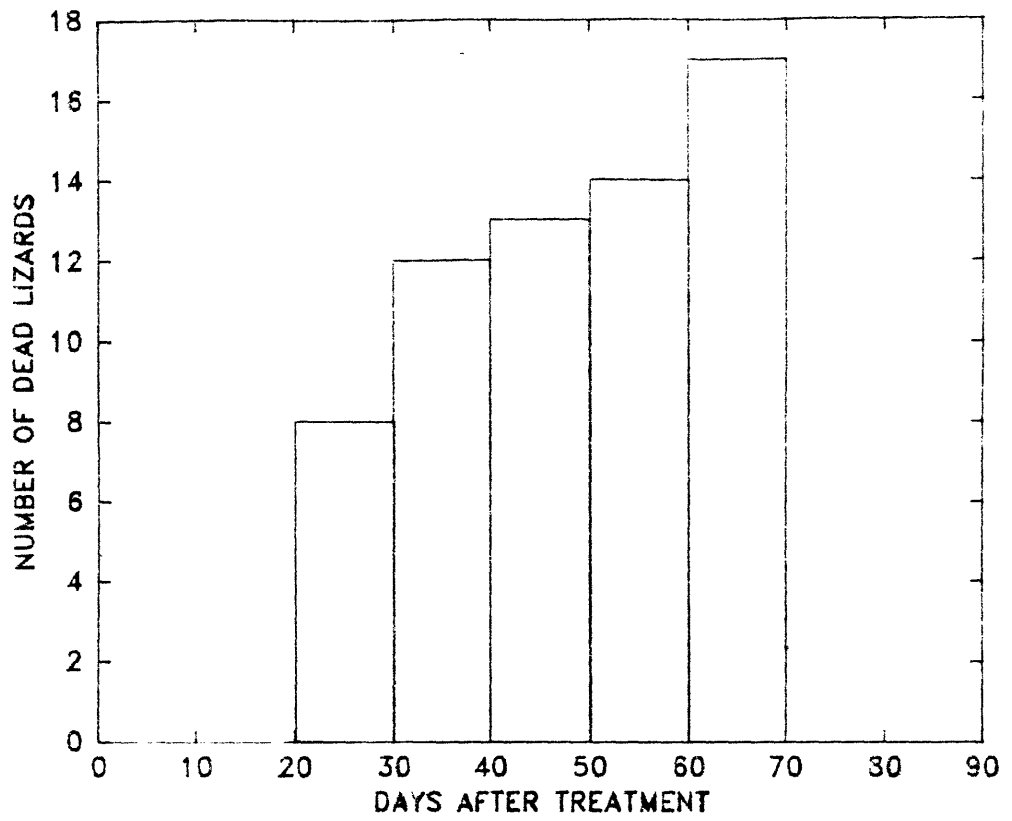
Figure 52 : Relationship between cumulative length of tail and

