

Distribution of energy reserves in a viviparous skink: Does tail autotomy involve the loss of lipid stores?

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Abstract Caudal autotomy is an effective defensive strategy used by many lizards to facilitate escape during predatory encounters. However, it has several potentially severe consequences, including a range of energetic costs that are believed to result from the depletion of caudal lipid reserves during tail loss. In this study we examined the possible effect of caudal autotomy on the energetic reserves of a small viviparous skink, *Niveoscincus metallicus* (O'Shaughnessy 1874). Animals of each sex were collected on three occasions to assess the distribution of lipid stores. In addition, the frequency and position of naturally occurring tail breaks were determined. Both abdominal and caudal lipid stores are present in *N. metallicus*; however, caudal fat bodies comprise the majority (55–78%) of these fat reserves. Temporal variation in fat body mass, both abdominal and caudal, was evident. There was a significant relationship between the two fat stores, which was distorted in pregnant females, when relatively more fat was stored in the tail. Examination of the distribution of caudal fat in the tail revealed that the majority (90–95%) occurs within the proximal third of the tail. The remainder is located in the middle portion of the tail, with no reserves in the most distal tail section. During late pregnancy, females store relatively more fat closer to the body. The frequency of tail loss in a natural population of *N. metallicus* was extremely high (78%). Tail breaks were normally distributed along the length of the tail (i.e. most near the middle and fewer distal and proximal breaks). Thus there was a relatively high chance of some lipid depletion as a result of tail loss, but because 76% of breaks occur in the middle and distal thirds of the tail, there is a high probability that tail loss results in only minimal (i.e. <10%) lipid depletion. This is the first instance where both the energetic 'value' of the tail and the likelihood of lipid depletion during tail loss have been determined in a lizard. Overall, the combination of the aggregation of caudal fat reserves and position of naturally occurring tail breaks may enable *N. metallicus* to combine caudal fat storage and tail autotomy with minimal conflict.

Key words: autotomy, cost of reproduction, fat body, *Niveoscincus metallicus*, predation, reproduction, Scincidae, tail loss.

INTRODUCTION

Autotomy of body parts to evade potentially fatal predatory encounters is a defensive mechanism employed by a variety of invertebrates (e.g. crustaceans, cnidarians, spiders, insects; Robinson *et al.* 1970; Edmunds 1974; Roth & Roth 1984) and vertebrates (e.g. squamate reptiles, salamanders; Wake & Dresner 1967; Arnold 1988). Tail autotomy in lizards is an effective defensive tactic that is used to facilitate escape from predators when other strategies such as crypsis and fleeing have failed (Arnold 1988). Although caudal autotomy provides an immediate survival benefit, the ensuing consequences of tail loss may reduce an individual's subsequent fitness (Arnold 1988). Tail loss in lizards has been associated with reduced locomotor performance (Ballinger *et al.* 1979; Punzo 1982; Formanowicz *et al.* 1990; Martin & Avery

1998; Downes & Shine 2001), lowered social status (Fox & Rostker 1982; Martin & Salvador 1993), diminished probability of surviving subsequent predator encounters (Dial & Fitzpatrick 1984; Daniels *et al.* 1986; Downes & Shine 2001) and decreased survival under natural conditions (Wilson 1992; Niewiarowski *et al.* 1997; Fox & McCoy 2000).

Squamate reptiles accumulate energetic reserves in the form of fat bodies located in either or both of the abdomen and tail (Derickson 1976). These energy stores may be utilized for reproductive investment (Hahn & Tinkle 1965; Diaz *et al.* 1994; Doughty & Shine 1998), metabolism over winter or periods of nutritional stress (Avery 1970; Derickson 1974; Daniels 1984), and general growth and maintenance (Derickson 1974). In species where abdominal fat bodies are absent, caudal lipid reserves constitute the entire lipid reserve (e.g. *Sphenomorphus* group of lygosomine skinks; Greer 1986); however, caudal fat may be the major fat store even when abdominal fat is also present (Clark 1971; Dial & Fitzpatrick 1981; Vitt & Cooper 1986). Consequently, tail loss may result in the direct depletion of lipid stores and a range of

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Accepted for publication April 2002.

energetic costs including restricted rates of growth (Ballinger & Tinkle 1979; Smith 1996) and reduced reproductive output (Smyth 1974; Dial & Fitzpatrick 1981; Wilson & Booth 1998). Further indirect costs may be incurred from the diversion of energetic resources, originally allocated to growth or reproduction, towards tail regeneration (Congdon *et al.* 1974; Vitt *et al.* 1977; Dial & Fitzpatrick 1981).

The seemingly conflicting strategies of caudal fat storage and tail autotomy have intrigued numerous authors (Clark 1971; Dial & Fitzpatrick 1981; Daniels 1985; Doughty & Shine 1998; Wilson & Booth 1998). The high regularity of tail loss in species in which lipid reserves are primarily stored as caudal fat (Clark 1971; Dial & Fitzpatrick 1981; Vitt & Cooper 1986; Wilson & Booth 1998) suggests that mechanisms should exist to limit the impact of autotomy. For example, ground skinks (*Scincella [Lygosoma] laterale*) ingest shed tails, presumably to recoup lost lipid stores (Clark 1971) and in certain instances geckos (*Phyllodactylus marmoratus*) can limit the length of tail dropped to reduce the amount of fat lost (Daniels 1985).

