
‘Costs’ of Caudal Autotomy in the Metallic Skink, *Niveoscincus metallicus*



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ABSTRACT

Caudal autotomy is a defensive mechanism utilised by squamate reptiles to survive predatory attacks. Although tail loss is an effective escape mechanism in lizards, autotomy may result in severe 'costs' being inflicted upon the animal. However, since the tail is capable of regeneration, these 'costs' may only be transient. An animal's ability to balance the costs and benefits of autotomy determines the adaptive advantage of tail loss. The locomotory, thermoregulatory, energetic, reproductive and behavioural 'costs' of caudal autotomy were investigated in the metallic skink, *Niveoscincus metallicus*.

Niveoscincus metallicus is a small ground-dwelling skink that inhabits a wide range of microhabitats. It is a viviparous species that possesses a sinusoidal locomotory mode, and both caudal and abdominal fat reserves. High levels of tail loss are evident in most populations. Caudal autotomy was found to have two main impacts on *N. metallicus*: 1) restriction of mobility; and 2) depletion of energetic reserves. However, the species was found to possess several behavioural and anatomical modifications to limit the 'costs' incurred.

Tail autotomy was found to severely restrict locomotory performance in *N. metallicus*. Terrestrial locomotion, sprinting and stamina, was found to be preferentially inhibited by caudal autotomy. Climbing ability was not affected by tail loss. In females, locomotory inhibition caused by caudal autotomy was relatively short-lived. However, in males there was no evidence of restoration of locomotory performance during this study. This was the first investigation of the temporal impact of caudal autotomy on performance in lizards.

Behavioural modification was evident following caudal autotomy. Tailless *N. metallicus* were found to compensate for diminished locomotory abilities by selecting more cryptically located basking sites and remaining closer to refuge. This modification of basking preference was assumed to be the result of the animal adopting an alternative defensive strategy.

Thermoregulatory behaviour was not modified following tail loss. However, females were found to lower their thermal preferences during gestation, presumably to enhance embryonic development. It was concluded that reproductive success represented higher priority than tail regeneration.

Niveoscincus metallicus was demonstrated to store the majority (~50-75%) of its energetic reserves in its tail. Most (~90%) of these reserves were located within the proximal third of the tail. Depletion of abdominal fat stores was found to be related to periods of reproductive investment. There was some evidence that abdominal fat reserves were preferentially allocated to reproductive effort.

Caudal autotomy during vitellogenesis was associated with a reduction in the clutch size of tailless females. This reduced reproductive investment was related to the diversion of energy towards tail regeneration rather than the direct depletion of caudal fat stores. These tailless females were found to modify their reproductive strategy by producing a smaller number of larger and 'better' quality offspring. However, tail autotomy during gestation did not influence the weight or size of offspring. Maternal tail size and the presumed environment during gestation was not related to the phenotype of a female's offspring.

The frequency and position of tail loss were found to vary between altitudes and populations. Predation pressure or basking behaviour failed to explain these differences. Predation efficiency, frequency of repeated tail breaks and the age structure of the population all appeared to be related to the frequency and position of tail loss. *Niveoscincus metallicus* was found to be capable of 'economy of autotomy', preferentially losing the more distal portions of its tail that do not contain significant fat stores.

It is concluded that caudal autotomy inflicts several costs on *N. metallicus*. However, the existence of behavioural and anatomical modifications limits the impacts of these 'costs'. This study suggests that the costs and benefits of caudal autotomy have co-evolved in *N. metallicus*, allowing it retain a successful defensive mechanism while limiting the associated 'costs'.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

An animal's ability to evade and subsequently survive predatory attacks is central to its survival. Behaviours that enhance the likelihood of successful escape will be adaptively advantageous and may therefore be expected to be the result of strong selection pressures. Autotomy, the sacrifice of expendable body portions during predatory encounters, exemplifies such a behaviour (Bellairs and Bryant 1985). Among squamate reptiles this process is referred to as caudal autotomy, since the tail is the autotomised structure (Arnold 1988). Caudal autotomy is an ancestral feature within squamates; however, the loss or partial loss of the ability to shed the tail has occurred in several lineages (e.g. agamids, chamaeleons, varanids, and iguanids) over the course of evolution (Arnold 1984, 1988). Skinks, geckos and lacertids constitute the vast majority of species that are capable of caudal autotomy (Arnold 1984, 1988).

The basic premise of caudal autotomy in lizards is that the tail is shed when the animal is grasped by a predator during a predatory encounter. This acts both to release the lizard from its pursuer and to divert the attention of the predator while the lizard escapes (Arnold 1988). The evolution in certain species of accompanying behaviours and morphological traits has enhanced the effectiveness of tail autotomy. For example, accentuating behavioural displays, colour markings and the 'offering' of the tail may all serve to direct the focus of the predatory attack towards the tail (Cooper and Vitt 1985, Daniels *et al.* 1986, Arnold 1988). The detached tail usually writhes violently, providing a decoy that maintains the attention of the predator. Such thrashing tails confuse the predator, leaving it in two minds whether to continue to pursue the injured prey or consume the small morsel of food left behind (Arnold 1988). If the latter option is chosen, the furious movements of the shed tail increase its handling time, providing the wounded lizard with the extra moments necessary in order to make its escape (Dial and Fitzpatrick 1983, Arnold 1988).

Staged predatory encounters within the confines of a laboratory highlight the effectiveness of caudal autotomy as an escape mechanism. Tailed lizards are able to divert the attack of a predator away from the essential head and body, using autotomy to make a successful getaway (Dial and Fitzpatrick 1984, Daniels *et al.* 1986). However, tailless lizards without the option of autotomy are usually the subject of fatal predatory attacks focused towards the head and body (Daniels *et al.* 1986). Although caudal autotomy does not always result in escape, it appears that enough individuals do benefit from it to make it worthwhile (Arnold 1988). This is evidenced by the high frequency of tail loss exhibited in most natural populations and the high regularity of detached tails, but not their owners, in the stomachs and crops of predators (Arnold 1988).

The ingenious simplicity of caudal autotomy masks the complex underlying anatomical and physiological modifications that have evolved in order to facilitate it. Tail autotomy is made possible by pre-determined sites of weakness within the caudal vertebrae and associated fracture planes within the surrounding soft tissues and skin (Bellairs and Bryant 1985). These adaptations result in the potentially violent and rapid detachment of the tail occurring with minimal blood loss and tissue trauma (Bellairs and Bryant 1985). The healing process begins immediately with extensive immunological reactions, and the formation of a scab on the tail stump within 48 h (Bellairs and Bryant 1985). Most species also possess impressive tail regeneration abilities, and are capable of completely replacing the tail within 2-12 months (Bellairs and Bryant 1985). Although the regenerated tail possesses structurally homologous muscle and soft tissue structures, a cartilaginous rod replaces the caudal vertebrae (Bellairs and Bryant 1985). The replacement cartilage may be less flexible than the preceding caudal vertebrae, potentially limiting the tail's effectiveness in locomotion and subsequent predatory encounters (Arnold 1988).

Caudal autotomy, despite its undeniable benefit, appears to be a rather paradoxical defensive mechanism. Tail loss may have a wide range of consequences in lizards in areas such as locomotory ability, reproduction, energetics, thermoregulation and subsequent survival (see Arnold 1988 for review). There are two main elements of these 'costs': reduced mobility following tail loss; and depletion of caudal energy reserves.

In lizards, caudal fat reserves may represent the primary or a supplementary source of energetic stores. Besides reducing the total available energy reserves, tail autotomy imposes a severe energetic 'cost' to fuel the process of tail regeneration (Bellairs and Bryant 1985). In order to supply the lipids required for tail regeneration, energy stores that would otherwise be available for reproductive effort and body growth are diverted into caudal replacement (Ballinger and Tinkle 1979, Dial and Fitzpatrick 1981, Arnold 1988). Habitat use, food intake and thermoregulatory behaviour may all be altered to compensate for the shortfall in energy supplies and create the optimal environment for regeneration to occur at its maximal rate (Martin and Salvador 1992, 1993a, b; Martin and Avery 1997).

In the majority of lizards, the tail is intimately involved in the regulation of stride frequency and the attainment of maximal speed (Hamley 1990, Ritter 1992, Martin and Avery 1998). Its absence has been shown to significantly retard locomotory performance (Ballinger *et al.* 1979, Punzo 1982, Formanowicz *et al.* 1990). Such inhibition of movement results in a cascade of indirect costs which have important implications for activity (Formanowicz *et al.* 1990, Martin and Avery 1998), resource and habitat use (Martin and Salvador 1992), home range size and access to partners, (Martin and Salvador 1993c; Salvador *et al.* 1995, 1996), and both foraging and escape tactics (Martin and Salvador 1993b, Martin and Avery 1997). These secondary costs have received infrequent attention by most authors. However, much insight can be gained from the extensively researched area concerning the 'costs' of reproduction in viviparous lizards. This research area parallels that observed with caudal autotomy, as both result in a reduction in locomotory performance (e.g. Shine 1980), with the possibility of flow-on effects such as those listed above (e.g. Schwarzkopf and Shine 1992).

Despite the numerous and substantial 'costs' incurred by an individual as a result of caudal autotomy, tail loss occurs at an unerringly high frequency in nature. As long as the benefit gained from autotomy outweighs the costs incurred, the strategy of caudal autotomy becomes adaptively advantageous (Arnold 1988). Therefore, in order to achieve a comprehensive understanding of the process, the relative values of the costs

and benefits need to be quantified. However, due to the relatively fixed nature of the benefit of autotomy, i.e. the survival of an immediate predatory encounter, most research in this area has been directed towards the costs of tail loss. The ‘costs’ of caudal autotomy are potentially numerous, and may persist for the rest of the individual’s life. Through the study and quantification of these costs, it is anticipated that the magnitude of the benefit of caudal autotomy can be defined. If Arnold’s (1988) argument is correct, the repeated quantification of the ‘costs’ of tail loss will allow the benefit of such an action to be assessed. The benefit will narrowly exceed the maximum total cost incurred. This research thesis sets out to quantify the potential ‘costs’ of caudal autotomy using the metallic skink, *Niveoscincus metallicus*, as a model species.

1.2 NIVEOSCINCUS METALLICUS AS A MODEL SPECIES

The metallic skink, *Niveoscincus metallicus*, was selected as the model species for this thesis. There are several aspects of the biology and ecology of this species that make it suitable for this purpose.

- 1) Many aspects of the biology and ecology of *Niveoscincus metallicus* have been extensively investigated (e.g. Melville 1994, 1998; Swain and Jones 1994, 1997; Jones and Swain 1996; Melville and Swain 1997a, b, 1999b, in press; McCoull in prep).
- 2) *Niveoscincus metallicus* is capable of losing its tail at any point along its length. The frequency of tail loss in the species can be high and variable between populations (R. Swain, unpublished data).
- 3) The metallic skink is not an aggressive species, so tail loss is more likely to be an indicator of predation than the result of intraspecific aggression (Vitt *et al.* 1974, Jennings and Thompson 1999).
- 4) The widespread distribution of the species and its abundance in the majority of habitats up to the alpine treeline (Rawlinson 1974; Melville and Swain 1997a, b, 1999b), means that the variation in the frequency of tail loss exhibited across its range may be correlated with different predator types and predation intensities.

- 5) As a predominately ground-dwelling species, this animal relies on a sinusoidal mode of locomotion that depends heavily on the tail (Melville 1998). Tail autotomy, therefore, has the potential to inflict substantial locomotory costs.
- 6) *Niveoscincus metallicus* is a shuttling heliotherm that behaviourally regulates its body temperature. It inhabits a wide variety of habitats where it basks both overtly and cryptically, providing substantial potential for individuals to alter their thermoregulatory behaviour in response to tail loss (Melville and Swain 1997a).
- 7) Both abdominal and caudal fat stores, believed to be utilised in general somatic growth and reproduction, are present in *Niveoscincus metallicus*. Thus, tail loss could have important energetic costs on this species.
- 8) The species is viviparous and the 3-4 month gestation period (Jones and Swain 1996, Swain and Jones 1997) enhances the possibility of tail loss resulting in some degree of reduced reproductive output or offspring quality.
- 9) *Niveoscincus metallicus* possesses some degree of facultative placentotrophy (Thompson *et al.* 1999a; Swain and Jones in press a), with maximal placental nourishment occurring during late pregnancy. Tail autotomy at this stage has the potential to influence the subsequent size of the offspring due to reduced levels of facultative placentotrophy.

1.3 THE GENUS *NIVEOSCINCUS*

Skinks constitute the majority of the otherwise impoverished Tasmanian reptilian fauna (Heatwole 1976). Tasmania, Australia's most southerly and only island state, possesses a cool to cold temperate climate which supports eighteen species of lizards (17 skinks, 1 agamid) and three species of snake (Elapidae).

Until recently, substantial confusion surrounded the taxonomic relationships among the Tasmanian lizard fauna. However, several taxonomic studies by Hutchinson and co-workers (Hutchinson *et al.* 1988, 1989, 1990; Hutchinson and Schwaner 1991) resulted in several members of the genus *Leiolopisma* being assigned to the newly erected and largely Tasmanian genus, *Niveoscincus* ('snow skinks'). Eight species are currently recognised, six of which (*N. microlepidotus*, *N. greeni*, *N. ocellatus*, *N. orocryptus*, *N. palfreymani* and *N. pretiosus*) are endemic to Tasmania. The distribution of *N.*

metallicus extends from Tasmania to the south-eastern corner of Victoria, while *N. coventryi* is the only member of the genus restricted to the Australian mainland, occurring in a small area of south-eastern Victoria. Until as recently as the start of the last decade, the only substantial work on the snow skinks was provided by Rawlinson (1974), but this predated the revised taxonomy. However, there is now an extensive amount of recent literature on phylogenetic relationships (Hutchinson *et al.* 1988, 1990, Hutchinson and Schwaner 1991, Melville 1998; Melville and Swain 1998, in press), ecology and behaviour (Wapstra and Swain 1996; Melville and Swain 1997a, b, 1999a, b, in press), and reproductive ecology and physiology (Swain and Jones 1994, 1997, in press a, b; Jones and Swain 1996; Jones *et al.* 1997, 1998; Olsson and Shine 1998a, b, 1999; Wapstra *et al.* 1999; Thompson *et al.* 1999a, Olsson *et al.* 2000, Wapstra in press).

1.4 NIVEOSCINCUS METALLICUS

Members of the genus *Niveoscincus* are small to medium sized lygosome lizards, characterised by the possession of a well developed prefrontal shield, paired or fused frontoparietals, a distinct prefrontal shield, and a moveable lower eyelid with a moderate to large transparent palpebral disc (Hutchinson *et al.* 1989). All members of the genus possess well-developed pentadactyl limbs and a viviparous mode of reproduction (Hutchinson *et al.* 1989, 1990).

The metallic skink, *Niveoscincus metallicus*, is the most widely distributed member of the genus with its distribution extending across the majority of Tasmania and its coastal islands, Bass Strait islands and the south-eastern corner of Victoria. Predominately ground dwelling in nature, it inhabits a diverse range of habitats that extend over a broad altitudinal range (sea level to 1415 m a.s.l.) from dry sclerophyll woodlands to subalpine heaths (Melville and Swain 1999b). It is well adapted to disturbed habitats and is commonly found in large abundance in suburban gardens and roadside vegetation. *Niveoscincus metallicus* is a relatively cryptic species that occupies shaded microhabitats with medium to dense vegetation cover, soil, and thick litter (Melville and Swain 1999b). It is an active forager with a largely arthropod-based diet, spending a large proportion of time foraging amongst the undergrowth (Melville and Swain 1999b). Despite its apparent requirement for some degree of arboreal vegetation (Rawlinson

1974), it remains largely confined to the leaf litter, only climbing onto rocks or logs to bask (Melville and Swain 1997a, 1999b). It is a shuttling heliotherm with an active diurnal pattern; utilising both rocks and logs close to the ground to behaviourally thermoregulate (Melville and Swain 1997a).