cumulative weight of lipid (expressed as proportion of total length

and total tail lipid respectively) of male and female Ctenotus

taeniolatus collected in March and December. Regression lines for

males in December are represented by dashed lines and for the

remaining lizards by the intact line. (male/Dec = triangle,

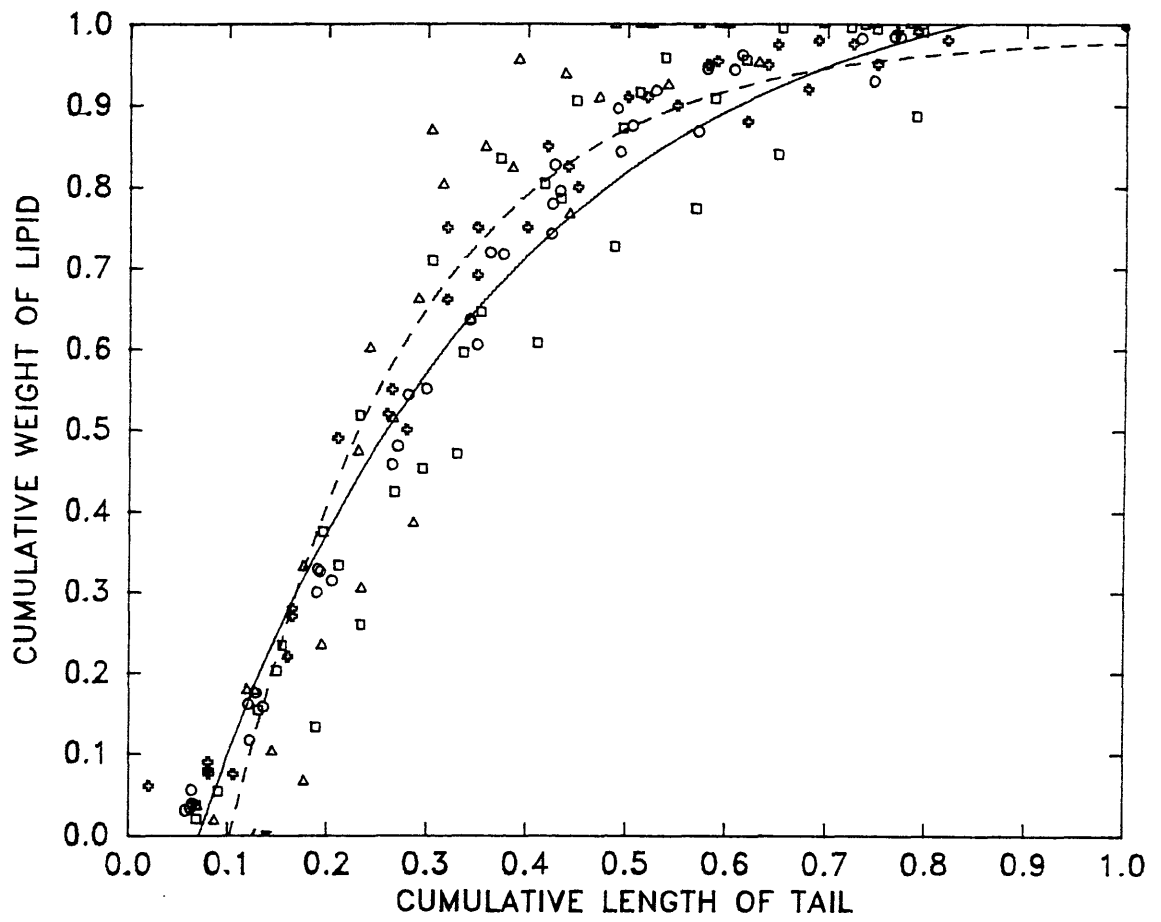male/March = cross, female/December = square, female/March =

circle).