It has generally been assumed, although never demonstrated, that the amount of caudal fat lost is related to the length of tail shed. However, the validity of this assumption has not been thoroughly investigated. Daniels (1985) stated that the gecko *P. marmoratus* lacked lipid stores in the distal portion of its tail, which suggests that tail loss may not always result in the depletion of caudal fat. Most studies that have investigated the energetic consequences of autotomy have removed the majority of the tail (Dial & Fitzpatrick 1981; Wilson & Booth 1998), and consequently a substantial portion of caudal fat. However, because complete tail autotomy is relatively rare in some natural populations (Daniels 1985; Wilson & Booth 1998), the severe consequences of autotomy that have been demonstrated in the laboratory may be of reduced ecological relevance. If the majority of naturally occurring tail breaks result in only minor caudal lipid depletion in lizards, the strategies of caudal fat storage and tail autotomy might be used in combination without conflict.

We investigated the relative importance of abdominal and caudal lipid stores in the metallic skink (*Niveoscincus metallicus*), enabling an energetic 'value' to be assigned to the tail. To determine if variation in the position of tail breaks influenced the energetic consequences of autotomy, we examined the distribution of caudal fat along the length of the tail. We then estimated the position of naturally occurring tail breaks for comparison against the distribution of caudal energy reserves in order to gauge the likelihood of tail loss resulting in significant fat loss. Seasonal sampling was incorporated in the study. However, our purpose was not to undertake an assessment of the energetic costs of reproduction per se, but rather to

establish whether the distribution of lipid reserves is consistent throughout the activity season.

METHODS

Study species

The metallic skink (*Niveoscincus metallicus*) is a small viviparous lizard (45–65 mm adult snout–vent length (SVL)) that has a widespread distribution across a range of habitats from sea level to subalpine environments (1400 m a.s.l.) in Tasmania and south-eastern Victoria, Australia (Melville & Swain 1999). It is a relatively cryptic species that occupies shaded microhabitats with medium to dense vegetation cover and thick litter (Melville & Swain 1999). It is predominantly a shuttling heliotherm and utilizes both rocks and logs close to the ground as basking sites (Melville & Swain 1997). Tail autotomy is generally used as a defensive mechanism against predators only after crypsis and fleeing have failed. *Niveoscincus metallicus* has both abdominal and caudal fat bodies and is able to autotomise its tail along the majority of its length.

Distribution of energetic reserves

We collected adult *N. metallicus* (>45 mm SVL; Swain & Jones 1994; Jones & Swain 1996) by noosing from around Clarence Lagoon (1000 m a.s.l.; 42°04'S, 146°19'E), a small glacial lake on the central plateau of Tasmania, Australia. Animals of both sexes were collected in late November 1999 (late spring; $n = 8\delta$, 8φ), early February 2000 (late summer; $n = 10\delta$, 10φ), and mid-March 2000 (early autumn; $n = 10\delta$, 10φ). All lizards collected had original or completely regrown tails. They were transported to the laboratory and killed by rapid cooling to -20°C (Cogger 1992). Measurements of SVL and tail length (± 0.1 mm) were taken for each individual. The paired abdominal fat bodies were removed by dissection and weighed (wet mass ± 0.1 mg). Dry mass was measured for 15 abdominal fat bodies that were dried for 24 h at 60°C and regression analysis was used to establish the relationship between wet mass and dry mass. Dry mass was then estimated for all other samples.

In males, the dimensions of one testis were measured (maximum length and width ± 0.1 mm) and testis volume (mm^3) calculated using the formula for the volume (V) of an ellipsoid, $V = 4/3\pi a^2b$, where a is half the width and b is half the length. Testis volume has been shown to be a reliable indicator of male reproductive status in *N. metallicus* (Swain & Jones 1994). In females, reproductive status was

recorded (i.e. pregnant or postpartum) and developing embryos staged according to Dufaure and Hubert (1961).

To estimate the mass of caudal fat bodies, the tail was removed through the most proximal fracture plane and its wet mass recorded (± 0.1 mg). The entire tail was then dried for 24 h at 60°C and re-weighed to obtain its dry mass. Preliminary trials indicated that tails were completely dry at this time. Each tail was then immersed in ether for a minimum of 4 days to dissolve the lipid stores, then placed in a fume cabinet for 24 h to allow the ether to dissipate, leaving a completely dry tail minus the caudal lipid stores. The dry tails were then reweighed (± 0.1 mg) and the weight difference before and after the ether treatment taken as an estimate of the dry mass of caudal lipid stores. This method was completed on intact tails in November; however, in February and March the tails were cut into three equal-length sections to determine the distribution of caudal fat in each third of the tail. We verified our method by applying the same procedure to skin flaps, front and hind limbs, and abdominal fat bodies. The limbs of *N. metallicus* share the same structural components as the tail, but lack lipid reserves. There was no mass change in the limbs or skin following ether treatment; however, the abdominal fat bodies were completely dissolved, leaving only the surrounding membrane.