Niveoscincus metallicus is one of the smaller members of the genus with an adult snout-vent length (SVL) of 45-65 mm, weighing 2-5 g, with a tail that can reach up to 130-140% of the SVL (Chapter 7). Its colour and markings are highly variable, ranging from brown to dark black (dorsal surface), with vertebral strips or flecks and a mid-lateral streak. Due to its distribution over a wide range of habitats and areas, *N. metallicus* co-exists with most other members of the genus. However, it is distinguished from other members of the genus by the presence of large mid-body scales (22-29 rows) and possession of a long slender body with relatively small limbs. The second feature allows it to co-exist with the other members of the genus, which are largely saxicolous or arboreal in nature (Melville and Swain in press).

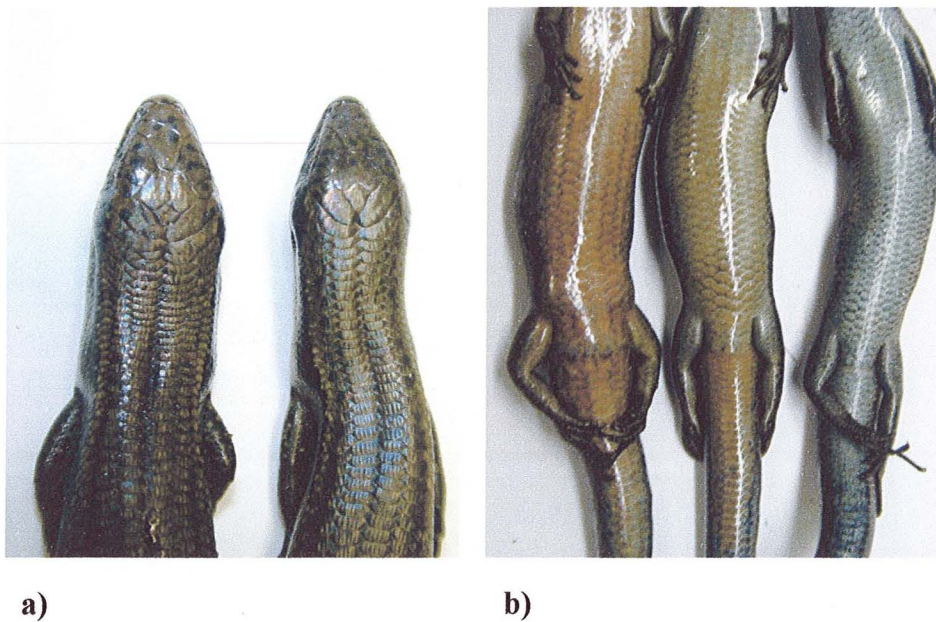


Figure 1.1 Sexual dimorphism in *N. metallicus*. a) males (left) have broader heads and wider necks compared to females (right); b) ventral colouration of males (left) is generally more intense than females (middle and right), and cloacal opening also wider in males than females.

A degree of sexual dimorphism is present amongst adults of the species. Males generally attain longer and larger body sizes, possess more pronounced heads than females and generally have more intensive ventral colouration (Figure 1.1). The significance of such colouration is unknown (Swain and Jones 1994). However, the eversion of the hemipenes remains the only highly reliable method for sex determination in this species. *Niveoscincus metallicus* is an annual breeding viviparous skink, with clutch sizes generally ranging from 1-8 (average 3.5-4) (Rawlinson 1974, Jones and Swain 1996).

Like all other members of the genus, the metallic skink exhibits an asynchronous reproductive cycle (Swain and Jones 1994, Jones and Swain 1996). Vitellogenesis begins in late summer (February), the first matings occur in April with sperm stored overwinter by females until ovulation and fertilisation occurs in spring (September) following emergence (Jones and Swain 1996). A second mating period may occur after emergence (Swain and Jones 1994, Jones and Swain 1996). Gestation is completed by late December to early February depending on environmental conditions (Figure 1.2).

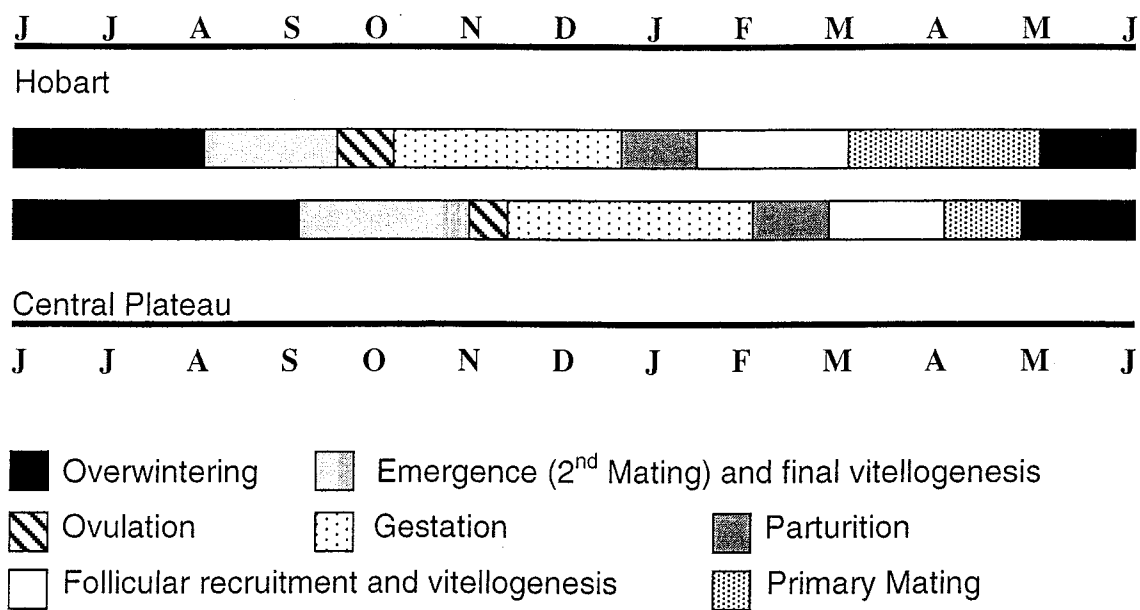


Figure 1.2 Asynchronous timing of female reproductive events for *N. metallicus* populations at Hobart and the Central Plateau (adapted from Jones and Swain 1996, C. McCoull, pers. comm.).

Young are fully developed and independent at birth and range from 15-25 mm SVL and parental care is absent (Bennett 1997, C. McCoull, pers. comm.). *Niveoscincus metallicus* exhibits both lecithotrophy and placentotrophy (Jones *et al.* 1998), and the presence of facultative placentotrophy has also been demonstrated (Swain and Jones in press a).

1.5 RESEARCH OBJECTIVES

The primary aim of this research thesis is to identify and quantify the locomotory, energetic, behavioural, reproductive and ecological ‘costs’ associated with caudal autotomy in the metallic skink, *Niveoscincus metallicus*. *Niveoscincus metallicus* was considered to be an ideal model species for such an investigation (Section 1.2). A number of laboratory based investigations along with a field based study were instigated in order to achieve the major aim of the project. These were based on a series of questions that were deemed to be fundamental.

- 1) Does caudal autotomy inhibit locomotory performance? (Chapter 3)
- 2) Does tail loss result in modified thermoregulatory behaviour? (Chapter 4)
- 3) How important is the tail for fat storage, and in what manner is the fat distributed along the length of the tail? (Chapter 5)
- 4) Are energetic costs imposed by the loss of caudal fat reserves? (Chapter 5)
- 5) Do juveniles with tail loss experience inhibited growth rates or survival? (Chapter 5)
- 6) Does maternal tail loss influence clutch size or offspring fitness? (Chapter 6)
- 7) Does the frequency or nature of tail loss vary between different habitats? (Chapter 7)
- 8) Do tailless lizards modify their behaviour towards crypsis to reduce the probability of predation? (Chapter 7)

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 DESCRIPTION OF STUDY SITE

Tasmania is Australia's most southerly and only island state, separated from the south-east tip of mainland Australia by a 200 km stretch of water, known as Bass Strait. It is situated between latitudes 40 and 43.5°S and longitudes 140-150°E and experiences a cool to cold temperate, and largely unpredictable, maritime climate.

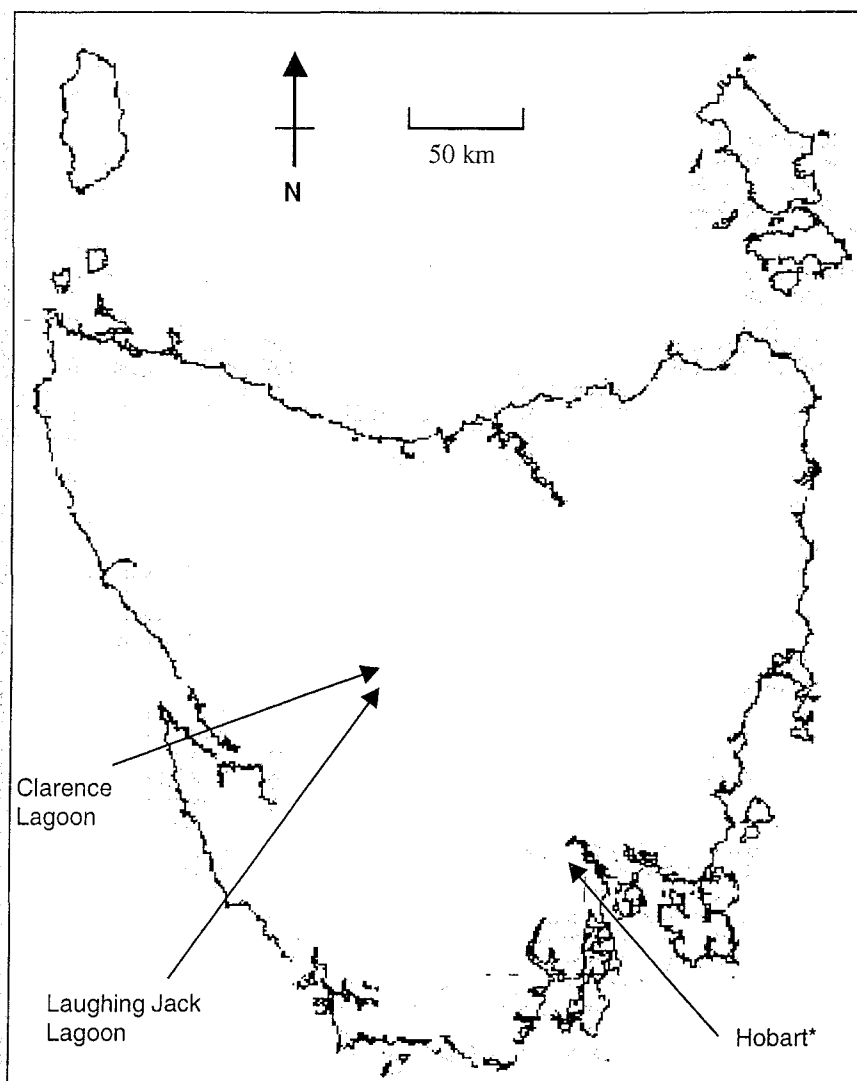


Figure 2.1 Map of Tasmania showing the location of the field sites. The asterisk (*) indicates that the South Hobart and Dynnyrne field sites (refer to Chapter 7) are at the same locality.

All animals used in the course of this study for laboratory purposes were collected from around Clarence Lagoon (146°19'E 42°04'S), a small glacial lake located approximately 1000 m a.s.l. on the edge of the Central Plateau World Heritage area in Central Tasmania (Figure 2.1). However, a second Central Plateau field site and two localities in Hobart were also used in Chapter 7 (Figure 2.1). Clarence Lagoon is situated behind the remnants of a glacial moraine and the southern shore is lined with a narrow band of dolerite boulders. Like most of the Central Plateau, it is characterised by extreme and unpredictable weather, with the possibility of snow in every month of the year. The annual rainfall is high, with daytime temperature ranges of 9.6-22.3 °C in summer and 3-11.8 °C in winter. Shallow soil surrounds the lake, allowing large dolerite boulders to break through to the surface in many areas. The site consists of a number of interwoven microhabitats, including subalpine heaths and forests, tall mixed forests, open sclerophyll, rainforests and rock screes (Figure 2.2).

The vegetation in each habitat may differ markedly, with subtle differences in ground vegetative cover, canopy cover, sunlight and temperature within each microhabitat. However, *N. metallicus* appears to be able to readily move between, and utilise, all available microhabitats (pers. obs.). The area is largely undisturbed, due mainly to the difficulty of access for visitors and the general public. The metallic skink, *Niveoscincus metallicus*, is present in extremely high numbers at the site. Several other reptiles, such as *N. pretiosus*, *N. ocellatus*, *Drysdala coronoides* (white-lipped snake) and *Notechis ater* (tiger snake), are also commonly found at Clarence Lagoon.



Figure 2.2 The field site at Clarence Lagoon
a) Sub-alpine heathland and dolerite boulders by the lagoon edge
b) High altitude woodland in from the lagoon edge
c) Rainforest habitat in enclosed areas

2.2 LIZARD COLLECTING TECHNIQUES

Two methods were implemented in order to collect animals during the course of the study. The primary method of capture involved the use of a 'noosegun', a modified fishing rod with a loop of fishing line at the tip which acted as the noose. The noose was positioned around the lizard's head and quickly tightened. The animal was either retrieved from the noose by hand or released into a bucket. This method proved to be the most reliable method of capture at all field sites; however, its use was restricted to overtly and covertly basking lizards. Capture by hand was the other method used, mainly in combination with noosing to catch animals that fell from the noose or fled under rocks during a noosing attempt.

Once lizards were collected, they were transported back to the laboratory in plastic containers with ample leaf litter and cover. A total of about 200 animals were collected from Clarence Lagoon, while a further 368 lizards were caught and immediately released from 4 field sites during the course of the project (see Chapter 7). The removal of this number of animals had no observable impact on the population and, where possible, animals and their young born in captivity were released at the site of capture at the completion of the project. On return to the laboratory lizards were housed under standard laboratory conditions (Section 2.3).

2.3 GENERAL LABORATORY HOUSING

The majority of the lizards used in laboratory investigations were kept in the School of Zoology lizard housing facility (Figure 2.3). Fluorescent lighting within the housing area provided 14 h of light each day at an intensity of ~20 000 lux. An air-conditioning system maintained the ambient room temperature around 12-14° C. Animals were housed in groups of up to five in plastic terraria (20 x 30 x 10 cm) with a mesh cover and an absorbent substrate. *Niveoscincus metallicus* is not an aggressive species and commonly basks in social groups of up to 5-6 (pers. obs.), allowing this number to be housed together in the laboratory without any incidence of aggression. Basking surfaces, in the form of upturned terracotta pots that also provided cover, were placed under 25W basking lights controlled by automatic timers which provided

10 h of basking light per day. The basking light, which was suspended over one end of the terrarium, created a temperature gradient of 12-35° C within each container. All adult lizards were fed 2-3 times weekly on a diet of mealworms (*Tenebrio larvae*), catfood and mashed banana. Water was available *ad libitum*. These conditions will be referred to as standard housing conditions.