Figure 53 : Proportion of tail remaining in <u>Ctenotus</u> <u>taeniolatus</u> with freshly damaged tails.
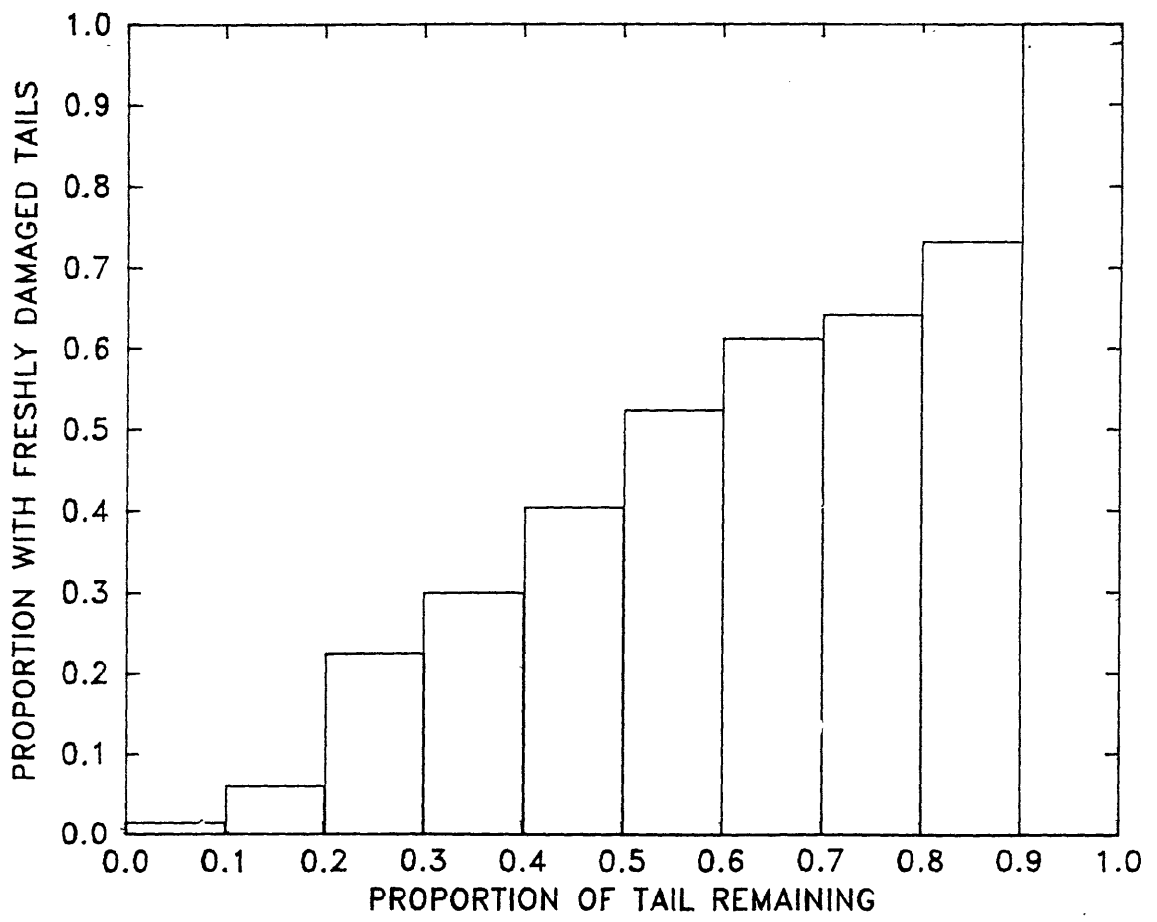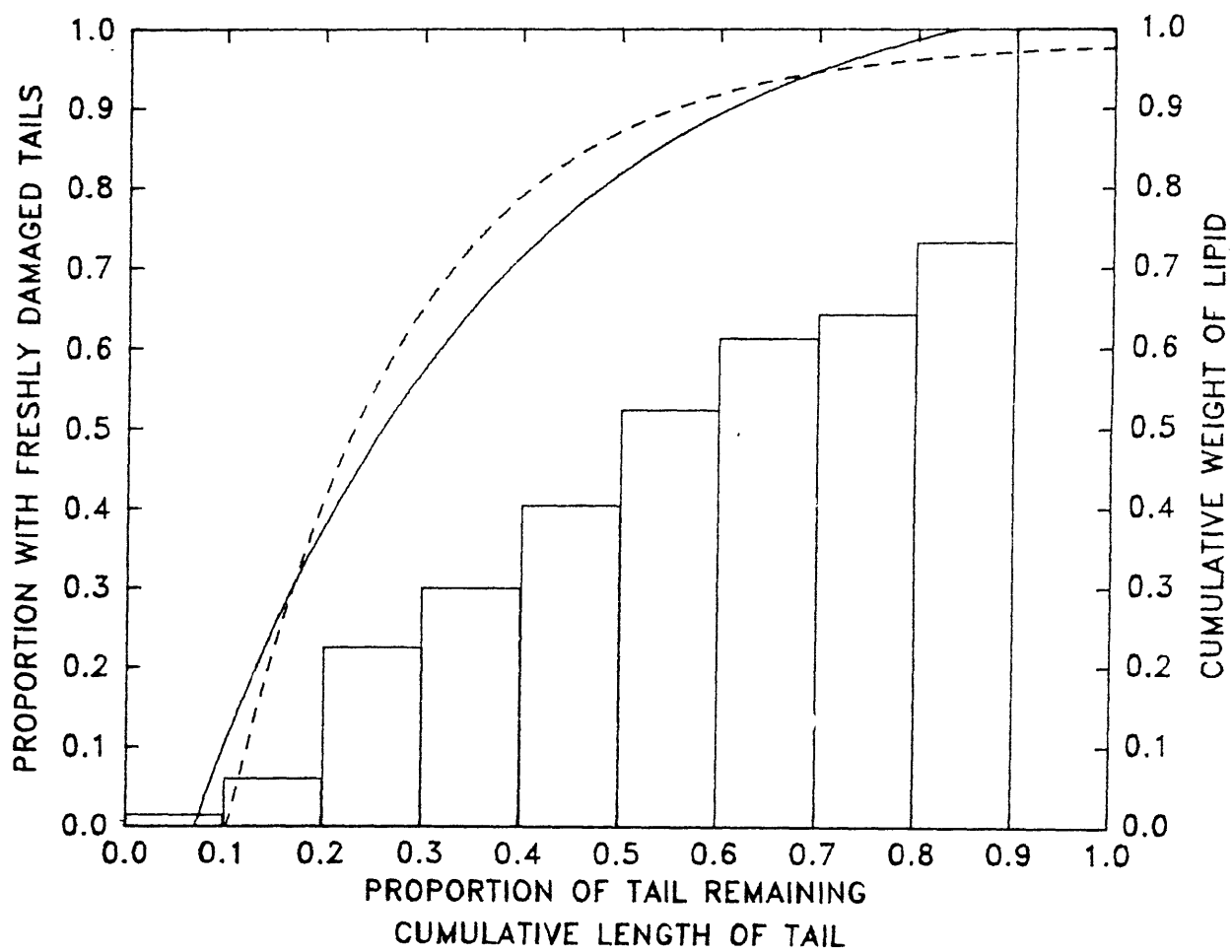
Figure 54 : Comparison of proportion of tail remaining in <u>Ctenotus</u> <u>taeniolatus</u> with freshly damaged tails with the distribution of lipid within a tail as in figure 52. Dashed lines represent distributions for male in December and intact line represents the remaining lizards.