Frequency and position of tail autotomy

To determine the frequency and relative position of tail loss in *N. metallicus*, we collected 100 animals from Clarence Lagoon between 11 and 18 January 2000. For each lizard the presence of any tail break was noted and measurements were taken of SVL and tail length (TL; ± 0.1 mm). The distance from the vent to the tail break (break length (BL); ± 0.1 mm) was also measured for animals with evidence of previous tail damage. This enabled the proportion of animals with previous tail loss to be determined. Each animal was given a temporary non-toxic paint mark to prevent resampling and animals were released at the site of capture. For lizards that exhibited signs of tail damage, the original tail length (OTL) was estimated by generating the linear regression equation for SVL *vs* TL for all animals with complete original tails. Position of tail loss was estimated by BL/OTL, where 0 indicates a break at the tail base and 1 indicates a break in the distal tip of the tail. Because the tail base (break length) may elongate during tail regeneration (Tinkle 1967), the true position of tail loss might be slightly more proximal than the estimate. However, it is unlikely that this discrepancy would cause our estimate to deviate substantially from the actual position of tail loss.

Data analysis

The data were checked for all relevant assumptions before statistical analysis; no transformations were required. Linear regression was used to investigate several relationships including those between lipid stores and body size (SVL or tail length), caudal and abdominal fat reserves, dry and wet mass of abdominal fat reserves, and tail length and body size (SVL). We compared the relationship between the two fat stores for each sex-month combination by testing for homogeneity of slopes. Analysis of covariance (ANCOVA) was used to examine the relationship between tail length and body size for animals collected to assess the frequency and position of tail loss (tail length as dependent variable, sex as factor, and SVL as the covariate).

Body size (SVL or tail length) was investigated as a possible covariate for analyses involving fat reserves; however, there was no significant relationship between the mass of each fat store and body size ($P > 0.05$ for all sex-month combinations; except abdominal fat *vs* SVL for males during February, $R^2 = 0.62$; $F_{1,9} = 12.9$, $P = 0.007$) and therefore it was not considered in any analysis. Sexual and temporal variation in fat reserves (overall and caudal distribution) were investigated using ANOVA (sex and time as factors). Where significant interactions were found to exist, the main effects were examined by treating each sex-month combination as a group and performing ANOVA (group as factor) post-hoc tests.

We used ANOVA to examine temporal variation in male reproductive status and sexual differences in the position of tail breaks. Normality of the position of tail breaks along the length of the tail was investigated using frequency histograms, boxplots and normal quantile plots. The probability of tail breaks occurring at particular positions along the length of the tail was estimated using the area under a standard curve (for the given sample mean and standard deviation). These values were used to estimate probable loss of caudal fat following tail autotomy.

RESULTS

Variation in energetic reserves

There was a significant linear relationship between the mass of abdominal fat bodies before and after the drying treatment (dry mass = $0.81 \times$ wet mass - 0.559; $R^2 = 0.78$; $F_{1,14} = 46.96$, $P < 0.001$). This regression equation was used to estimate the dry mass of abdominal fat to allow direct comparison with caudal lipid stores.

The reproductive status of *N. metallicus* differed for

the three sampling periods (Fig. 1). Females were in early pregnancy (stage 30–32 embryos) in November, late pregnancy in February (stage 40), and 4 weeks postpartum in March (Fig. 1). Male reproductive status, as measured by testes volume, varied significantly (ANOVA: $F_{2,25} = 14.87$, $P < 0.001$), with testis size decreasing progressively (Tukey's post-hoc test; Fig. 1).

There was a significant sex-month interaction for both abdominal (ANOVA: sex \times month: $F_{2,50} = 13.6$, $P < 0.001$) and caudal fat body mass (ANOVA: sex \times month: $F_{2,48} = 3.6$, $P = 0.034$). Post-hoc analysis revealed that both sexes in November and females during late pregnancy (February) had significantly smaller abdominal fat bodies than males in February and either sex in March (Fig. 1). Males during February had larger caudal fat bodies than either sex in November (Fig. 1). Reproductive status