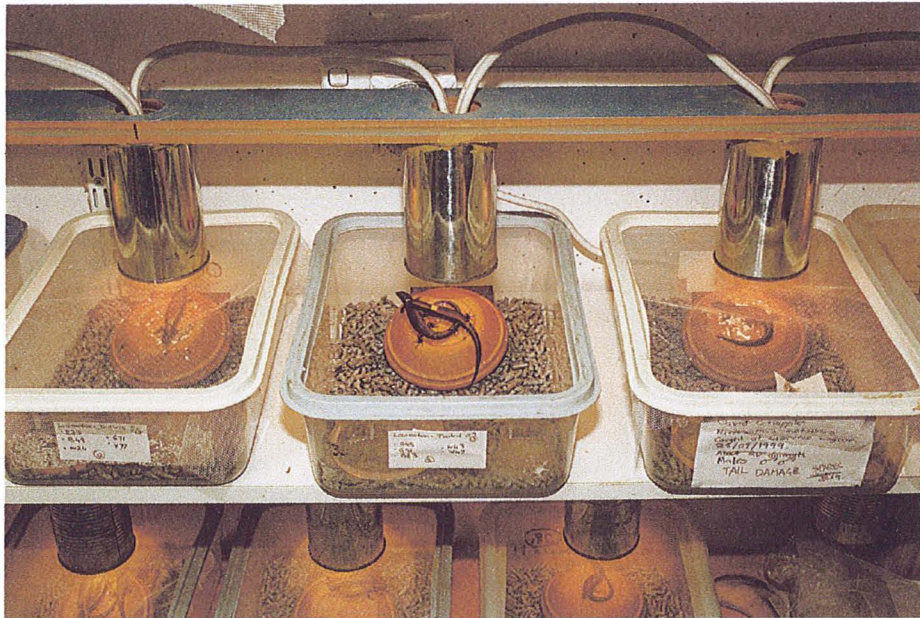


Figure 2.3 Laboratory housing conditions

2.4 JUVENILE HOUSING CONDITIONS

All pregnant females used in laboratory experiments gave birth during the course of the project. Maternal housing terraria were checked once or twice daily for newborns. Once females had given birth, they were gently palpated to confirm that parturition was complete. The newborns were removed from the cage and measurements taken of clutch size, offspring weight (± 0.1 mg), snout-vent length (distance from snout to cloacal opening ± 0.1 mm) and tail length (± 0.1 mm). The sprint speed at birth was also recorded (m sec^{-1}) (Chapters 3 and 6).

Newborns were housed in plastic terraria (30 x 20 x 10 cm) with a maximum of 4-6 individuals per terrarium. The basking lights were as described in Section 2.3, and all individuals appeared to gain equal access to basking surfaces and food. Juveniles were fed daily on a diet of mashed banana and catfood, which was placed undercover

to encourage feeding and ensure maximal growth. Water was available *ad libitum*. Most juveniles were held until the first available opportunity for release at the site of maternal capture. However, some juveniles were retained in the laboratory for use in a number of experiments.

CHAPTER 3

LOCOMOTORY PERFORMANCE

3.1 INTRODUCTION

The ability of an animal to navigate its way effectively through its environment is crucial to its daily survival and capacity to function normally. The behavioural traits and locomotory performance abilities that allow animals to utilise their environment are believed to be the result of continual selection pressures (Arnold 1983, Garland and Losos 1994, Bauwens *et al.* 1995). In lizards, morphology and locomotory performance are intimately related, and an animal's limb and body morphology may therefore influence the potential habitats it can utilise (Melville and Swain 1999b, in press). Consequently, the morphological traits exhibited by an animal may have a profound influence on an animal's behaviour and ecology (Arnold 1983, Emerson and Arnold 1989). In lizards, caudal autotomy results in a tail that is structurally modified from the original (i.e. supported by cartilage not bone), thus permanently altering the morphology of the lizard. Hence, following autotomy, lizards may display modified behaviour which may substantially impact upon both their locomotory performance and habitat use.

In the majority of lizards, the tail is functionally important during locomotion. Various authors have highlighted the locomotory 'costs' of tail autotomy through its influence upon stride length (Hamley 1990, Martin and Avery 1998), body curvature (Martin and Avery 1998), balance (Ballinger 1973) and attainment of maximal sprint speed (Martin and Avery 1998). The impaired movements of tailless lizards can be investigated through several key aspects of lizard biomechanics. Most lizards move by lateral undulations of the vertebral column (Hamley 1990, Ritter 1992). This lateral bending creates a standing wave within the trunk region of the animal, which forms a travelling wave along the tail (Hamley 1990). The coupling of hind limb retraction and tail flexion dictates that stride frequency and the frequency of tail oscillation must be equal (Hamley 1990). Tail loss acts to reduce the efficiency of hind limb retraction and consequently decreases stride length (Hamley 1990, Martin

and Avery 1998). Tailless lizards, therefore, usually have shorter stride lengths during locomotion and, due to the relationship between stride length and frequency, have to ‘work harder’ to maintain the same speeds (Hamley 1990). These factors make it harder for tailless lizards to attain their maximal sprint speeds and, due to the increased effort required to maintain normal performance levels, endurance capacity may be reduced.

Locomotory impairment resulting from the absence of the tail has been shown to affect terrestrial (Ballinger *et al.* 1979, Punzo 1982, Formanowicz *et al.* 1990), arboreal (Brown *et al.* 1995) and aquatic (Daniels 1985b) forms of locomotion, as well as endurance capacity (Daniels 1985b). The inhibited movement that may result from tail loss may have flow-on effects for functions such as thermoregulation (Chapter 4), reproduction (Chapter 6), habitat use and behaviour (Chapter 7). Although the impact of tail autotomy on the performance capabilities of lizards is well known, the time taken for the complete restoration of these abilities has not been investigated. Animals with completely regenerated tails possess locomotory abilities equal to those with original tails (pers. obs.). However, defining the tail length where this first occurs warrants investigation since the time to reach this point determines the duration of locomotory costs.

This chapter sets out to investigate whether tail loss has the ability to impact upon the performance abilities of *Niveoscincus metallicus*, both its immediate effect and the persistence of this impact through time. Pregnant females usually exhibit inhibited mobility (e.g. Shine 1980); therefore, sexual variation in the effect of autotomy due to reproductive status was also investigated. Three locomotory aspects were studied: sprint speed, climbing ability and locomotory endurance. *Niveoscincus metallicus* is a predominately ground-dwelling species with a long-slender body and reduced limbs that utilises sinusoidal movements during locomotion (Melville and Swain in press). The possibility that the impact of tail loss differs between performance traits as a result of this locomotory mode was investigated. Due to the large lateral flexions of the body and tail during locomotion, tail loss was expected to result in severe performance ‘costs’. Since sprint speed, and presumably the two other performance

criteria, are highly repeatable traits (Huey and Dunham 1987), the animals were tested on three occasions during tail regeneration to determine the duration of any locomotory costs imposed. Three questions concerning the locomotory impact of tail autotomy were investigated in this chapter.

- 1) Does tail loss in *Niveoscincus metallicus* result in a significant decrease in locomotory performance, due to the important role of the tail in locomotion? If so, does its impact vary between sexes or performance traits?
- 2) Are full performance abilities regained once the tail reaches a critical length that enables normal lateral movement during locomotion?
- 3) Do *post-partum* females have superior performance abilities compared to pregnant females?

3.2 MATERIALS AND METHODS

3.2.1 Collection and preparation of animals

Sixty animals, 30 males and 30 females, were collected from Clarence Lagoon during late September and early October 1999 (Sections 2.1, 2.2). All were adult and sexually mature (i.e. SVL over 45 mm; Swain and Jones 1994, Jones and Swain 1996), and possessed either an original or completely regenerated tail.

For each sex, animals were randomly assigned to one of two groups, control or experimental, and housed under standard conditions with 5 lizards per cage. Each animal was identified by a small piece of coloured adhesive cloth tape attached to the dorsal surface; each lizard was assigned a unique colour and number combination. These visual identifiers were replaced after each moult. Measurements of SVL (± 0.1 mm), tail length (± 0.1 mm), tail break length (distance from vent to break ± 0.1 mm) and tail regeneration length (distance from break point to tip ± 0.1 mm) were recorded for each individual.

In order to obtain an initial baseline measurement of the performance capabilities of each animal, locomotory performance was recorded for each performance criterion (Sections 3.2.3-3.2.5). Once an initial reading was obtained, tails were removed from animals in the two experimental groups. Tail autotomy was achieved through preliminary cooling, followed by pinching the tail near its base to break it along a caudal fracture plane. Stress and blood loss was minimal, with the resultant tail stump 8-14 mm in length. All animals exhibited signs of wound healing within a few days, with the formation of a characteristic scab and concealment of the wound by a layer of skin (Bellairs and Bryant 1985). Visible tail regeneration commenced within three weeks of tail autotomy. Each control group was cooled and handled in a similar manner to the experimental groups, except that the tail was not removed. All animals were allowed to recover at room temperature for 45 minutes before being returned to standard conditions (Section 2.3).

All animals, both control and experimental groups, were retested within 36 h for each performance criterion, and subsequently after one month and three months. The testing regime involved sprint and climbing trials on day one, separated by a minimum of three hours, with endurance trials performed the following morning. Recent food intake may inhibit locomotory performance (Garland and Arnold 1983, Huey *et al.* 1984), so animals were not fed in the 24 h prior to each testing period. All females were pregnant when captured. The testing periods corresponded with mid- and late-pregnancy, with the final trials performed when all females were *post-partum*. This variation in reproductive stage was expected to influence locomotory performance over the course of the study (Shine 1980, Bauwens and Thoen 1981, Olsson *et al.* 2000).

3.2.2 Test Temperatures

Locomotory performance abilities exhibit a considerable degree of thermal sensitivity (Bennett 1980, Hertz *et al.* 1983, Waldschmidt and Tracy 1983, Crowley 1985, Mautz *et al.* 1992). Consequently maintenance of a constant body temperature is vital in order to assess the effect of tail loss on locomotory performance. All lizards were

heated to their optimal performance temperature of 26° C (Melville 1998, C. McCoull pers. comm.) prior to each locomotory trial.

Lizards were placed, in groups of up to five, in watertight metal containers immersed in a Grant Instruments™ waterbath, which was heated using a Raetek Instruments™ TH1 Thermoregulator™. Water temperature was maintained at 26° C, with a small propeller continuously mixing the water. The water temperature was verified prior to each trial with a hand held thermometer. All animals were warmed for at least 30 minutes before each trial, and between first and second trials. This method of raising body temperature allows more accurate and stable body temperatures to be achieved than other methods that heat from a single surface only.

3.2.3 Sprint Performance

Maximal sprint speed was determined by running each lizard along a heated 'racetrack', 1.5 m in length. Three 120 W spotlights, situated underneath the metal floor of the racetrack and linked to a temperature sensor probe, allowed the track temperature to be precisely controlled at 26° C ($\pm 1^\circ$ C). This heat source prevented the animals from losing body temperature during the trial. The metal surface of the track was lined with fine sandpaper to allow lizards to gain traction while sprinting. Once heated (Section 3.2.2), each lizard was prompted to sprint down the racetrack using a small brush. Three photodiodes, positioned at 50 cm intervals along the length of the track, and linked to a Macintosh computer, produced two estimates of sprint speed for each trial. Each lizard was tested twice per performance occasion, with the fastest time over a 50 cm interval used to calculate maximum sprint speed (m sec^{-1}). Data from lizards that refused to run were excluded from the dataset.

3.2.4 Climbing ability

An estimate of the climbing ability of each lizard was obtained by recording the time taken to climb a 40 cm long wooden rod with a diameter of 2.5 cm. The surface of the rod was roughened to improve traction using sandpaper and positioned at a 45° angle.

Tests were conducted within a test arena (67 x 61 x 21 cm) lined with a sand substrate, which cushioned the fall of any lizard that jumped or fell from the rod while climbing. Lizards were warmed to the test temperature (Section 3.2.2) and placed at the base of the wooden rod. They were encouraged to climb through gentle taps on the base of the tail. The time taken to climb the rod was determined using a handheld stopwatch and values were converted to climbing speeds (cm sec^{-1}). On each sampling occasion, animals were tested twice with the fastest time used to calculate maximum climbing speed. Trials where lizards refused to climb or fell off before reaching the end of the rod were excluded from the dataset.

3.2.5 Locomotory endurance

The endurance capacity of individuals was evaluated using a treadmill with a neoprene belt that provided traction. The treadmill, 50 cm long and 20 cm wide, was set at a constant speed of 10 cm sec^{-1} . At this speed, all animals moved willingly and exhibited no visible signs of distress. Prior to each trial, animals were warmed to the test temperature (Section 3.2.2), and then placed on the treadmill. Lizards were encouraged to run at the constant speed of the treadmill through gentle taps at the base of the tail. The trial ended when either the lizard refused to continue running or lagged behind and reached the rear of the treadmill. The duration of the trial was recorded using a handheld stopwatch and was used as a measure of the locomotory stamina capacity for the animal. Due to the potential stress and fatigue caused by multiple trials, each individual was tested only once per sampling occasion.

3.2.6 Neonatal tail loss and sprint speed

The immediate effect of post-natal tail autotomy on the sprint speed of neonates was assessed using newborns from control females held in captivity (Chapters 3 and 4). Maternal cages were checked twice daily, with the sprint speed of newborns assessed immediately following birth. All sprint trials were conducted as described in Sections 3.2.2 and 3.2.3, except that only a single trial was performed due to the tiring effect of such trials on newborns. Measurements were taken as described in Section 2.4. The

relative tail length (tail length/SVL) of each individual was also calculated. Following the initial trial, two individuals from each clutch were chosen at random, with complete tail autotomy induced in one sibling as per Section 3.2.1. Both tailed and tailless neonates were retested and re-measured within 24 h to assess the impact of tail autotomy on locomotory performance at birth. However, locomotory performance was not followed over the course of tail regeneration due to the decreased repeatability of sprint speed after 2 weeks (pers. obs.). As newborns do not exhibit any sexually dimorphic traits in relation to morphology and sex determination is difficult at this stage (C. McCoull, pers. comm.), an investigation of sexual differences in relation to caudal autotomy was not attempted.

3.2.7 Data analysis

The influence of caudal autotomy was studied through the investigation of three main areas: a) the immediate impact of tail loss (1-way ANCOVA); b) recovery of locomotory ability following tail autotomy (Repeated Measures ANCOVA); and c) sexual variation in the effect of autotomy (comparison of male and female results for a and b). The influence of female reproductive stage on performance ability was also studied (T-Test). Statistical analyses were conducted using the SAS System for Windows[®] v6.12, according to the following procedure.

The immediate effect of tail loss was evaluated with a one-way ANCOVA on the performance trial after tail loss (24 h) using the initial trial data as the co-variate. This initial trial (baseline measurement) was used as the co-variate instead of SVL due to its ability to account for variation in performance abilities due to size, and also initial differences in the locomotory capacities of each group. The assumption that each treatment had identical group regression slopes was tested by assessing the significance of the treatment*co-variate interaction. In every instance this assumption was met, allowing the analysis to continue. The linearity of the relationship between the performance trait (dependent variable) and initial speed/time (co-variate) was evaluated by examining a plot of the residuals versus the co-variate and assessing the normality of residuals. This assumption was met for each trait. Finally the

independence of residual variances and the response variable was assessed by examining a plot of residuals versus predicted values and comparison of the variances of residuals among groups.

The recovery effect subsequent to tail autotomy was analysed using a repeated measures ANCOVA design, with the initial response as the co-variate. The appropriate correlation structure (compound symmetry, autoregressive or unstructured) was evaluated by selecting the structure which had the values of Akaike's Information Criterion and Schwarz's Bayesian Criterion which were closest to zero. The significance of the co-variate was then assessed to determine whether an ANCOVA design was necessary. In each instance, the co-variate (initial response) proved to be significant. The assumption of equal slopes was then tested, using a conservative P value of 0.01 in order to negate the possibility of significant differences being found due to small sample size (McPherson 1990; L. Barmuta, pers. comm.). If this assumption was not met, the analysis did not proceed further, but when met the main effects were then evaluated. Visual inspection of a plot of residuals versus predicted residuals was used to assess homogeneity of variance and data normality.