9.3 DISCUSSION

9.3.1 Effect of autotomy on overwintering

A considerable amount of circumstantial evidence, including results presented in section 7.0 of the present study, along with some experimental studies (Clark 1971, Smyth 1974, Robertson 1976) suggests the importance of stored lipids in supplying energy needs over inactive, non-feeding periods. However, only one previous study has successfully attempted to examine the effects of autotomy on the ability to survive overwinter. Daniels (1981) found that tailless geckos (Phyllodactylus marmoratus) survive significantly less time when compared with tailed geckos. Thus it appears that caudal lipid is important to the survival of that lizard overwinter. However, the situation in C.taeniolatus is more drastic, as this skink does not possess abdominal fat stores and relies primarily on tail lipid for its energy reserves. Experiments with C.taeniolatus conducted under controlled and natural conditions, suggest that without its tail this species is unable to survive over winter, and further that although it possesses lipids in the carcass these are not used during starvation at low temperatures.

9.3.2 Effect of autotomy on reproduction

Again, a considerable amount of circumstantial evidence, including results presented in section 7.0 of the present study, suggests the importance of stored lipids in supplying the energy needs of reproduction, few studies have tested this hypothesis (summary presented in table 47). All of these studies showed that the removal of a fat store, whether the tail or fat body, had a detrimental effect on reproduction; in fact in some cases eggs were not produced (Hahn and

Tinkle 1965, Smyth 1974, present study). *Lampropholis guichenoti* appears to be the exception; however, in experiments with these lizards egg mass was not measured, so whether or not energy content of the clutch changed is unknown. In lizards that have caudal lipid stores it is clear that removal of the tail does have an effect on the energy content of a clutch, and that this effect is greatly exaggerated if the tail is the only source of stored lipid, to the extent that there may be up to 100% reduction in clutch size (*Hemiergis peronii*, Smyth 1974; *C.taeniolatus*, present study).

The mechanism behind the reduction of reproductive effort when lipid stores are removed is still not clear. One hypothesis is that the fat body is not essential to reproduction, except when food is in short supply, such as occurs in the first reproduction of *Uta stansburiana*. In that case removal of the major lipid store results in either a reduction in reproductive effort or an inhibition of vitellogenesis (Hahn and Tinkle 1965). However, the possibility of second or third clutches after fat body excision was not investigated. An alternative hypothesis is apparent in the work of Smith (1968). In *Ameiva festiva* and *A.quadrilineata*, tropical lizards that have a continuous reproductive cycle and with only short periods (8 days) of inactivity throughout the year, reproductive effort is still reduced by removal of abdominal fat bodies (Smith 1968), indicating that in these species fat bodies are essential to reproduction in spite of their continual activity and the presumed reliability of the food source. Further, after fat body excision female *Ameiva* possessed insatiable appetites compared with control lizards, with no ensuing reduction in the number of corpora atretica (Smith 1968). Similarly, in *Morethia boulengeri*, a lizard that possesses and uses lipids from the fat body and the tail, removal of the tail, the less important lipid store, still caused a

reduction in clutch size (Smyth 1974) indicating that in this species such a reduction is more likely a result of decreased lipid stores rather than the lack of essential fat soluble vitamins or micronutrients that may be associated with lipid stores. Thus, the more important the removed lipid store is to the energy budget the more drastic reduction there is in reproductive effort.