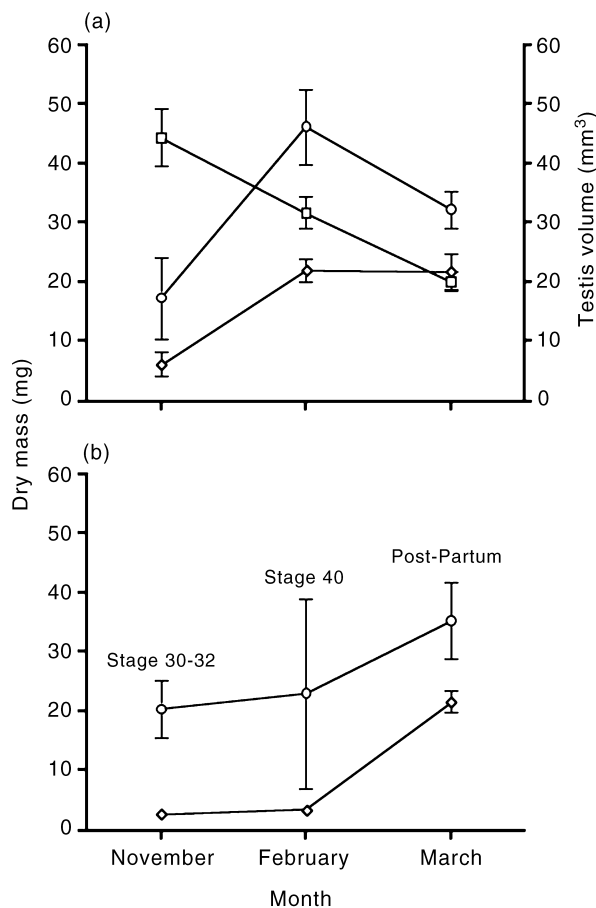


Fig. 1. Variation in reproductive status and fat body mass in (a) male and (b) female *Niveoscincus metallicus* (November $n = 8\delta$, 8ϕ February $n = 10\delta$, 10ϕ March $n = 10\delta$, 10ϕ). Male (volume of one testis in $\text{mm}^3 \pm \text{SE}$; □) and female reproductive status (pregnancy stage after Dufaure & Hubert 1961) are indicated at each sampling period. (◇) Abdominal and (○) caudal fat body mass ($\text{mg} \pm \text{SE}$) were determined at each sampling period.

therefore appeared to influence the mass of energetic reserves in *N. metallicus*. Abdominal and caudal fat stores significantly increased between November and February in males as the testis regressed but stabilized between February and March as the testes continued to regress (Fig. 1). Likewise, abdominal lipid reserves increased significantly after parturition in females (Fig. 1).

The proportion of total lipid reserves stored in the tail was investigated (Table 1). Three data points were excluded from the analysis, as both total stores ($< 3 \text{ mg}$) and percentage tail fat (0–3%) were low, suggesting that these animals were in unusually poor condition. A significant sex-month interaction was found (ANOVA: sex \times month: $F_{2,47} = 4.4$, $P = 0.018$). Tukey's post-hoc test revealed that caudal fat constituted a larger proportion of total fat in pregnant females (November and February) than in males or postpartum females (Table 1, Fig. 1).

The regression relationship between abdominal and caudal fat was not consistent for each sex-month combination across the season (test for homogeneity of slopes ANOVA: $F_{5,43} = 2.57$, $P = 0.040$). Examination of the plots of abdominal fat mass against caudal fat mass indicated that pregnant females (November and February) had a steeper regression slope than post-pregnant females in March or males in any month; this

Table 1. Percentage ($\% \pm \text{SE}$) of total lipid stores located in the tail for male and female *Niveoscincus metallicus*

Month	Male	Female
November	55.6 ± 12.06 (8)	77.9 ± 11.24 (8)
February	66.6 ± 3.43 (10)	75.7 ± 10.93 (10)
March	60.4 ± 2.74 (10)	58.2 ± 3.57 (10)

Sample sizes are indicated in parentheses.

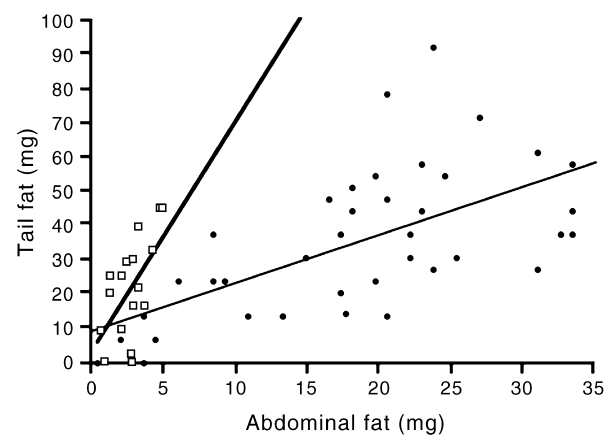


Fig. 2. Relationship between abdominal and caudal fat stores (mg) for *Niveoscincus metallicus* (●,—; overall, excluding pregnant females) and pregnant females (□,—; November and February). The equations for the linear regression are provided in the text.

was clearly a consequence of their greatly reduced abdominal reserves. Consequently, separate regression equations were calculated for pregnant females in November and February (tail fat = $6.83 \times$ abdominal fat + 3.97; $R^2 = 0.36$; $F = 8.57$, $P = 0.010$) and all other combinations (Tail fat = $1.42 \times$ abdominal fat + 8.58; $R^2 = 0.37$; $F = 21.16$, $P < 0.001$; Fig. 2). One pregnant female was identified as an outlier because of high leverage and was excluded from this analysis.