Comparison of the results from the 1-way and Repeated Measures ANCOVA for males and females was used to assess sexual differences in the impact of tail autotomy. Likewise, variation in the effect of tail loss between the three performance criteria was evaluated by comparison of the results obtained from each criteria. When there were no treatment differences between the two groups of females, a t-test was completed on the pooled data for late pregnancy (1 month) and *post-partum* (3 months) females to determine whether performance ability is influenced by reproductive stage.

The influence of tail loss on the sprint speed of juveniles was assessed using a Randomised Complete Block design ANOVA on the difference in sprint speed between the two sampling occasions. Maternal size (or clutch) was treated as the block, with the treatment (tail loss) allocated to lizards within each block.

Homogeneity of variances was assessed through a plot of fitted values against standardised residuals. The normality of the data was evaluated through visual inspection of the plot of residuals versus error.

3.3 RESULTS

3.3.1 Adult performance capabilities

The relative tail lengths (tail length/SVL) of the experimental animals varied over the course of the experiment (Table 3.1). Females, upon capture, had lower relative tail lengths compared to males; however, this appears to be a sampling artifact as males and females without tail loss generally have equivalent tail lengths (Section 7.3.1). Following tail removal, the initial regeneration of the tail was rapid. Three months after caudal autotomy the tail was about half its original size in males and two thirds its original size in females (see Section 5.3.2 for analysis of regeneration rate).

Table 3.1 Relative tail length (tail length/SVL \pm s.e.) of experimental animals on each of the testing occasions.

Time	Male (n = 15)	Female (n = 15)
Initial	1.14 \pm 0.035	0.94 \pm 0.048
24 h	0.22 \pm 0.009	0.18 \pm 0.010
1 Month	0.26 \pm 0.002	0.28 \pm 0.021
3 Months	0.53 \pm 0.020	0.67 \pm 0.020

Sprint Speed

The effect of tail loss on sprinting ability differed between males and females (Figure 3.1). Immediately following tail loss, males exhibited a significant decrease in sprint performance (ANCOVA: $F_{1,22} = 20.18$, $P = 0.0001$). However, no proximate influence of tail autotomy on sprint speed was observed in females (ANCOVA: $F_{1,17} = 3.01$, $P = 0.1031$).

In males, the inhibitory effect of caudal autotomy was maintained throughout the course of the study (Repeated ANCOVA: $F_{1,20} = 21.31$, $P = 0.0002$), although sprint speed changed with time ($F_{2,42} = 12.73$, $P = 0.0001$). However, the variation in sprint performance over time was similar for both control and experimental animals ($F_{2,42} = 0.65$, $P = 0.5254$). Females also exhibited variation in sprint speed during their time in captivity (Repeated ANCOVA: $F_{2,31} = 13.90$, $P = 0.0001$); however, each group maintained equivalent levels of sprint performance (Treatment: $F_{1,15} = 0.29$, $P = 0.5964$; Interaction: $F_{2,31} = 1.67$, $P = 0.2051$). Since there was no difference between female treatment groups the data were pooled and a t-test was completed to investigate whether sprint speed changed significantly following pregnancy. The test revealed that there was a significant decrease in sprint speed following parturition ($t = 2.11$, $df = 17$, $P = 0.0001$).

It appears therefore that tail autotomy has a significant impact on the sprinting ability of males but not females. This locomotory inhibition in males was still evident even three months after caudal autotomy. However, following parturition females do not appear to regain their sprint ability after the removal of the burden of the clutch.

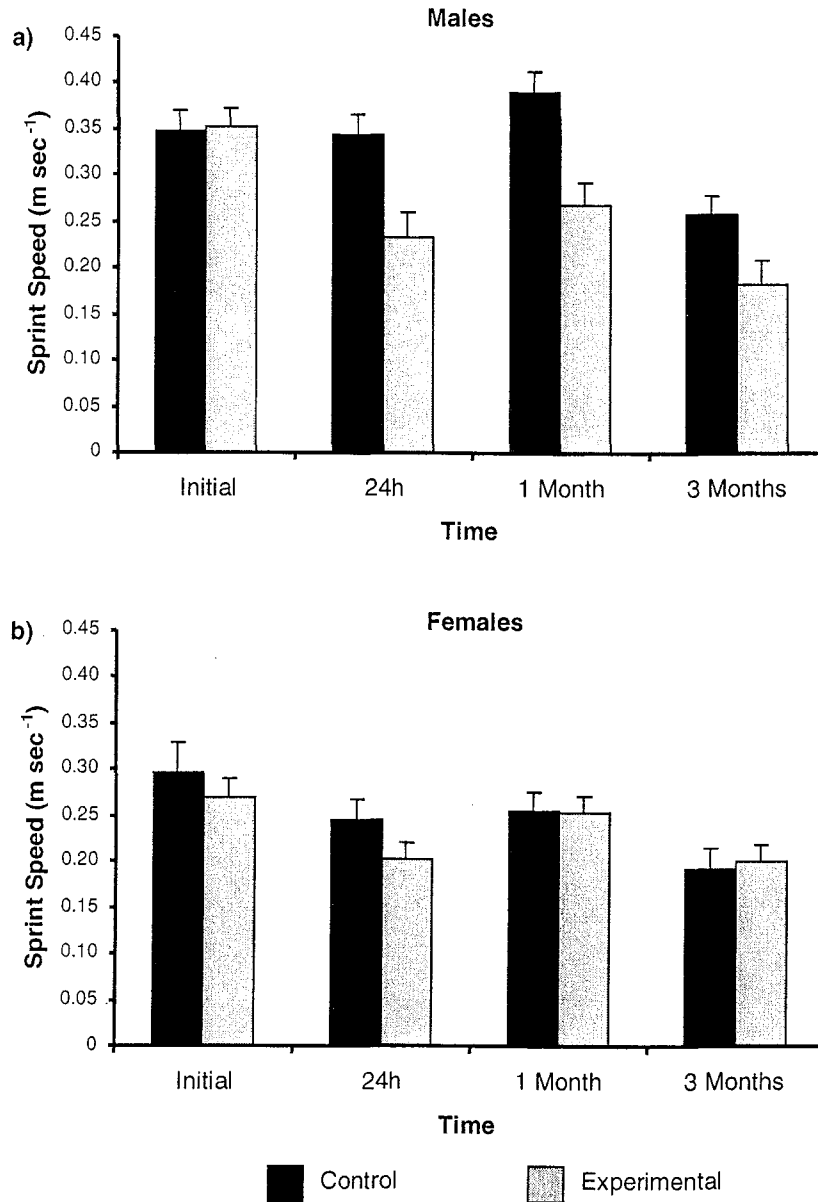


Figure 3.1 Sprint speed of a) males and b) females on four occasions: initial, 24 h, one month and three months. Tail autotomy occurred prior to the 24 h test occasion, therefore the difference between the initial and 24 h time points indicates the immediate impact of tail loss, with recovery recorded at two time points over the subsequent 3 months. All values except the initial time point represent least squares means (\pm s.e.).

Climbing ability

Tail autotomy did not influence the climbing performance of either sex (Figure 3.2). The climbing ability of both males (ANCOVA: $F_{1,26} = 2.75$, $P = 0.1104$) and females ($F_{1,21} = 3.94$, $P = 0.0618$) did not decrease significantly immediately following tail

loss. Although males with tails had considerably faster climbing speeds than tailless males, this was due primarily to the superior initial climbing ability of the control individuals. The diminished climbing ability of females after autotomy was not found to be significant due to the large degree of variation between individuals.

Both groups of males maintained their initial climbing abilities throughout the three months of the study (Repeated ANCOVA; Treatment: $F_{1,24} = 1.56$, $P = 0.2236$; Time: $F_{2,49} = 2.77$, $P = 0.0723$; Interaction: $F_{2,49} = 2.04$, $P = 0.1410$). However, since the slopes of the two groups of females were not found to be equal, a repeated measures ANCOVA was not possible. Tailed females, however, appeared to retain slightly faster climbing speeds than tailless females during tail regeneration. The climbing ability in both groups appeared to decrease gradually until the one month time interval (late pregnancy), before increasing in *post-partum* females (3 month interval), possibly due to removal of the burden of the clutch. A t-test on the pooled data for each group confirmed that there was a significant increase in climbing ability in females following parturition ($t = 2.08$, $df = 21$, $P = 0.0006$).

Caudal autotomy, therefore, does not appear to impose any locomotory constraints on the climbing capability of *N. metallicus* in either sex. Pregnancy, however, has an inhibitory effect on climbing ability in females, with *post-partum* females exhibiting a substantial increase in climbing speed following parturition.

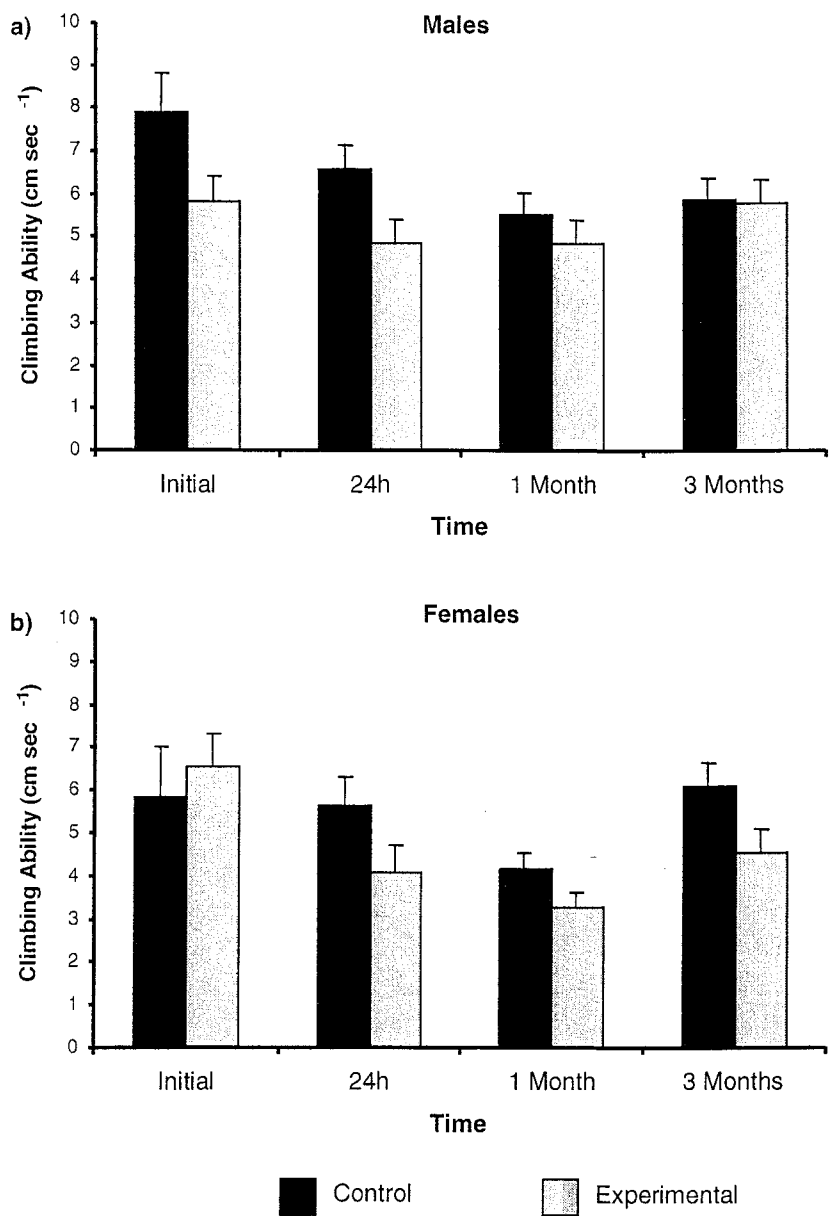


Figure 3.2 Climbing ability of a) males and b) females on four occasions: initial, 24 h, one month and three months. Tail autotomy occurred prior to the 24 h test occasion, therefore the difference between the initial and 24 h time points indicates the immediate impact of tail loss, with recovery recorded at two time points over the subsequent 3 months. All values except the initial time point represent least squares means (\pm s.e.).

Stamina

Intuitively if an animal has to work harder following tail loss to maintain the same speed (Hamley 1990, Martin and Avery 1998), its stamina is likely to be diminished. This was observed in *N. metallicus* as the endurance capacity of animals running on a

treadmill decreased immediately following tail loss (Figure 3.3). This decrease was significant for females (ANCOVA: $F_{1,20} = 8.11$, $P = 0.0107$), but just non-significant in males ($F_{1,23} = 4.27$, $P = 0.0514$).

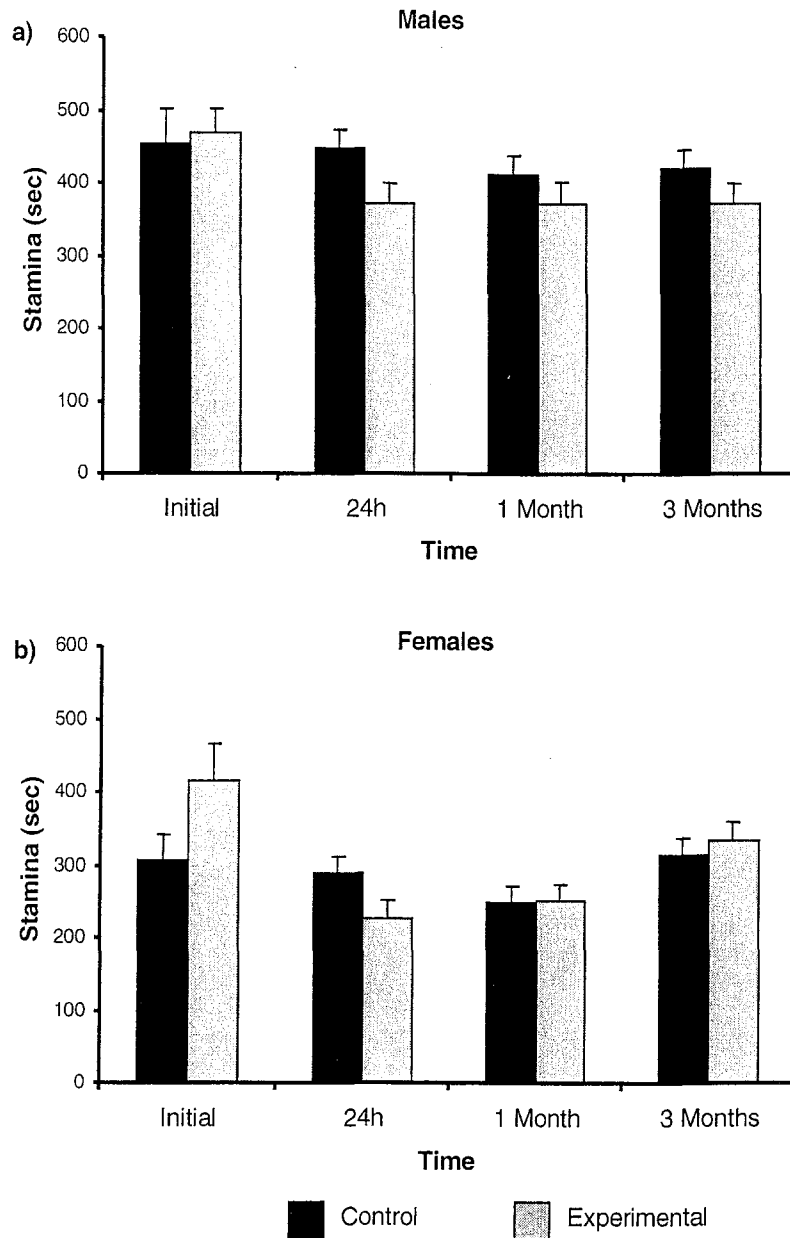


Figure 3.3 Stamina (time on treadmill in seconds) of a) males and b) females on four occasions: initial, 24 h, one month and three months. Tail autotomy occurred prior to the 24 h test occasion, therefore the difference between the initial and 24 h time points indicates the immediate impact of tail loss, with recovery recorded at two time points over the subsequent 3 months. All values except the initial time point represent least squares means (\pm s.e.).