A corollary to these hypotheses is apparent in experiments in which the tail alone is removed, and is detailed in the work of Congdon et al. 1974, Vitt et al. 1977 and Dial and Fitzpatrick 1981. These authors suggest that the partitioning of energy to reproduction or tail regeneration is dependent on the functional significance of the tail, so that if the absence of the tail does not significantly decrease fitness then energy will be used for reproduction and the tail will be regenerated slowly; if on the other hand the presence of the tail does significantly increase fitness then tail regeneration will proceed more rapidly at the expense of reproduction. In the present study it was found that C.taeniolatus did regenerate its tail, including lipid deposits, at the cost of all or part of a clutch of eggs. In some individuals this rate was rapid when compared to those stated for Coleonyx brevis (Vitt et al. 1977), and in others it was slow with rates similar to those reported for Eumeces skiltonianus (Vitt et al. 1977), and although males and females were not different, significant differences were apparent among years. This variation in regeneration rate is most likely due to the varying ability of lizards to feed, as conditions were not controlled within these experiments. However, it is apparent from these experiments that available energy in tailless C.taeniolatus was allocated to tail regeneration and lipid deposition within the tail in preference to reproduction, a result also reported for Coleonyx brevis (Dial and Fitzpatrick 1981), a gecko with a very

different life history pattern from <u>Ctenotus</u>.

Table 47 : Summary of experiments designed to test the effect of lipid removal on reproduction in lizards.

Species	Fat stores	Treatment	Results	Source
Uta stansburiana	fat body	fat body removed early yolking	reduced clutch size; increased corpora atretica	Hahn and Tinkle 1965
		fat body removed prior to yolking	no yolking occurred after 40 days	
Ameiva festiva, _A.quadrilineata_	fat body	fat body removed early yolking	increased corpora atretica; increased feeding	Smith 1968
Morethia boulengeri	fat body, tail, carcass	tail removed early yolking	reduced clutch size 14%; no change in mean egg mass;	Smyth 1974
Hemiergis peronii	tail, carcass	tail removed early yolking	reduced clutch size 55%; increased corpora atretica	Smyth 1974
Coleonyx brevis	fat body, tail, carcass	tail removed pre-vitellogenesis	clutch size unchanged; egg mass reduced 14%; egg energy reduced 19%	Dial and Fitzpatrick 1981
Ctenotus taeniolatus	tail, carcass	tail removed early yolking	reduced clutch size 50-100%; increased corpora atretica; no change in mean egg weight	present study
Lampropholis guichenoti	fat body, tail, carcass	tail removed early yolking	no change in clutch size	present study

9.3.3 Relevance of autotomy

Although the frequency of autotomy has for many years been routinely used as an index of predation (Rand 1954, Parker and Pianka 1975, Tinkle 1967, Tinkle and Ballinger 1972 and many others), the arguments behind such interpretations are now thought to be fallacious, as lizards can have undamaged tails when predation is zero, or when predators are 100% efficient, successfully capturing all individuals attacked (Schoener 1979). Consequently a high incidence of autotomy does not necessarily indicate high predation intensities but rather a high incidence of lizards which successfully avoid predation. In addition, the probability of losing the tail is a function of the length of exposure to predation (Tinkle and Ballinger 1972, Jaksic and Fuentes 1980, Schoener and Schoener 1980, present study) and to the frequency of other activities that could lead to autotomy, e.g., intraspecific aggression (Jaksic and Fuentes 1980, Schoener 1979).