Distribution of caudal fat

In February and March, the distribution of caudal fat along the length of the tail was determined (i.e. amount in proximal, middle and distal tail thirds). Significant sex-month interactions were found for the proportion of fat in both the proximal (ANOVA: sex \times month: $F_{1,36} = 7.6$, $P = 0.009$) and middle tail sections (ANOVA: sex \times month: $F_{1,36} = 7.9$, $P = 0.008$). Post-hoc analysis revealed that during late pregnancy (February) females stored a larger portion of caudal fat in the proximal third and less in the middle third than postpartum females. Caudal fat reserves were not generally located in the distal portion of the tail; therefore, no analysis was possible. The overall distribution (excluding late pregnant females) of caudal fat reserves and that for late pregnant females is presented in Table 2. The majority (90–95%) of caudal fat in *N. metallicus* is located in the proximal third of the tail, with the remainder situated in the middle portion (Table 2).

Frequency and position of tail loss

Seventy-eight of the 100 animals collected from Clarence Lagoon exhibited signs of previous tail loss. The frequency of tail loss (78%) did not differ between males (48/62 = 77.4%) and females (30/38 = 78.9%). Sexual differences in the relationship between TL and SVL were not evident in the 22 animals with complete

Table 2. Percentage (% \pm SE) of total caudal fat stored in each tail third for *Niveoscincus metallicus*

Tail section	Overall	Late pregnant females
Proximal	89.4 \pm 1.55	96.2 \pm 1.29
Middle	10.5 \pm 1.54	3.5 \pm 1.35
Distal	0.1 \pm 0.03	0.3 \pm 0.36

Data for both sexes from February and March have been pooled for presentation (the overall value excludes females in February). The distribution of tail fat for females during late pregnancy (stage 40 embryos; Dufaure & Hubert 1961) is also shown.

original tails (ANCOVA on tail length with SVL as the covariate; $F_{1,21} = 0.46$, $P = 0.51$), so a common regression equation was calculated (TL = $1.09\text{SVL} + 11.98$; $R^2 = 0.61$; $F_{1,21} = 31.24$, $P < 0.001$). This equation was used to estimate the location of the tail break for each animal with previous tail autotomy. The proportion of animals with tail breaks located in each third of the tail did not differ substantially between the sexes (males: 0.30, 0.39, 0.31; females: 0.31, 0.44, 0.25; proximal, middle, and distal thirds, respectively).

Probability of lipid depletion from autotomy

The position of tail loss did not differ significantly between males and females (ANOVA: $F_{1,77} = 0.7$, $P = 0.42$); the data were therefore combined for further analysis. Tail breaks were found to be normally distributed along the length of the tail (with mean position = 0.51 and standard deviation = 0.243, $n = 78$; Fig. 3). The probability of tail breaks in the Clarence Lagoon population occurring at particular positions along the length of the tail was estimated using the area under a standard curve. The chance of a tail break occurring within the distal third of the tail where no fat is stored is 0.252. Consequently, most autotomy events involved the loss of some caudal energy reserves (74.8% occurred in the proximal and middle thirds). However, only 24% of breaks occurred within the proximal section of the tail, where most fat is stored. Thus, although breaks were most frequent (50.8%) in the middle portion of the tail where up to 10% of caudal fat is stored, most tail breaks involved losses of no more than 10% (76% in the middle and distal thirds).

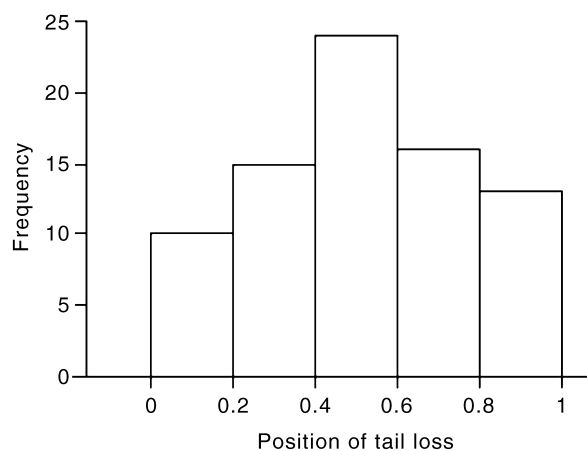


Fig. 3. Estimated position of tail breaks in *Niveoscincus metallicus* at Clarence Lagoon ($n = 78$). The mean break position is 0.51 (standard deviation = 0.243). 0 indicates a break located near the base of the tail and 1 indicates a break near the distal tip.

DISCUSSION

Caudal lipid reserves represented the major site (55–78% of total reserves) of energy storage in *N. metallicus*. Comparable values have been recorded for the skinks *Scincella laterale* (48–75%; Clark 1971) and *Eumeces* (50% in three species; Vitt & Cooper 1986), and the gecko *Coleonyx brevis* (60%; Dial & Fitzpatrick 1981). However, although caudal lipid stores may constitute a substantial proportion of the energy reserves in lizards, the majority of studies have relied solely on abdominal fat bodies to assess the size of energetic reserves. The relationship between the two fat stores in *N. metallicus* was generally consistent, except for pregnant females, which stored significantly less fat in the abdomen. This difference may represent variation in the deposition and utilization of each store (Derickson 1974), indicating the preferential use of abdominal fat for reproductive investment (Avery 1970; Smyth 1974). Alternatively, the low overall lipid reserves at this time may have distorted the relationship between abdominal and caudal fat stores. Clearly, however, studies that examine only one storage site to analyse reproductive investment in species with both abdominal and caudal stores may reach misleading conclusions.