Males, both control and experimental, maintained their initial endurance capacity throughout the study (Repeated ANCOVA; Treatment: $F_{1,21} = 2.19$, $P = 0.1541$; Time:

$F_{2,43} = 2.35$, $P = 0.1077$; Interaction: $F_{2,43} = 2.56$, $P = 0.0889$). However, during tail regeneration experimental females regained their endurance capabilities. This was evident from a significant treatment*time interaction (Repeated ANCOVA: $F_{2,37} = 3.40$, $P = 0.0440$), with significant variation between time intervals ($F_{2,37} = 15.63$, $P = 0.0001$), but not treatment groups ($F_{1,18} = 0.18$, $P = 0.6789$). Since there was no difference between treatment groups, the data were pooled and a t-test was completed to reveal that there was a significant increase in the locomotory stamina of females following parturition ($t = 2.09$, $df = 20$, $P = 0.0001$).

The restoration of locomotory endurance following tail loss appears to occur rapidly in females. However in males, the slight, but non-significant, decrease in stamina was maintained over the three month duration of the study. Therefore, it appears that sexual differences in the rate of recovery may exist. The burden of the clutch in pregnant females seems to diminish endurance, as following parturition there was a significant increase in the time females could run on a treadmill.

3.3.2 Juvenile sprint speed

This experiment used fourteen clutches of juveniles to determine the impact of tail loss within 24 h of birth. Two juveniles from each clutch were used, with one being assigned to each of the two treatment groups: tail removed (experimental) or tail left intact (control). A one-way ANOVA showed that the relative tail lengths of juveniles assigned to each group did not differ ($F_{1,27} = 0.15$; $P = 0.701$) (Table 3.2).

Table 3.2 Mean relative tail lengths (\pm s.e.) of control and experimental newborns at birth (before) and after tail loss in experimental animals.

Group	n	RTL Before	s.e.	RTL After	s.e.
Control	14	1.18	0.013	1.18	0.013
Experimental	14	1.18	0.016	0.14	0.011

Juveniles assigned to the experimental group exhibited considerable decreases in sprint speed following tail loss (Figure 3.4). A randomised complete block ANOVA confirmed this decrease in sprint speed as significant ($F_{1,23} = 72.96$; $P = 0.0001$). This

reduction in sprint speed was independent of any maternal (clutch) effects ($F_{11,23} = 0.60$; $P = 0.7961$). Tail autotomy at birth therefore inhibits the locomotory performance of newborns regardless of which clutch they originate from.

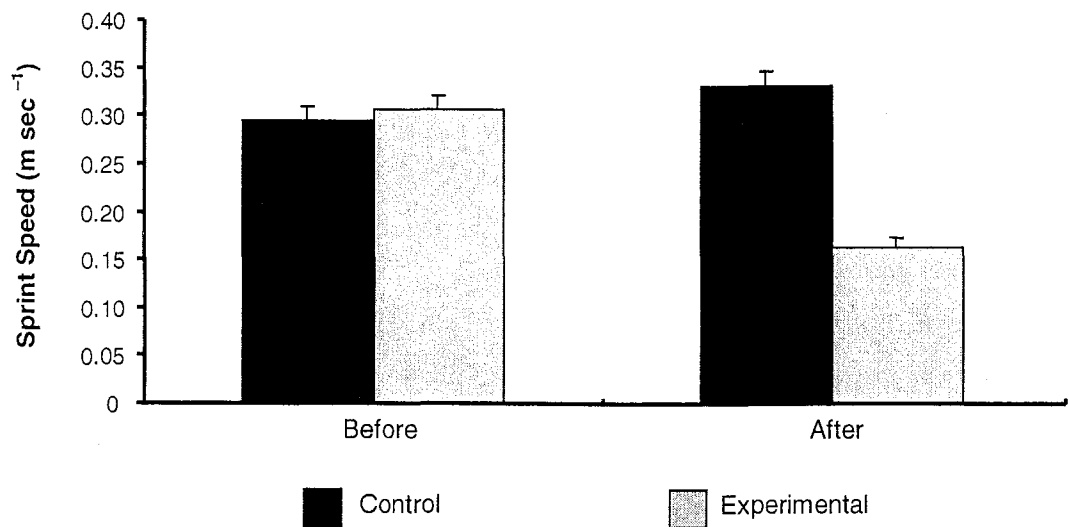


Figure 3.4 The average sprint speed of juveniles ($n=14$) before and after inducement of tail loss in experimental animals (mean \pm s.e.).

3.4 DISCUSSION

The inhibitory effect of tail autotomy on locomotory performance has been widely documented in a variety of species (Ballinger *et al.* 1979, Punzo 1982, Formanowicz *et al.* 1990, Martin and Avery 1998). Each of these studies, however, has been limited to an investigation of the immediate impact of tail loss on sprint performance, without attention to any possible sexual or temporal consequences of autotomy. This chapter demonstrates that the ramifications of caudal autotomy may vary between adults of both sexes, and juveniles, and between a number of performance traits. The recovery of locomotory capabilities following tail loss may be dependent on the rate of tail regeneration and the particular performance trait in question.

The maximum sprint speed of male *N. metallicus* decreased by 34% immediately following tail removal. This reduction in sprint performance is consistent with the proximal impact of tail loss observed in a number of species such as *Cnemidophorus*

sexlineatus (36%; Ballinger *et al.* 1979), *Cophosaurus texanus* (32%; Punzo 1982), *Uma notata* (42%; Punzo 1982), *Scincella lateralis* (35%; Formanowicz *et al.* 1990) and *Psammodromus algirus* (40%; Martin and Avery 1998). However, in each of these studies either no mention was made of the sex of the animals used or the possibility that sexual differences may exist was ignored. Likewise, the duration of these effects were not reported (discussed later). Although in the present study the sprint speed of juveniles was halved immediately following tail loss, caudal autotomy in females failed to result in any observable decline in sprinting ability. Sexual differences, therefore, appear to exist in *N. metallicus* with the impact of tail autotomy, a result not previously reported and one which may have implications for those studies listed above. The reproductive stage of females at the time of tail removal, mid-pregnancy, may be responsible for the absence of locomotory inhibition.

Pregnant females, both oviparous and viviparous, commonly exhibit reduced sprinting ability and mobility (Shine 1980, Van Damme *et al.* 1989a, Cooper *et al.* 1990, Sinervo *et al.* 1991). This impact of reproductive status has also been demonstrated in a number of *Niveoscincus* species, including *N. metallicus* (Melville 1994, Wapstra 1998, C. McCoull pers. comm.). The physical burden of the clutch and the large lateral distension of the body has been suggested to limit both the degree of lateral flexion and agility (Shine 1980). The performance abilities of pregnant females are already diminished, therefore it is likely that the influence of tail loss on an already inhibited performance trait may be curtailed. Consequently, tail autotomy whose major influence on performance ability is in regard to lateral bending during locomotion (Hamley 1990, Ritter 1992, Martin and Avery 1998), may only be of minor relevance in pregnant females.

The endurance capacity of females, however, was substantially decreased as a result of tail loss. The period for which pregnant females were able to maintain a consistent running speed was halved following caudal autotomy. Tail length and the rigidity of the caudal musculature function to determine the frequency of tail oscillation and the force of hind limb retraction (Hamley 1990). The degree of hind limb retraction acts to dictate stride length in lizards (Hamley 1990, Martin and Avery 1998). As a result

of the intimate coupling between stride length and stride frequency (Hamley 1990, Martin and Avery 1998), animals with reduced stride lengths have to increase stride frequency to maintain velocity. This necessitates an increased level of exertion resulting, presumably, in decreased levels of stamina. Although no evidence was obtained to confirm this possibility, females in this study may have been able to ‘work harder’ over short distances by increasing stride frequency to maintain sprint speeds at levels similar to that prior to tail loss. However, this increased physical and energetic exertion would not have been able to be sustained for an extended period, resulting in a decreased level of stamina observed in the current study. This hypothesis, however, requires further investigation.

Tailless males, similarly, exhibited endurance capabilities much lower than those of their tailed counterparts. Although barely statistically insignificant ($P = 0.0514$), the 70 second decrease in stamina may reflect a relevant and substantial locomotory ‘cost’. If so, even without the physical and physiological burden of pregnancy, males seemed to be unable to ‘work harder’ over short sprint distances or maintain constant speeds for an extended period of time. Pregnancy in viviparous reptiles, therefore, may provide a ‘cushioning’ effect to the impacts of caudal autotomy. Consequently, pregnant females without tails may be no more vulnerable to predation due to decreased escape speed than those with complete tails.

Niveoscincus metallicus, although morphologically adapted to a ground-dwelling lifestyle, possesses a substantial ability to climb (Melville and Swain, in press; current study). The climbing speeds of neither males nor females were affected by the absence of the tail. Consequently, *N. metallicus* exhibits substantial performance costs from autotomy in relation to sprint speed and stamina which are not evident when they are climbing.

This conclusion is not without precedence. Although only a few authors have investigated multiple performance criteria, there is evidence that the effect of tail autotomy does vary between performance traits. Daniels (1985b) found that autotomy in the water skink, *Sphenomorphus quoyii*, inhibited swimming speed and stamina but

not terrestrial sprint speed. Likewise, Brown *et al.* (1995) found that the climbing ability of the European wall lizard, *Podarcis muralis*, decreased substantially following caudal autotomy; however, there was a corresponding increase in sprint speed. Although the tail may be useful for ensuring balance while climbing (Ballinger 1973), it may hold lesser importance for this performance trait. Since the feet are always firmly attached to the substrate while climbing, problems of uncontrolled lateral oscillations of the hindquarters may be less relevant (Arnold 1984). Consequently, the absence of a tail to act as an inertial damper in order to control hind limb retraction may be less of a concern during arboreal locomotion. Anecdotal evidence suggests that higher frequencies of tail loss are correlated with species that employ climbing as their primary locomotory mode (Arnold 1984). This suggests that tail loss may impose less of a locomotory 'cost' on climbing species, or that the predation intensity or efficiency is greater for these species. In this study, where testing of arboreal locomotion involved climbing a relatively thin rod, lateral bending as a driving force of locomotion, may have been of little importance.

Locomotory performance traits such as sprint speed are generally considered to be highly repeatable (Huey and Dunham 1987), but in my study sprint speed decreased with time in captivity. This may have been due to decreasing levels of motivation (e.g. Olsson *et al.* 2000) or the result of *ad libitum* feeding. *Niveoscincus metallicus*, like most other *Niveoscincus* species, has a high captive feeding rate (Olsson *et al.* 2000, pers. obs.). This resulted in animals possessing abdominal fat bodies 5-10 times their normal size after three months in captivity (Section 5.3.2). For several performance criteria in this study there was a significant decrease in locomotory performance which was independent of both reproductive status and tail loss. The increased burden caused by these large abdominal fat bodies may have resulted in the gradual reduction in performance, a situation similar to that observed during pregnancy.

Olsson *et al.* (2000), however, used this situation to their advantage to investigate the cause of locomotory inhibition observed in pregnant females. They utilised the unique reproductive cycle in *Niveoscincus microlepidotus* that results in pregnant and

non-pregnant females being available simultaneously. Using *ad libitum* feeding in non-pregnant females, they were able to produce a situation where these females possessed abdominal fat bodies of comparable weight and position to the developing embryos in pregnant females. They found that animals with these artificially enhanced fat bodies ran faster than pregnant females, suggesting that physiological, not physical processes may be responsible for the reduced sprint speed in this instance. This suggestion was further supported by the presence of a time lag between parturition and restoration of locomotory ability. Gestation in all species of *Niveoscincus* is relatively lengthy and may require time to overcome physiologically. Both caudal autotomy and time in captivity may affect an animal's physiology. Muscular strength, metabolic capacity and motivation may all be decreased. Therefore, investigation purely of the biomechanics of lizard locomotory performance may be insufficient to account for the observed decrease in sprint performance following caudal autotomy. However, motivation or willingness to perform was not recorded in the present study.

The performance capabilities of squamate reptiles exhibit a considerable degree of thermal sensitivity, with a clearly defined temperature range for optimal performance (Hertz *et al.* 1983, Crowley 1985). However, unlike most lizards, species of *Niveoscincus* generally maintain temperatures that differ from that considered optimal for locomotory performance (Melville 1994, 1998; Kik 1998; Kabat 1999; present study, Chapter 4). All performance trials in the present study were conducted at the previously determined optimum temperature of 26 °C (Melville 1998; C. McCoull, pers. comm.). Kabat (1999) reported that the reduction in endurance capacity of pregnant *Niveoscincus microlepidotus* was exaggerated at temperatures above the thermal optimum. The possibility exists, therefore, that caudal autotomy may have had a more profound effect on locomotory performance at temperatures considered sub-optimal for performance. Consequently, *N. metallicus* at high altitude (i.e. Central Plateau) which usually experience lower, and presumably suboptimal, morning body temperatures compared to those at lower altitudes (i.e. Hobart) may endure enhanced levels of locomotory impairment as a result of caudal autotomy.

The recovery of locomotory abilities following caudal autotomy has not previously been investigated. Intuitively it would be expected that the performance capabilities of an individual should return over the course of tail regeneration. The time taken for this to occur dictates the duration of locomotory ‘cost’. Whether the duration of ‘cost’ is similar for each performance trait is currently unknown. In this study caudal autotomy was found to impact upon the sprinting and endurance abilities of males, and the stamina of females. No recovery, however, was observed in males for either performance trait after three months. At this point the tail had regenerated to about half of its original length. Females, however, regained full endurance abilities within one month of tail loss, when the tail was approximately a third of its original length. This restoration of stamina was still evident following parturition. Olsson *et al.* (2000) found comparable differences associated with sex in the related species *Niveoscincus microlepidotus*. They found a significant negative correlation between the proportion of tail regrown and sprint speed in males, suggesting a gradual restoration of performance ability. However, in pregnant females sprint speed was not influenced by tail length, suggesting that locomotory abilities may return rapidly following tail loss in females. Differences in the recovery rate of males and females might be due, at least in part, to inherent sexual differences in locomotory biomechanics. Consequently, locomotory ‘costs’ associated with caudal autotomy may differ substantially between males and females. However, further work is needed to expand upon this preliminary investigation of the duration of locomotory costs in *N. metallicus* and determine the tail length at which these performance costs are no longer evident and verify the sexual differences in recovery observed in this study.

CHAPTER 4

THERMOREGULATORY BEHAVIOUR

4.1 INTRODUCTION

Temperature, and its regulation, is believed to constitute the single most important factor in a reptile's ecology (Heatwole 1976). This is largely due to the thermal sensitivity of the physiological processes which determine the majority of a reptiles's ecology and behaviour. Temperature has the potential to influence a range of behavioural and physiological processes in lizards, such as mobility (Bennett 1980; Hertz *et al.* 1983, 1988; Waldschmidt and Tracy 1983; Mautz *et al.* 1992), defensive behaviour (Hertz *et al.* 1982, Christian and Tracy 1981, Losos 1988, Van Damme *et al.* 1990) and reproduction (Beuchat 1986, Brăna 1993, Andrews *et al.* 1997). Consequently, reptiles usually maintain body temperatures that reflect their current physiological status. Different physiological processes may have different thermal 'optima', which necessitates active regulation of body temperature to suit the physical status of the animal.