However, bearing these limitations in mind, tail-break frequencies are useful, particularly if one is interested in how often lizards are in the position of being alive but with no or reduced energy stores. In natural populations from NSW and parts of Queensland up to 60% (Table 45) of C.taeniolatus have regenerated tails indicating that at some time autotomy had occurred; in the New England region percentages were not as high (maximum 46%; Table 45). Tail-break frequencies for the only other skink without abdominal fat bodies were similar to these (Hemiergis decresiensis, Robertson 1981), while those reported for skinks with abdominal fat bodies were higher (Robertson 1981, Vitt et al. 1977, Vitt 1983, unpublished data on Lampropholis delicata and Leiolopisma platynota). Although these values are dependent on the age structure of the samples examined, these data point to the possibility that although the presence of autotomy in C.taeniolatus is quite high,

it is less than that found in skinks which have lipids stored in places other than the tail.

To further consider the significance of autotomy to C.taeniolatus it is important to consider the position of autotomy, as Ctenotus is capable of shedding its tail at any of the fracture planes present in each vertebra and as lipid deposits are not evenly distributed down the tail (Fig. 52). The few studies that have tried to estimate the position of autotomy have all used tail-break ratios of completely (Daniels 1981) and partially (Vitt 1983) regenerated tails, calculations which assume that the part of the tail remaining after autotomy changes directly with body length. So that this assumption was not made, only lizards with freshly broken tails, as described in section 9.2.4, were used in the present study. These data indicate that the majority of lizards that survive attack have lost the distal portion of their tail with approximately 30% losing the very tip, while only 6% lost the entire tail. When these data are combined with those available on distribution of lipid within the tail (Fig. 54) it is apparent that few lizards lose large proportions of their tail lipid store, e.g., lizards have to lose 80% of their tail before they lose 50% of their lipid store; only 20% of lizards are in this category.

10.0 SIGNIFICANCE OF TAIL AUTOTOMY TO C.taeniolatus - A DISCUSSION

Tail adaptations in lizards may take two forms (i) tail autotomy followed by regeneration or (ii) tail retention, with little or no regeneration (Vitt et al. 1977). Present theory suggests that lizards in which tails are functionally important should either retain the tail, not using it as a means of predator escape, or practise tail autotomy followed by rapid regeneration (Vitt et al. 1977, Dial and Fitzpatrick 1981). This second alternative, which first appears evolutionarily paradoxical, usually involves the use of trade-offs with resource apportionment to somatic and reproductive recipients (Dial and Fitzpatrick 1981), so that reproduction has energetic priority over tail regeneration in short-lived iteroparous species while the reverse is held for long-lived species. Vitt et al. (1977) have produced a flow chart summarising the important events influencing the evolution of tail adaptations in lizards.

At first glance, C.taeniolatus seems to fit into an average pathway as predicted by Vitt et al. (1977) and Dial and Fitzpatrick (1981). C.taeniolatus matures in its second year (third season) and lives for at least 5 years, with a short, single, annual breeding season, so by lizard standards it can be termed long-lived and possibly late maturing. It practises tail autotomy as a response to predator attack with as high as 60% of lizards with tail breaks. In quadrupedal lizards it is highly likely that the loss of a tail increases the escape speed (Daniels 1983) rather than decreasing it, as occurs in bipedal lizards (Ballinger 1973b, Ballinger et al. 1979, Punzo 1982), with the thrashing tail acting as a distraction to the predator (Dial and Fitzpatrick 1983). It can be highly advantageous for a lizard to shed the tail under such

circumstances. However, the tail of C.taeniolatus is the most important store of lipid, as this lizard possesses no abdominal fat bodies and the carcass lipid is unavailable. Measurements from natural populations and controlled experiments indicate that tail lipid is necessary for survival over winter and for the production of a clutch of eggs, so that if the entire tail is removed in the early stages of vitellogenesis then tail regeneration, with an accompanying deposition of lipids, takes place in preference to the continued production of the clutch. Further, the tail can function as a whip (Appendix), the flicking movement of which propels the tail and distal portions of the body away from a chasing predator, such as a snake or other lizard, in the final stages of escape. Also, although mating has not been observed in this study, it is likely that at least a portion of the tail is necessary during copulation. Fox and Rostker (1982) have shown that in Uta stansburiana even partial tail loss can result in reduced social status. All of the above, point to the fact that the tail of C.taeniolatus is actively functional, that autotomy is probable and that if whole tail autotomy occurs before winter or in the early stages of vitellogenesis a significant decrease in fitness may result.