Variation in energetic reserves

The study of energy stores and their utilization in relation to environmental variables and reproductive events has been used to enhance our knowledge of reptilian life histories and reproductive cycles (Derickson 1976; Olsson *et al.* 1997; Doughty & Shine 1998). Periods of reproductive investment are generally negatively correlated with fat body mass (e.g. Hahn & Tinkle 1965; Diaz *et al.* 1994; but see Wapstra & Swain 2001). Although an analysis of reproductive investment was not the primary purpose of our study, our data suggest that similar negative relationships exist in *N. metallicus*, at least for females. We found that females had greatly reduced abdominal reserves during gestation. They replaced these rapidly in autumn, even though they were then yolking follicles for the next year's litter. These changes indicate a large energetic investment associated with gestation in *N. metallicus*, as in other species (Birchard *et al.* 1984; Beuchat & Vleck 1990). Likewise, the relatively low fat reserves when the testes were enlarged in November may relate to the energetic cost of sperm production (Olsson *et al.* 1997). However, the apparent correlation between testes regression and both abdominal and tail lipid stores is probably spurious. It is not maintained in February to March and, more importantly, peak testes size was probably missed between November and February. Swain and Jones (1994) reported that testes

reached their maximum size in the late December – January period, during the period when lipid stores are rising. In *N. metallicus*, sperm are stored in the epididymides for mating in late autumn and early spring (Swain & Jones 1994), so the observed use of fat stores is not related to this activity.

Energetic reserves and tail loss

Despite the apparently high energetic 'value' of the tail, the majority of *N. metallicus* individuals at Clarence Lagoon exhibited evidence of tail damage. However, the high frequency of tail autotomy may be offset in *N. metallicus* by the proximal aggregation of caudal lipid stores and the infrequent occurrence of tail breaks that result in a substantial loss of fat. Although the accumulation of caudal fat reserves close to the body may represent a lipid conserving mechanism (Daniels 1985), such aggregation might be required to enable rapid mobilization of these fat stores during periods of reproductive investment or hibernation. This is supported by the increased aggregation of caudal lipid close to the body during late pregnancy in females. Alternatively, there may be insufficient space in the more distal sections of the tail to accommodate a substantial mass of fat.

The location of breaks was normally distributed along the length of the tail in our study population (Fig. 3). Several explanations might account for the relative lack of tail breaks at the extreme base and tip of the tail. Tail autotomy in lizards occurs through fracture planes located in caudal vertebrae because of a combination of muscle contraction and the external force supplied by the predator (Bellairs & Bryant 1985). However, fracture planes are absent near the tail base so as to protect major locomotory muscles and the hemipenes in males (Bellairs & Bryant 1985; Russell & Bauer 1992; Arnold 1994; Barbadillo *et al.* 1995; Zani 1996; Barbadillo & Bauwens 1997; Russell *et al.* 2001). Consequently, autotomy cannot occur at the extreme base of the tail. Moreover, the force required to break the tail at fracture planes increases with tail width (Fox *et al.* 1994), so more force is required to achieve autotomy at the most proximal fracture planes near the tail base. One of the major functions of the shed tail is to distract the predator while the lizard escapes (Arnold 1988). Because the effectiveness of the shed tail as a decoy depends both on its length and movement (Dial & Fitzpatrick 1983), autotomy near the tip of the tail may not be adequate to distract the predator. However, tail breaks generally occur near where it is grasped by the predator (but see Daniels 1985; Arnold 1988; for exceptions) and as a result the type of predator and predation efficiency (Medel *et al.* 1988) may influence the position of tail loss.

Considered together, the aggregation of caudal fat

stores and their infrequent loss during autotomy in natural situations may provide an explanation for how the strategies of autotomy and caudal fat storage can be combined in *N. metallicus* and other lizards. Although the overall probability of some lipid depletion from tail loss is high in *N. metallicus*, the likelihood of substantial loss is comparatively low. Consequently, *N. metallicus* appears able to retain an effective anti-predation strategy with minimal direct cost in terms of energy stores. However, although this particular cost of autotomy may be limited, there may be other costs associated with, for example, thermoregulation, social standing or locomotion, and the cost of regenerating the tail may be substantial. *Niveoscincus metallicus* provides an excellent model for investigating these possibilities.

ACKNOWLEDGEMENTS

We thank Colin McCoull for his assistance in the field and developing the ether treatment technique and Leon Barmuta for statistical advice. Paul Doughty provided constructive criticism on an earlier draft of this manuscript. This study was conducted under Animal Ethics Permit No. A0005657 from the University of Tasmania.