The selective occupation and movement between thermal microclimates within a habitat, coupled with behavioural traits that control heat gain and dissipation, allow a lizard to actively regulate its body temperature. Selection and regulation of body temperature is believed to fall under the control of hypothalamic temperature receptors whose properties and states determine an animal's thermal setpoints (Tosini and Avery 1993). These setpoints are the body temperatures at which basking is initiated (lower setpoint) and ceased (upper setpoint) (Tosini and Avery 1993). Since the regulation of body temperature exhibits some degree of neural control, the physical state of the animal has the potential to influence the thermoregulatory characteristics of the individual.

Perhaps the most documented instance of the physical state of an individual influencing its thermoregulatory properties is in relation to pregnancy in viviparous lizards. The viviparous mode of reproduction is generally believed to have evolved to

allow maternal regulation of the embryonic temperature during incubation within cold climates (Shine 1985, 1995). Support for this hypothesis is exhibited by viviparous squamates which alter their thermoregulatory behaviour during gestation (Stewart 1984, Beuchat 1986, Brăna 1993, Daut and Andrews 1993, Tosini and Avery 1996, Andrews *et al.* 1997). Two hypotheses have been put forward to explain this switch in thermoregulatory behaviour during pregnancy: the encumbrance hypothesis; and the thermal stress hypothesis (Andrews *et al.* 1997). The encumbrance hypothesis suggests that the reduced mobility of females during pregnancy (e.g. Shine 1980) inhibits the ability to thermoregulate precisely. Alternatively, it is argued that conflicting maternal and embryonic thermal optima may lead to thermal stress of the embryos when held at normal maternal temperatures. This may result in mothers modifying their body temperatures to those that are conducive to optimal embryonic development. In such situations of compromise and trade-offs, 'costs' are inevitable.

Caudal autotomy in lizards has the potential to parallel the situation experienced during pregnancy in viviparous lizards. *Lacerta monticola*, a European lacertid, has been shown to alter aspects of its thermoregulatory behaviour in response to tail loss (Martin and Salvador 1993a). Although its thermal characteristics were not modified following tail loss, its basking behaviour in the field changed. Both the thermal stress and encumbrance hypotheses provide potential explanations for such behaviour. For example, mobility may be restricted as a result of tail autotomy (see Chapter 3), potentially compromising the individual's ability to thermoregulate (encumbrance hypothesis). In addition, the regeneration of a structure the size of the tail requires extensive energetic expenditure and the physiological processes that drive tail regeneration are highly temperature dependent. Both temperature and photoperiod have been shown to influence the rate of tail replacement (Turner and Tipton 1972, Bellairs and Bryant 1985, Ndukuba and Ramachandran 1988). However, the thermal optimum for tail regeneration may conflict with the 'normal' optimum temperature of the animal (thermal stress hypothesis).

Intuitively, it would be expected that a lizard would limit the duration of any potential 'costs' incurred through tail loss by maintaining a temperature which would maximise its rate of tail regeneration. A shuttling heliotherm such as *N. metallicus* may attempt

to achieve this in a variety of ways, including modifying the time spent at extreme high and low temperatures, the frequency of basking events and the precision with which the temperature is regulated. Apart from these behavioural modifications, the animal may also alter aspects of its thermoregulatory characteristics.

Both Kik (1998) and Kabat (1999) have demonstrated that *Niveoscincus microlepidotus* lowers its thermal setpoints and preferred body temperature during pregnancy. Therefore, flexibility exists in the regulation of temperature and potentially it would be possible for *N. metallicus* to alter its thermoregulatory characteristics in response to tail loss. However, limiting the duration of the 'costs' incurred may not be the sole focus of any response. Downes and Shine (1998) demonstrated experimentally that predator avoidance was a higher priority than thermoregulation in the gecko, *Oedura lesueurii*. Likewise, if the thermal stress hypothesis is correct, optimal embryonic development possesses a higher priority than any maternal thermoregulatory consideration. An investigation of the influence of tail autotomy on thermoregulatory behaviour in males and pregnant *N. metallicus* may reveal important information about the overall 'costs' of caudal autotomy and shed light on thermoregulatory priorities in this species. Several questions were formulated in order to investigate this possibility.

- 1) Do individuals modify aspects of their thermoregulatory behaviour to enable the maximal rate of tail regeneration to occur?
- 2) Do pregnant females alter their thermoregulatory characteristics to enable optimal embryonic development?
- 3) Does tail loss influence a female's thermoregulatory response to pregnancy?
- 4) What do the results from the previous three questions reveal about the priorities and/or importance of caudal autotomy in males and females?

4.2 MATERIALS AND METHODS

4.2.1 Thermoregulatory Characteristics

4.2.1.1 Collection and preparation of animals

A subset of the animals collected for use in performance trials (Section 3.2.1) was used to investigate the effects of caudal autotomy on both the thermoregulatory characteristics and behaviour of *Niveoscincus metallicus*. Due to the constraints of using cloacal temperature probes to measure body temperature in such small skinks, only individuals over 52 mm in SVL were used in the study. Eight randomly selected individuals from each of the four groups (i.e. males tailed/tailless, females tailed/tailless) were tested on each sampling occasion, with the thermoregulatory characteristics and behaviour of each group tested once prior to tail loss (Section 3.2.1), within 1 week of tail loss, and on two subsequent occasions at one month and three months into tail regeneration. General housing conditions and preparation of the animals was as described in Section 3.2.1.

4.2.1.2 Eccritic temperatures and basking setpoints

A large wooden, open-topped terrarium (120 cm x 120 cm x 30 cm) was used as the test arena. It was subdivided into 8 separate sections (55 cm x 30 cm) by wooden partitions, each identified by a number (1-8). A 2-3 cm layer of sand acted as the substrate. Tiles positioned on wooden blocks and located approximately 7 cm under a heat source (25 Watt light bulb) constituted basking sites in each section. This basking setup provided a temperature gradient of 15-40° C, allowing behavioural thermoregulation to occur.

Body temperatures of the lizards were recorded throughout the daily activity period (9 am-5 pm). Small temperature probes (0.5 mm diameter) were inserted into the cloaca and securely held in position with a strip of adhesive cloth tape around the tail. Each probe was connected to a data logger by a 1.5 m lead that allowed uninhibited movement around the arena, permitting shuttling heliothermy. The data logger was

linked to a Macintosh computer, which used a pre-written program to record the body temperature of all 8 lizards at 5 minute intervals.

Animals were familiarised with the testing arena with cloacal probes in place, approximately half an hour prior to the commencement of each trial. They were not fed in the 24 h prior to the trial, and water but not food was available during the eight hour testing period.

For each animal the overall mean temperature (average T_b over the entire activity period), mean upper and lower basking setpoints (average T_b where initiated and ended basking event), maximum temperature (highest T_b recorded), time spent at high ($>30^\circ\text{C}$, $>35^\circ\text{C}$) and low ($<25^\circ\text{C}$) temperatures, and time spent within one standard deviation of the mean temperature, were recorded (Figure 4.1). These values were calculated from the 97 data points obtained for each animal over the course of the 9 am – 5 pm activity period.

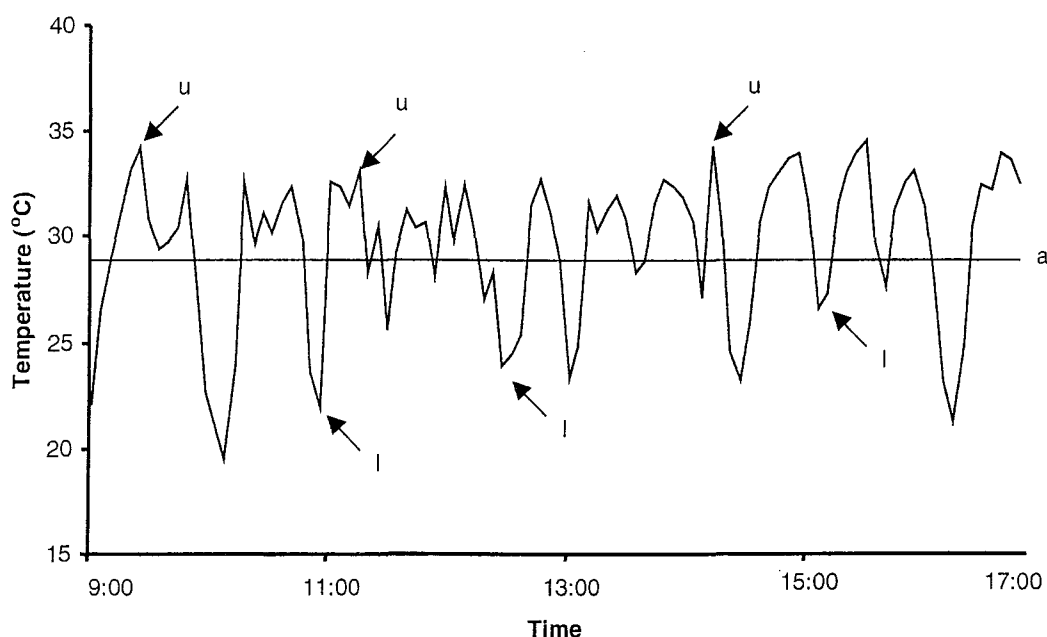


Figure 4.1 Representative temperature recording over the course of the activity period (9am – 5pm). The line marked 'a' indicates the average body temperature. The arrows indicate three examples of upper and lower setpoints (marked u and l respectively).

4.2.2 Basking behaviour

4.2.2.1 Collection and preparation of animals

Forty lizards, 20 males and 20 pregnant females, were collected from Clarence Lagoon in late November 1999 (Section 2.2) to investigate the consequence of tail loss on the basking frequency of individuals. For each sex, animals were randomly assigned to one of two groups, control or experimental, with tail autotomy induced in members of the experimental group. Complete caudal autotomy was achieved under anaesthesia, 5% isoflurane at 1L O₂ min⁻¹ administered for 15 minutes (Bennett 1996). Once the animal was anaesthetised, the tail was removed through a fracture plane at its base using forceps. Stress and blood loss was minimal, with all animals rapidly regaining consciousness. The resultant tail stump was 8-14 mm in length. Animals were allowed to recover at room temperature for 45 minutes. Within one week all lizards exhibited signs of wound healing and scab formation (Bellairs and Bryant 1985), with visible regeneration apparent within 2 weeks. Control animals were anaesthetised and handled in an identical manner, except for removal of the tail.

Following tail removal all lizards, both experimental and control, were weighed (\pm 0.01 g) and measurements taken of SVL, tail length and break length (\pm 0.1 mm). Each lizard was marked with a piece of adhesive cloth tape with a unique colour/number combination.

4.2.2.2 Laboratory housing conditions

The lizards used in this experiment were not housed under standard laboratory conditions, but instead were housed in pairs (members of the same group) in open-topped terraria (67 cm x 61 cm x 21 cm). The terraria were located in an undergraduate teaching laboratory under normal ambient room temperatures. Initially each terrarium contained two basking tiles, each located approximately 13 cm beneath a 40 W basking light. However, this produced too much heat and one heat source was removed; both tiles were then placed under the remaining basking light. Both lizards appear to gain equal access under the single basking source with no evidence of agonistic interactions. Temperature gradients of 15-38° C were available within each

terrarium. Basking lights operated for 10 h per day, with ambient light available through windows of the laboratory providing the natural photoperiod. The experiment was conducted between early December 1999 and mid February 2000. Absorbent bedding acted as the substrate, and two plastic pot plant halves created refuge sites for the lizards. Water was available *ad libitum*, and animals were fed twice per week with mealworms dusted with calcium powder. After some initial problems making the terraria escape proof, an overhang was created around the top of each box; this successfully prevented further escape.

4.2.2.3 Observations

The frequency of basking was investigated at four points over the course of tail regeneration in tailless individuals of each sex. At the start of the experiment, females were in mid-pregnancy (Stage 31-32), with parturition occurring between the 2nd and 3rd assessment periods.

The terraria were set up to allow only overt basking, so that basking behaviour could be readily observed from a distance. All 40 lizards were observed at 15 minutes intervals over an eight-hour testing period. Every 15 minutes a circuit of the twenty terraria was completed, and each lizard was recorded as performing one of three distinct behaviours.

- 1) **Basking-** Lizards lying on a basking tile and adopting one of two primary thermoregulatory postures:
 - a) lying with limbs positioned laterally beside body with dorso-ventral compression of the body; or
 - b) lying with limbs held back against the side of the body.
- 2) **Foraging-** slow searching movements, walking around the terrarium or drinking.
- 3) **Hiding-** Animal not visible, having sought refuge under the cover provided or within the absorbent gravel.

At the completion of the testing period, a frequency score out of 33 (the total number of daily observations) was obtained for each behaviour. Tests were conducted at 3-4 week intervals on fine or slightly overcast days with the outside temperature between 20-25° C. Observation of the animals did not appear to affect the propensity of any individual to perform a particular behaviour.

4.2.3 Data analysis

Data analyses were performed on the SAS System for Windows® v6.12. The impact of tail loss on each thermoregulatory characteristic or behaviour was analysed using a repeated measures factorial ANOVA design. The assumptions of homogeneity of group variances and normality were assessed by visually inspecting plots of group standard deviations versus group means and estimated versus predicted residual values, respectively. *Post-hoc* contrasts were used to investigate pre-planned comparisons between time points.

4.3 RESULTS

Caudal autotomy did not influence either the thermoregulatory characteristics or behaviour of *N. metallicus* (Tables 4.1 - 4.4, Figure 4.2). Tailless lizards maintained the same thermal setpoints and average body temperatures as tailed lizards. The time individuals spent at extreme high or low temperatures was not altered due the absence of the tail, nor was the precision with which temperature was maintained. Likewise, the frequency of basking events was unaffected as a result of autotomy. Caudal autotomy therefore does not appear to have any significant influence on the thermoregulatory behaviour in *N. metallicus*.

However, despite the absence of any tail loss effect some interesting results were obtained. Distinct sexual differences in both the thermal characteristics and basking behaviour were found to exist in *N. metallicus*. Pregnant females tended to spend more time basking than males (Figure 4.2), and generally did not allow their body temperatures to reach extremely high or low levels (Tables 4.2-4.4). Despite these behavioural differences the precision with which body temperature was maintained

Table 4.1 Mean upper and lower thermal setpoints ($^{\circ}\text{C} \pm \text{s.e.}$) for tailed (C- control) and tailless (TL) animals. The thermal setpoints prior to tail autotomy (initial) and on three subsequent occasions during tail regeneration (1 week, 1 month and 3 months) are presented. The results for the Repeated Measures ANOVA are presented.

Time	Group	Initial	Week 1	1 Month	3 Months	Tail Loss		Time		Interaction	
						<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>
Upper Setpoint	Males C	34.7 \pm 0.69	35.2 \pm 0.44	35.3 \pm 0.89	35.7 \pm 0.28	0.55 (1,12)	0.474	1.08 (3,36)	0.356	0.54 (3,36)	0.598
	Males TL	34.4 \pm 0.45	35.1 \pm 0.47	34.9 \pm 0.68	34.7 \pm 0.32						
	Females C	31.5 \pm 0.56	32.5 \pm 0.32	32.3 \pm 0.43	34.1 \pm 0.37	1.22 (1,13)	0.290	6.15 (3,39)	0.004*	0.92 (3,39)	0.422
	Females TL	33.0 \pm 0.51	33.1 \pm 0.71	32.5 \pm 0.94	34.2 \pm 0.21						
Lower Setpoint	Males C	23.2 \pm 0.58	24.8 \pm 0.77	25.6 \pm 0.18	27.9 \pm 0.37	0.10 (1,12)	0.759	29.50 (3,36)	0.001*	0.52 (3,36)	0.636
	Males TL	23.7 \pm 0.67	24.6 \pm 0.31	24.9 \pm 0.46	27.8 \pm 0.24						
	Females C	24.1 \pm 0.48	25.8 \pm 0.27	25.8 \pm 0.81	27.4 \pm 0.29	0.82 (1,13)	0.381	10.79 (3,39)	0.001*	0.28 (3,39)	0.780
	Females TL	25.1 \pm 0.46	26.3 \pm 0.82	25.8 \pm 0.92	28.0 \pm 0.29						

Table 4.2 Mean daily and maximum body temperature ($^{\circ}\text{C} \pm \text{s.e.}$) for tailed (C- control) and tailless (TL) animals. These temperatures were determined prior to tail autotomy (initial) and on three subsequent occasions during tail regeneration (1 week, 1 month and 3 months). The results for the Repeated Measures ANOVA are presented.