However, on closer examination of the biology of C.taeniolatus it becomes apparent that the position of the break and the time this occurs are crucial to the understanding of the significance of autotomy in this species.

Firstly, one must consider the ability of C.taeniolatus to overwinter. Certainly, if a lizard loses its entire tail at the beginning of or during winter, in all probability it will die either from freezing or from lack of nutrients. However, even though some predators do actively search out lizards in their refuges (McFarland 1982), Daniels (1981) has found that starved or cold geckos

(Phyllodactylus marmoratus) retained their tails for longer than well-fed or warm geckos. Further, estimations of the energy needed to overwinter and the quantity of energy in the form of stored lipids present in the tail at the beginning of winter suggests that on average an adult female lizard requires between 12 and 20% of tail lipid present at the beginning of winter to overwinter for 90 days (male, 17-30%) and between 25 and 35% for 140 days (male, 35-50%) (Table 48). This means that an average lizard can lose 70%, and sometimes more, of the tail and still have enough lipid stored to overwinter (Fig. 52). The situation for juveniles is more drastic, as lizards less than 1 g would have great difficulty surviving a long winter even if they had a complete tail, and in an average winter would probably require at least 80% of their tail. These predictions as yet, however, do not take into account the different thermal requirements for activity and feeding of juveniles and it may be that when such refinements can be made the estimates of energy required by small lizards will be less, and the predictions concerning the proportion of the tail required will be similarly reduced. However, bearing these inadequacies in mind, at least for adults it appears that of lizards with freshly broken tails less than 10% would be seriously affected by the energy requirements for overwintering (Fig. 53). These results taken with the result that lizards are less likely to lose their tail at this crucial time suggests that the probability of lizards being adversely effected by autotomy is very small.

Secondly, in terms of the ability of C.taeniolatus to reproduce it is clear that whole tail autotomy at a time prior to vitellogenesis will result in a reduction of the clutch for that year. However, estimates of the change in energy as measured by the change in the tail lipid in females and males over this time suggest that as much as 45% of the tail is used during the reproductive period for females and 30% for males

(Table 49). This means that lizards can lose up to 70% of their tail (Fig. 52) and still have enough lipid to produce a clutch of eggs and a new tail, provided that their ability to mate and feed is not adversely affected.

It is likely that only 20% of lizards (Fig. 53) would be detrimentally affected by autotomy at this time. Further, as C.taeniolatus has at least 4 breeding seasons during its lifetime, the sacrifice of one of these may be of less significance than in lizards which have only one chance to reproduce.

Unfortunately it is not possible to make any predictions about the additive effects of autotomy over time; for example a lizard that loses part or all of its tail over winter may be able to survive winter but may not be able to recoup its losses so as to mate or produce a clutch in spring. The existence of lizards in such circumstances may increase the cost of autotomy to the population. However, as the theory stands at present it appears that although C.taeniolatus exhibits high levels of autotomy, because it practises economy of autotomy and because of its longer life, lizards are making few sacrifices when they shed their tail to escape a predator, and consequently there is no paradox.

The question as to why C.taeniolatus stores all of its usable lipid within the tail, when other very similar skinks store lipid in both abdominal fat stores and the tail is still unanswered. Robertson (1981) suggests that storing lipids in the tail alone may allow for development of a larger clutch. Although this has not been examined, it appears unlikely as fat bodies usually decrease in size with increasing egg size, taking up very little room when eggs are at their peak of development. Further, preliminary investigations suggest that the presence of abdominal fat bodies follows a purely taxonomic line (Greer,

pers.comm.) rather than one of convergent ecology, although the significance of this can be determined only with detailed knowledge of the behaviour and ecology of the Australian Scincidae.

Table 48 : Percentage of tail lipid required for overwintering.

| | 90 days | | 140 days | |
Body weight (g)	Female	Male	Female	Male
1	66.4	82.6	100.0	100.0
2	29.0	35.9	51.5	67.4
3	21.9	27.3	39.4	51.6
4	18.2	22.4	33.9	44.3
5	15.9	19.9	30.4	39.8
6	14.3	17.9	28.1	36.8
7	13.3		26.4	

Table 49 : Percentage of tail lipid required during reproduction.

Body weight (g)	Female	Male
3	40.4	26.1
4	44.9	29.5
5	40.4	30.9
6	40.4	21.0
7	40.4	