REFERENCES

- Arnold E. N. (1988) Caudal autotomy as a defense. In: *Biology of the Reptilia*, Vol. 16 (eds C. Gans & R. B. Huey) pp. 236–73. Alan Liss, New York.
- Arnold E. N. (1994) Investigating the evolutionary effects of one feature on another: Does muscle spread suppress caudal autotomy in lizards? *J. Zool.* **232**, 505–23.
- Avery R. A. (1970) Utilization of caudal fat by hibernating common lizards, *Lacerta vivipara*. *Comp. Biochem. Physiol.* **37**, 119–21.
- Ballinger R. E., Nietfeldt J. W. & Krupa J. J. (1979) An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). *Herpetologica* **35**, 114–16.
- Ballinger R. E. & Tinkle D. W. (1979) On the cost of tail regeneration to body growth in lizards. *J. Herpetol.* **13**, 374–5.
- Barbadillo L. J. & Bauwens D. (1997) Sexual dimorphism of tail length in lacertid lizards: test of morphological constraint hypothesis. *J. Zool.* **242**, 473–82.
- Barbadillo L. J., Bauwens D., Barahona F. & Sanchez-Herraz M. J. (1995) Sexual differences in caudal morphology and its relation to tail autotomy in lacertid lizards. *J. Zool.* **236**, 83–93.
- Bellairs d'A. A. & Bryant S. V. (1985) Autotomy and regeneration in reptiles. In: *Biology of the Reptilia*, Vol. 15 (ed. C. Gans) pp. 301–410. John Wiley & Sons, New York.
- Beuchat C. A. & Vleck D. (1990) Metabolic consequences of viviparity in a lizard, *Sceloporus jarrovi*. *Physiol. Zool.* **63**, 555–70.
- Birchard G. F., Black C. P., Schuett G. W. & Black W. (1984) Influences of pregnancy on oxygen consumption, heart rate and hematology in the garter snake, implications for the 'cost of reproduction' in live bearing reptiles. *Comp. Biochem. Physiol.* **77A**, 519–23.
- Clark D. R. (1971) The strategy of tail autotomy in the ground skink, *Lygosoma laterale*. *J. Exp. Zool.* **176**, 295–302.
- Cogger H. G. (1992) *Reptiles and Amphibians of Australia*. Reed Books, Sydney.
- Congdon J. D., Vitt L. J. & King W. W. (1974) Geckos: Adaptive significance and energetics of tail autotomy. *Science* **184**, 1379–80.
- Daniels C. B. (1984) The importance of caudal fat in the gecko *Phyllodactylus marmoratus*. *Herpetologica* **40**, 337–44.
- Daniels C. B. (1985) Economy of autotomy as a lipid conserving mechanism: An hypothesis rejected for the gecko *Phyllodactylus marmoratus*. *Copeia* **1985**, 468–72.
- Daniels C. B., Flaherty S. P. & Simbotwe M. P. (1986) Tail size and effectiveness of autotomy in a lizard. *J. Herpetol.* **20**, 93–6.
- Derickson W. K. (1974) Lipid deposition and utilization in the sagebrush lizard, *Sceloporus graciosus*: Its significance for reproduction and maintenance. *Comp. Biochem. Physiol.* **49A**, 267–72.
- Derickson W. K. (1976) Lipid storage and utilization in reptiles. *Am. Zool.* **16**, 711–23.
- Dial B. E. & Fitzpatrick L. C. (1981) The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia* **51**, 310–17.
- Dial B. E. & Fitzpatrick L. C. (1983) Lizard tail autotomy: Function and energetics of postautotomy tail movement in *Scincella lateralis*. *Science* **219**, 391–3.
- Dial B. E. & Fitzpatrick L. C. (1984) Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria: Scincidae). *Anim. Behav.* **32**, 301–2.
- Diaz J. A., Alonso-Gomez A. L. & Delgado M. J. (1994) Seasonal variation of gonadal development, sexual steroids, and lipid reserves in a population of the lizard *Psammmodromus algirus*. *J. Herpetol.* **28**, 199–205.
- Doughty P. & Shine R. (1998) Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology* **79**, 1073–83.
- Downes S. & Shine R. (2001) Why does tail loss increase a lizard's later chances of being consumed by snake predators? *Ecology* **82**, 1293–303.
- Dufaure J. P. & Hubert J. (1961) Table de developpement du lezard vivipare: *Lacerta (Zootoca) vivipara* Jacquin. *Arch. Anat. Micr. Morph. Exp.* **50**, 309–28.
- Edmunds M. (1974) *Defense in Animals: A Survey of Anti-Predator Defenses*. Longman, New York.
- Formanowicz D. R., Brodie E. D. & Bradley P. J. (1990) Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*. *Anim. Behav.* **40**, 782–4.
- Fox S. F. & McCoy K. J. (2000) The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana*. *Oecologia* **122**, 327–34.
- Fox S. F., Perea-Fox S. & Castro Franco R. (1994) Development of the tail autotomy adaptation in lizards under disparate levels of predation at high and low elevations in Mexico. *Southwest. Nat.* **39**, 311–22.
- Fox S. F. & Rostker M. A. (1982) Social cost of tail loss in *Uta stansburiana*. *Science* **218**, 692–3.
- Greer A. E. (1986) On the absence of visceral fat bodies within a major lineage of scincid lizards. *J. Herpetol.* **20**, 267–9.
- Hahn W. E. & Tinkle D. W. (1965) Fat body cycling and experimental evidence for its adaptive significance to ovarian