Time	Group	Initial	Week 1	1 Month	3 Months	Tail Loss		Time		Interaction	
						<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>
Mean T_b	Males C	29.5 ± 1.03	30.2 ± 0.70	30.7 ± 0.65	31.8 ± 0.37	0.20 (1,12)	0.661	6.30 (3,36)	0.004*	0.66 (3,36)	0.550
	Males TL	29.3 ± 0.72	30.6 ± 0.47	29.9 ± 0.71	31.2 ± 0.21						
	Females C	26.9 ± 0.55	28.9 ± 0.47	29.2 ± 0.69	30.6 ± 0.32	0.68 (1,13)	0.423	9.86 (3,39)	0.001*	1.17 (3,39)	0.331
	Females TL	28.6 ± 0.68	29.3 ± 0.75	28.8 ± 1.03	30.9 ± 0.14						
Max T_b	Males C	36.6 ± 0.69	36.8 ± 0.38	37.2 ± 0.46	37.8 ± 0.23	0.50 (1,12)	0.495	1.86 (3,36)	0.169	0.37 (3,36)	0.735
	Males TL	36.4 ± 0.43	36.8 ± 0.48	36.8 ± 0.71	37.0 ± 0.23						
	Females C	34.5 ± 0.49	34.6 ± 0.30	34.8 ± 0.57	34.8 ± 1.40	0.87 (1,13)	0.426	2.89 (3,39)	0.113	0.83 (3,39)	0.439
	Females TL	35.8 ± 0.53	36.0 ± 0.61	34.7 ± 0.92	36.6 ± 0.22						

Table 4.3 Proportion of time (\pm s.e.) spent at high temperatures (Over 30 °C and Over 35 °C) by tailed (C- control) and tailless (TL) animals. These proportions were determined prior to tail autotomy (initial) and on three subsequent occasions during tail regeneration (1 week, 1 month and 3 months). The results for the Repeated Measures ANOVA are presented.

Time	Group	Initial	Week 1	1 Month	3 Months	Tail Loss		Time		Interaction	
						<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>
Over 30 °C	Males C	50.1 \pm 11.47	60.8 \pm 6.72	61.8 \pm 6.73	71.8 \pm 3.86	0.30 (1,12)	0.593	3.32 (3,36)	0.053	0.63 (3,36)	0.545
	Males TL	54.1 \pm 7.00	59.4 \pm 5.78	49.1 \pm 7.35	69.0 \pm 2.48						
	Female C	23.5 \pm 6.78	46.8 \pm 7.84	51.6 \pm 8.37	60.5 \pm 2.54	0.21 (1,13)	0.652	5.63(3,39)	0.03*	3.39 (3,39)	0.038*
	Female TL	46.2 \pm 7.04	49.8 \pm 7.30	35.9 \pm 10.71	64.1 \pm 2.54						
Over 35 °C	Male C	15.3 \pm 8.03	12.7 \pm 4.35	14.6 \pm 4.28	5.7 \pm 1.40	0.54 (1,12)	0.477	1.77 (3,36)	0.200	0.18 (3,36)	0.788
	Male TL	19.5 \pm 4.69	10.0 \pm 1.64	16.4 \pm 6.07	8.3 \pm 1.09						
	Female C	1.3 \pm 0.61	1.2 \pm 0.84	1.2 \pm 0.84	9.4 \pm 2.39	0.24 (1,13)	0.757	4.44 (3,39)	0.030*	0.24 (3,39)	0.757
	Female TL	6.9 \pm 4.59	6.8 \pm 2.83	7.7 \pm 12.3	12.3 \pm 4.36						

Table 4.4 Proportion of time (\pm s.e.) spent at low temperatures (Under 25 °C) and within 1 SD (i.e. \pm ½ SD) by tailed (C- control) and tailless (TL) animals. These proportions were determined prior to tail autotomy (initial) and on three subsequent occasions during tail regeneration (1 week, 1 month and 3 months). The results for the Repeated Measures ANOVA are presented.

Time	Group	Initial	Week 1	1 Month	3 Months	Tail Loss		Time		Interaction	
						<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>
Under 25 °C	Males C	29.5 \pm 1.03	30.2 \pm 2.12	30.7 \pm 0.66	31.9 \pm 0.37	0.20 (1,12)	0.661	6.30 (3,36)	0.004*	0.66 (3,36)	0.550
	Males TL	29.3 \pm 0.72	30.6 \pm 0.48	29.9 \pm 0.71	31.2 \pm 0.21						
	Female C	31.4 \pm 5.50	13.9 \pm 2.33	18.1 \pm 5.78	8.0 \pm 2.12	0.41 (1,13)	0.536	8.04 (3,39)	0.002*	0.54 (3,39)	0.594
	Female TL	23.3 \pm 2.65	16.0 \pm 3.77	16.3 \pm 5.77	6.7 \pm 0.96						
Within 1 SD	Male C	31.7 \pm 5.76	39.4 \pm 2.12	37.3 \pm 2.13	35.9 \pm 4.20	0.13 (1,12)	0.726	0.22 (3,36)	0.796	1.18 (3,36)	0.325
	Male TL	39.9 \pm 2.72	36.2 \pm 2.91	37.2 \pm 4.23	35.3 \pm 2.08						
	Female C	42.8 \pm 3.78	41.9 \pm 2.98	35.2 \pm 3.57	35.0 \pm 3.78	0.58 (1,13)	0.459	1.08 (3,39)	0.489	0.79 (3,39)	0.4896
	Female TL	37.6 \pm 2.02	35.3 \pm 2.48	37.7 \pm 6.57	34.2 \pm 2.07						

(time within 1 SD of T_b) was similar in both males and pregnant females (Table 4.4). However, pregnant females had a narrower gap between their upper and lower setpoints (i.e. elevated lower setpoint, diminished upper setpoint), that presumably resulted in them spending less time at extreme temperatures. The combination of these factors probably resulted in the lower average body temperature in pregnant females that was evident in the experiment (Table 4.2).

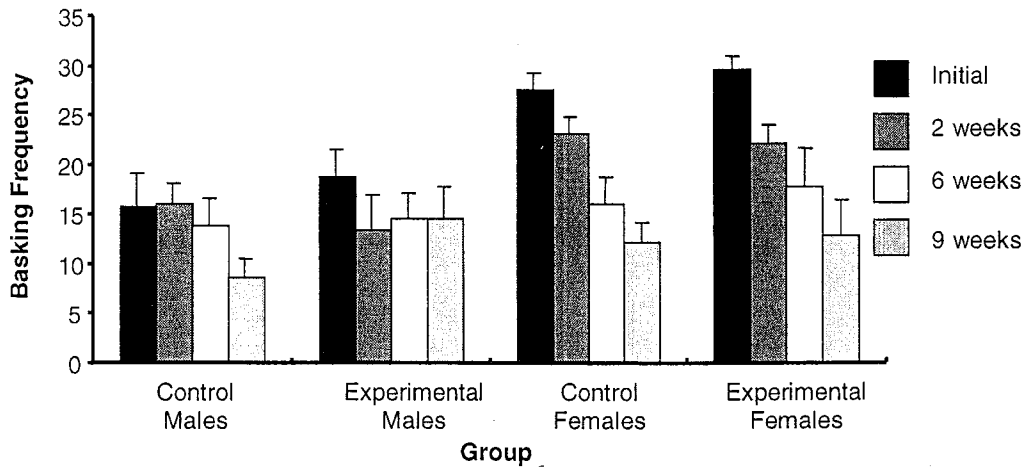


Figure 4.2 Frequency of basking behaviour over time for each of the four groups (score out of $33 \pm \text{s.e.}$). In females parturition occurred between week 2 and week 6.

Although sexual differences were present for the majority of the study, most aspects of thermoregulation were similar in males and *post-partum* females (Tables 4.1-4.4, Figure 4.2). Pregnancy therefore appeared to have a significant influence on both the thermoregulatory characteristics and behaviour of females. *Post-hoc* contrasts revealed that the thermal setpoints of females increased significantly following parturition (Upper: $P = 0.0142$; Lower: $P = 0.0122$). Parturition coincided with substantial increases in the amount of time spent at high temperatures (35°C : $P = 0.0176$) and a corresponding decrease in the frequency of time animals spent at low body temperatures ($P = 0.0043$). Females when pregnant spent considerably more of their time basking than when *post-partum* ($P = 0.0001$; Figure 4.2). The average body temperature of females increased significantly following parturition ($P = 0.0162$). However, the precision with which females regulated their body temperature was constant throughout the study. Pregnant females therefore appear to be able to shift

their body temperature and thermoregulatory characteristics without regulating their body temperature more precisely.

Thermoregulatory plasticity is evident in *N. metallicus*; however, unlike pregnancy, caudal autotomy does not result in any significant modification of the thermoregulatory strategy adopted. Generally the thermoregulatory behaviour of males and non-pregnant females is similar; however, pregnancy in females results in a substantial shift in behaviour. Hence, although modification of thermoregulatory behaviour is possible in *N. metallicus*, tail loss does not appear to possess the capacity to cause such an alteration in behaviour.

4.4 DISCUSSION

The potential 'costs' of caudal autotomy in lizards are numerous, with the capacity to severely restrict the daily activities of the animal, and possibly diminish its chances of future survival. These 'costs', however, are usually only transient, resulting in temporary penalties for the animal. The rate of tail regeneration presumably dictates the duration of these 'costs', because once the tail is replaced 'costs' are no longer evident. The physiological processes of caudal regeneration in lizards appear to be dependent both on photoperiod and temperature (Turner and Tipton 1972, Ndukuba and Ramachandran 1988). In heliothermic lizards that actively regulate their body temperature by moving between thermal microclimates in their environment, thermoregulatory behaviour should dictate the rate of tail replacement. Intuitively, therefore, it would be expected that individuals may alter their thermoregulatory behaviour following tail loss in order to maintain an optimum temperature conducive to rapid tail regeneration.

The initial question posed was whether tail autotomy had the ability to modify a lizard's thermoregulatory behaviour, presumably to enhance the rate of tail regeneration. The effect of tail loss on thermoregulatory behaviour in lizards has only been investigated once previously (Martin and Salvador 1993a). These authors investigated the impact of caudal autotomy on the thermoregulatory behaviour of the Iberian rock lizard, *Lacerta monticola*. They showed that the absence of the tail in

this animal had a negligible impact on its behaviour. The field and preferred temperatures of *L. monticola* were not altered as a result of caudal autotomy; neither was the time spent basking, the basking duration, nor the frequency of basking events. Habitat use and basking site selection appeared to be the only aspects of their thermoregulatory behaviour that changed as a result of tail loss (see Chapter 7). The metallic skink, *Niveoscincus metallicus*, displayed the same non-response as a result of tail loss, as it did not appear to change its thermoregulatory characteristics or basking behaviour following autotomy. The maximum and average body temperature, upper and lower thermal setpoints, and the time spent at extreme high and low temperatures were not affected by tail autotomy. Likewise, the frequency of basking events in the laboratory was unaffected. Thus, it is clear that thermoregulatory characteristics and behaviour are not influenced by tail loss in these two phylogenetically distant species, a lacertid and a skink.

Basking site selection appears to be the only aspect of thermoregulatory behaviour which is altered following tail loss (Martin and Salvador 1993a, Chapter 7). Following tail loss, both *L. monticola* (Martin and Salvador 1993a) and *N. metallicus* (Chapter 7) appeared to select different basking sites that were closer to cover and more cryptic in location (Martin and Salvador 1993a; Chapter 7). When put in the context of the thermal stress and encumbrance hypotheses (Andrews *et al.* 1997), the latter appears the more likely explanation for this switch in behaviour. No modification of the thermal characteristics of the two species was observed following tail autotomy in the laboratory; therefore the thermal stress hypothesis can be ruled out as an explanation. However, since tail loss may substantially inhibit mobility in *N. metallicus* (Chapter 3), physical encumbrance might occur in this species. Chapter 7 demonstrates that, in some instances, *N. metallicus* with short tails select cryptically located basking sites. However, any such switch towards crypsis in *N. metallicus* is probably the result of their decreased mobility (Chapter 3) or an increased predation probability rather than a concerted effort to maximise the rate of tail regeneration (but see Chapter 7). Consequently, apart from a slight modification in the way tailless animals use their habitat, caudal autotomy does not appear to impose any thermoregulatory ‘cost’ to the *N. metallicus*.

The absence of any modification of thermoregulation in lizards, in spite of the numerous impacts of tail loss (Chapter 3, 5, 6), poses some intriguing questions. Why is there is no perceivable adjustment in thermoregulatory behaviour following caudal autotomy? It has been assumed that lizards, as ectotherms, possess different thermal optima for a variety of physiological processes. Body temperature is assumed to reflect an animal's current physiological status. However, since caudal autotomy is an extremely common occurrence in a number of species, adaptations may exist to enable rapid tail regeneration to occur at body temperatures that are 'normally' maintained. The ability to perform caudal autotomy is a plesiomorphic characteristic within squamate reptiles (Arnold 1984, 1988) and selection works on physiological traits like any other. The reason no alteration in thermoregulatory behaviour is evident following tail loss may, in fact, be because optimal rates of tail regeneration occur in the thermal conditions that are regularly maintained when the animal has an intact tail. A thermal optimum for tail regeneration that is similar to the temperatures that are normally maintained would enable rapid tail regeneration to occur, while limiting any thermoregulatory 'cost' or conflict that may result from the modification of thermal preferences. Evolutionary processes therefore might have acted to refine the process of tail autotomy to allow this effective defensive strategy to occur as frequently as does in *N. metallicus* (see Chapter 7).

Pregnancy has been widely reported to influence thermoregulatory behaviour; therefore the question (Question 2) was posed whether pregnancy in *N. metallicus* resulted in a similar switch in thermal preferences. The mean body temperatures observed for males (~30° C) and *post-partum* females (~30° C) are comparable to the preferred (29.05° C) and field body temperatures (31.26° C) reported previously for *N. metallicus* (Bennett and John-Alder 1986, Melville 1994). However, pregnant females were found to maintain significantly lower temperatures (~27-28° C) during gestation. Pregnancy in *N. metallicus* resulted in females spending less time at high temperatures, but more at time at lower temperatures. Although the precision with which body temperature was maintained was similar for both pregnant and *post-partum* females, both the upper and lower thermal setpoints were lower in pregnant females. Such modification in thermal preferences and behaviour has been reported for a wide range of squamate reptiles during pregnancy (Stewart 1984, Brăna 1993,

Daut and Andrews 1993, Tosini and Avery 1996, Mathies and Andrews 1997, Andrews *et al.* 1997). *Niveoscincus metallicus*, therefore, like most other viviparous lizards exhibits thermoregulatory plasticity in thermoregulatory behaviour during gestation.

My study suggests that the optimum temperature range for embryonic development in *N. metallicus* is between 26° C and 29° C, with an average temperature of around 27-28 °C. This optimum temperature is 4-5° C higher than that in its alpine relative, *N. microlepidotus* (Kik 1998, Kabat 1999). However, unlike *N. microlepidotus*, *N. metallicus* regulates its body temperature during pregnancy close to that conducive to maximal performance (26° C; Melville 1998, C. McCoull, pers. comm.). As seen in Chapter 3, locomotory impairment associated with caudal autotomy may be exaggerated at sub-optimal temperatures. By maintaining body temperatures close to this optimum, pregnant females enhance their survival chances in the event of a predatory attack. This may enable tailless pregnant females during pregnancy to retain a level of mobility comparable to that of their tailed counterparts, while not unduly increasing their risk of predation.