- follicle development in the lizard *Uta stansburiana*. *J. Exp. Zool.* **158**, 79–86.
- Jones S. M. & Swain R. (1996) Annual reproductive cycle and annual cycles of reproductive hormones in plasma of female *Niveoscincus metallicus* (Scincidae) from Tasmania. *J. Herpetol.* **30**, 140–6.
- Martin J. & Avery R. (1998) Effects of tail loss on the movement patterns of the lizard, *Psammodromus algirus*. *Funct. Ecol.* **12**, 794–802.
- Martin J. & Salvador A. (1993) Tail loss reduces mating success in the Iberian rock lizard, *Lacerta monticola*. *Behav. Ecol. Sociobiol.* **32**, 185–9.
- Medel R. G., Jimenez J. E., Fox S. F. & Jaksic F. M. (1988) Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos* **53**, 321–4.
- Melville J. & Swain R. (1997) Daily and seasonal activity patterns in two species of high altitude skinks, *Niveoscincus microlepidotus* and *N. metallicus*, from Tasmania. *J. Herpetol.* **31**, 29–37.
- Melville J. & Swain R. (1999) Habitat associations and natural history of the Tasmanian 'snow skinks' (*Niveoscincus* spp.). *Pap. Proc. R. Soc. Tas.* **133**, 57–64.
- Niewiarowski P. H., Congdon J. D., Dunham A. E., Vitt L. J. & Tinkle D. W. (1997) Tales of lizard tails: Effects of tail autotomy on subsequent survival and growth of free-ranging hatchling *Uta stansburiana*. *Can. J. Zool.* **75**, 542–8.
- Olsson M., Madsen T. & Shine R. (1997) Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proc. R. Soc. Lond. B.* **264**, 455–9.
- Punzo F. (1982) Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. *J. Herpetol.* **16**, 329–31.
- Robinson M. H., Abele L. G. & Robinson B. (1970) Attack autotomy: A defense against predators. *Science* **169**, 301–2.
- Roth V. D. & Roth B. M. (1984) A review of appendotomy in spiders and other arachnids. *Bull. Br. Arachnol. Soc.* **6**, 137–46.
- Russell A. P. & Bauer A. M. (1992) The m.caudifemoralis longus and its relationship to caudal autotomy and locomotion in lizards (Reptilia: Sauria). *J. Zool.* **227**, 127–43.
- Russell A. P., Bergmann P. J. & Barbadillo A. J. (2001) Maximal caudal autotomy in *Podarcis hispanica* (Lacertidae): The caudofemoralis muscle is not sundered. *Copeia* **2001**, 154–63.
- Smith G. R. (1996) Tail loss in the striped plateau lizard, *Sceloporus virigatus*. *J. Herpetol.* **30**, 552–5.
- Smyth M. (1974) Changes in fat stores of the skinks *Morethia boulengeri* and *Hemiergus peronii* (Lacertilia). *Aust. J. Zool.* **22**, 135–45.
- Swain R. & Jones S. M. (1994) Annual cycle of plasma testosterone and other reproductive parameters in the Tasmanian skink, *Niveoscincus metallicus*. *Herpetologica* **50**, 502–9.
- Tinkle D. W. (1967) The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Pub. Mus. Zool. Univ. Michigan.* **132**, 1–182.
- Vitt L. J., Congdon J. D. & Dickson N. A. (1977) Adaptive strategies and energetics of tail autotomy in lizards. *Ecology* **58**, 326–37.
- Vitt L. J. & Cooper W. E. (1986) Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): Age specific differences in costs and benefits. *Can. J. Zool.* **64**, 583–92.
- Wake D. B. & Dresner I. G. (1967) Functional morphology and evolution of tail autotomy in salamanders. *J. Morph.* **122**, 265–306.
- Wapstra E. & Swain R. (2001) Reproductive correlates of abdominal fat body mass in *Niveoscincus ocellatus*, a skink with an asynchronous reproductive cycle. *J. Herpetol.* **35**, 403–9.
- Wilson B. S. (1992) Tail injuries increases the risk of mortality in free-living lizards (*Uta stansburiana*). *Oecologia* **92**, 145–52.
- Wilson R. S. & Booth D. T. (1998) The effect of tail loss on reproductive output and its ecological significance in the skink *Eulamprus quoyii*. *J. Herpetol.* **32**, 128–31.
- Zani P. A. (1996) Patterns of caudal autotomy evolution in lizards. *J. Zool.* **240**, 210–20.