Caudal autotomy in *N. metallicus* did not appear to influence the female thermoregulatory response to pregnancy. Ensuring optimal embryonic development and survival appears to represent a higher priority than tail regeneration in pregnant *N. metallicus* females. The high priority assigned to embryonic development, above any maternal or tail loss concerns, may be the result of the importance of the thermal environment during pregnancy. Swain and Jones (in press b) have demonstrated that, in *N. metallicus*, unfavourable thermal conditions during pregnancy can not be compensated for by nutritionally favourable conditions. Therefore, even if the mother is in good condition the thermal environment she encounters will have an overriding effect on the phenotype, viability and survival of the offspring. Consequently, in *N. metallicus* females, any alteration of thermoregulatory behaviour during gestation to potentially maximise tail regeneration would have an irrevocable impact on the developing embryos (e.g. Beuchat 1988, Schwarzkopf and Shine 1991, Shine and Harlow 1993, Daut and Andrews 1993, Mathies and Andrews 1997, Shine and Downes 1999, Swain and Jones in press b, Wapstra in press). Any 'costs' involved in

caudal autotomy are clearly overridden by the higher priority attached to reproductive success. This explanation based on the thermal stress hypothesis (Andrews *et al.* 1997), is a more plausible explanation for the observed decrease in body temperature than the encumbrance hypothesis, since locomotory inhibition was not severe in pregnant females (Chapter 3) and lack of mobility under laboratory conditions would probably not restrict the ability to thermoregulate effectively.

This study has demonstrated that: a) caudal autotomy does not influence thermoregulatory behaviour in *N. metallicus*; b) thermoregulatory plasticity is evident in response to pregnancy; and c) tail loss does not alter the female thermoregulatory response to pregnancy. These three findings allow determination of the priorities of *N. metallicus* following caudal autotomy. It is clear that thermoregulation in this species represents a higher priority than rapid tail regeneration, unless the thermal optima for the regenerative processes are equivalent to that normally maintained. However, it is obvious that embryonic development and reproductive success are higher priorities than either female thermoregulation or tail regeneration. Factors, therefore, that ultimately improve an individual's overall fitness (reproductive success; present study) and survival (predator avoidance; Downes and Shine 1998) are the highest priorities of squamate reptiles. However, for *N. metallicus* at least, processes relating to tail autotomy and regeneration represent a low priority compared to those that directly influence lifetime fitness or survival.

CHAPTER 5

ENERGETICS OF TAIL AUTOTOMY

5.1 INTRODUCTION

Natural selection theory stipulates that individuals that possess certain morphological or behavioural traits that enable them to survive and maximise their reproductive output will selectively proliferate within the population. However, completing the daily activities that ensure this outcome often requires considerable energetic expenditure. Daily functions performed by squamate reptiles may be fuelled partly by lipid energy reserves (Derickson 1976). These reserves may be present as either abdominal and caudal fat stores, with the caudal reserves constituting either the primary (see Greer 1986) or auxiliary source of energy stores. Caudal fat bodies have been demonstrated to be utilised in somatic body growth (Congdon *et al.* 1974, Ballinger and Tinkle 1979, Smith 1996), periods of nutritional stress (Daniels 1984), overwintering (Avery 1970, Derickson 1974, Smyth 1974) and reproductive investment (Smyth 1974, Derickson 1974, Dial and Fitzpatrick 1981). Therefore, the potential arises for tail autotomy to inflict energetic ‘costs’ upon an animal through the depletion of essential energy reserves.

Several energy related ‘costs’ have been identified in relation to tail loss, including decreased survival (Wilson 1992, Niewiarowski *et al.* 1997, Fox and McCoy 2000), inhibited growth (Congdon *et al.* 1974, Ballinger and Tinkle 1979, Smith 1996), and a reduced level of reproductive investment and/or output (Smyth 1974, Dial and Fitzpatrick 1981, Wilson and Booth 1998; but see Chapter 6). These ‘costs’ are believed to result from trade-offs between the process of tail regeneration and both body growth and reproductive effort. This may be due to the diversion of energetic resources, which would otherwise have been utilised for either growth or reproduction, to fuel the energy demands of tail regeneration (Ballinger and Tinkle 1979, Dial and Fitzpatrick 1981). Although tail autotomy facilitates the escape of the individual from potentially fatal predatory encounters, the strategy of shedding vital fat reserves appears counter-intuitive. It would be reasonable, therefore, to expect the

evolution of either behavioural or morphological adaptations that act to limit the loss of energy stores.

Such adaptations and modifications are indeed evident in numerous species of lizards. For example, some species are capable of relinquishing the minimal portion of tail necessary to ensure escape from predators (Daniels 1985a). This process, known as 'economy of autotomy', limits the amount of caudal fat lost as a result of tail autotomy (Daniels 1985a). The skink, *Lygosoma laterale*, has been observed to return, when possible, to consume its shed tail, presumably to recoup lipid stores that would otherwise be lost (Clark 1971). A third possible, though unproven, modification relates to the distribution of caudal fat reserves along the length of the tail. Logic suggests that, in species where the caudal fat reserves constitute a significant portion of the total energetic reserves, the tail fat should be preferentially distributed within the proximal region of the tail. Economy of autotomy might then provide a shed tail of adequate length to retain the attention of the predator, while limiting the magnitude of energetic depletion.

Whenever caudal autotomy does occur, however, the loss of fat reserves may be inevitable. In order to minimise the duration and extent of any energetic 'costs' and regain an area of lipid storage, the rate of tail regeneration should therefore be maximised. Presumably it is energetically expensive to replace a structure such as the tail, especially when energetic reserves are already depleted. This may result in the trade-off between growth and reproduction suggested previously. However, by enhancing food intake, sufficient energetic supplies may be attained to allow each of these activities to occur concurrently without conflict. The availability of energy reserves, however, may not be the sole requirement that determines the rate of tail regeneration, since several other factors, both intrinsic and extrinsic, have been demonstrated to influence this rate.

For example, the process of tail regeneration exhibits both temperature and photoperiod sensitivity (Turner and Tipton 1972, Ndukuba and Ramachandran 1988). Environmental chemicals may also have a profound effect on the rate at which regeneration occurs (Ramachandran and Ndukuba 1989, Suresh and Hiradhar 1990),

while the presence of energetically expensive blood parasites has been found to retard tail regeneration (Oppliger and Clobert 1997). Perhaps the most intriguing aspects of caudal regeneration relate to differences in the rate of regeneration associated with sex (Vitt 1981), life-history stage and species (Vitt *et al.* 1977). It has been suggested that in situations where the tail is functionally more important, tail regeneration occurs at an enhanced rate (Vitt *et al.* 1977).

Caudal autotomy in newborns provides an ideal situation in which to study the energetic ‘costs’ associated with tail loss. The experimental depletion of energetic reserves at birth leaves the neonate with two options: either optimise the rate of growth to obtain large size more quickly, or regenerate the tail as rapidly as possible to regain adequate locomotory abilities and an effective defense mechanism. Since *N. metallicus* newborns only have several weeks before they enter their first overwintering period either option may convey survival benefits. Attaining larger size may enhance the probability of survival, while tail regeneration may enable them to regain the ability to autotomise their tail and survive until hibernation. They would also regain their locomotory abilities, allowing them to forage and move throughout their environment to build up fat stores. If indeed tail loss does impose some form of energetic impact on the newborn, we would expect to see a trade-off between these two options. However, if juveniles are capable of achieving both rapid body growth and tail regeneration, energetic ‘costs’ related to tail loss may be low.

A series of laboratory experiments and investigations was instigated to study the energetic ‘costs’ of caudal autotomy in *Niveoscincus metallicus*. The energetic ‘value’ of the tail was evaluated through the determination of its fat content in relation to the total reserves (abdominal + caudal). The distribution of these reserves along the length of the tail was also assessed. Tail regeneration rates and fat body sizes of lizards held for other experiments (Chapters 3 and 4) were also used to determine tail regeneration rates and the energetic ‘cost’ of tail regeneration. Finally the effect of tail loss on the early growth rates of newborns was studied. These experiments were used to evaluate a number of questions concerning tail loss in *Niveoscincus metallicus*.

- 1) Does the high frequency of tail loss in *N. metallicus* (Chapter 7) result in either the tail representing only a secondary site of energetic reserves, or the preferential aggregation of caudal fat within the proximal section of the tail?
- 2) Do animals, three months after tail loss, with regenerating tails possess smaller abdominal fat bodies than animals with intact tails? If so, does this suggest that there is an energetic cost associated with regrowing the tail?
- 3) Is tail regeneration more rapid in males than females? If so, does this suggest that the costs associated with reproduction restricts the capacity of females to divert energy into tail regrowth.
- 4) Do newborns that experience tail loss immediately after birth exhibit inhibited growth rates compared to their tailed siblings?

5.2 MATERIALS AND METHODS

5.2.1 Energetic value and fat distribution within the tail

Ten individuals of each sex were collected from Clarence Lagoon as described in Section 2.2, during each of late November, early February and mid March. All lizards possessed either original or completely regenerated tails (see Section 5.3.1). For females these three sampling occasions corresponded to mid gestation, late gestation and post-parturition, respectively and decreased testicular development in males.

Upon return to the laboratory, all lizards were killed by placing them in a freezer for at least 24 h at -20° C. When convenient, the lizards were thawed and measurements taken of body mass (± 0.1 mg), SVL and tail length (± 0.1 mm). Animals were dissected by making a ventral incision along the midline, with lateral cuts near the cloaca and forelimbs, which allowed the skin flaps to be removed and expose the peritoneal cavity. The two abdominal fat bodies were located directly below the kidneys, just anterior to the cloacal opening. Each fat body was removed and weighed separately (± 0.1 mg). The digestive tract was removed, leaving only the reproductive organs within the posterior section of the peritoneal cavity. In females, the number of follicles or embryos and corpora lutea that were present in each oviduct (left and right) was recorded, before the follicles or embryos were removed and

weighed (± 0.1 mg). Developing embryos were staged according to Dufaure and Hubert (1961). For males, the external appearance of the testes was recorded, and their volume calculated using the formula for the volume of an ellipsoid, $V = 4/3\pi a^2b$, where a = half the shortest diameter and b = half the longest diameter.

The amount of tail fat was calculated through a simple process. The tail was removed at its base by running a pair of forceps posteriorly along the tail from the cloaca until the tail was autotomised through the fracture plane closest to the cloaca. The wet weight of the tail was recorded (± 0.1 mg). Each tail was then dried for a minimum of 24 h at 60° C and re-weighed to obtain a measure of dry weight. Preliminary trials showed that tails were completely dry at this time. Tails were then placed into ether for between 4-6 days to dissolve the caudal fat. After this time, each tail was removed from the ether and allowed to stand inside a fume cabinet to allow the ether to evaporate. Initial trials indicated that all ether had dissipated within 24 h, leaving a completely dry tail minus the caudal fat. The tails were subsequently re-weighed, with the differences in dry weight before and after the ether treatment taken to indicate the dry weight of caudal fat present. The validity of the method was evaluated using skin flaps, abdominal fat bodies and front and rear limbs. The limbs provide muscle, skin and bone as in the tail, but lack the fat reserves. Ether treatment produced no change in the dry weight of the skin flaps or limbs; however, only the outer membrane of the abdominal fat bodies remained after the ether treatment. In late November the method was completed on intact tails, but on the two subsequent occasions each tail was divided into three equal sections to obtain an indication of the relative fat content of the proximal, middle and distal thirds of the tail.

5.2.2 Tail regeneration rates of adults

Caudal regeneration was followed in the lizards used in Chapter 3; in females tail removal corresponded to the early-mid pregnancy period. Tail regeneration was followed at monthly intervals for periods up to 4 months. Measurements of weight (± 0.1 mg), SVL (± 0.1 mm), total tail length (± 0.1 mm) and regeneration length (± 0.1 mm), were recorded on each occasion.

The energetic cost of regenerating the tail was examined in the lizards used in Chapter 4 (Section 4.2.2). Three months after the removal of the tail, all animals were dissected to assess their abdominal fat bodies (as per Section 5.2.1) to determine whether caudal autotomy results in a decrease in energetic reserves.

5.2.3 Growth and tail regeneration rates of juveniles

Juveniles born in captivity from mothers held for use in Chapters 3 and 4 were used in this experiment. In order to limit any confounding factors, only juveniles from control tailed mothers were used. Maternal cages were checked for births twice daily. Upon discovery of a clutch of newborns, two individuals were chosen at random and assigned to either a control or experimental group. Within 24 h of birth, each lizard was weighed (± 0.1 mg) and measurements taken of SVL and tail length (± 0.1 mm). Each individual was then given a unique toe clip for identification. After these measurements were recorded, complete tail autotomy was induced in experimental animals as described in Section 3.2.1, and all animals re-measured within 24 h. All juveniles were subsequently re-measured every two weeks for eight weeks to obtain estimates of body growth and tail regeneration. Animals were housed under standard juvenile housing conditions (Section 2.4). Due to the difficulty of determining the sex of juveniles without dissection and the absence of juvenile sexual dimorphism (C. McCoull, pers. comm.), analysis of sex dependent growth rates was not completed.

5.2.4 Data Analysis

Analyses were performed using the SAS System for Windows[®] v6.12. Several types of statistical analysis were completed to determine the energetic value of the tail. A two-way ANOVA was completed to determine whether the relative tail lengths differed between sexes or collection occasions. Homoscedasticity of variances was investigated by visual inspection of plots of group standard deviations versus group means. Normality of the data was evaluated through the inspection of a plot of residuals versus predicted residual values. A series of simple linear regressions was then completed to evaluate the relationship between caudal and abdominal fat. The assumptions of homoscedasticity of error variances and non-correlation of errors were

assessed by examining a plot of studentised residuals against predicted values. Normality of the independent variables was assessed by visual examination of a plot of studentised residuals against normal cumulative distribution. A multiple comparisons of slopes ANOVA was used to determine whether the regression equations had equal slopes. Seasonal and sexual variation of abdominal and caudal fat stores were examined using a two-way ANOVA.

Frequency data were analysed by chi-squared tests for simple data sets where expected values were available or, when higher dimension contingency tables were involved, by log-linear modeling. Finally, a standardised residual was used to determine whether preferences existed for storing caudal fat in a particular section along the tail (after Terry *et al.* 1987).

$$r = (\text{observed} - \text{expected}) / (\text{expected})^{1/2}$$

A positive residual was an indication that the distribution of tail fat was biased towards a particular section, while a negative value indicated a non-preference for fat storage in that section.

Differences in the rate of tail regeneration between males and females were analysed with a 1-way ANOVA. Homoscedasticity of variances and normality of the data were assessed in the manner described above for the 2-way ANOVA. The energetic cost of regenerating the tail was determined using a 2-way ANCOVA with size (SVL) as the co-variate. The assumptions of homoscedasticity of variances and data normality were checked as for the 2-way ANOVA. The assumption of homogeneity of slopes was also evaluated.

The influence of tail loss on juvenile growth was assessed using a Randomised Complete Block design ANOVA on the increase in size (SVL) over an eight-week period. Maternal size (or Clutch) was treated as the block, with the treatment (tailloss) allocated to two lizards within each block. Homogeneity of variances was assessed through a plot of fitted values against standardised residuals. The normality

of the data was evaluated through visual inspection of the plot of residuals versus error.

5.3 RESULTS

5.3.1 Energetic value and fat distribution within the tail

The energetic value of the tail in *Niveoscincus metallicus* was determined on three occasions over the course of the experiment. Females were examined at mid-pregnancy, late-pregnancy and vitellogenesis during the collections in November, February and March, respectively (Table 5.1). The testicular volume of males was found to decrease over the season (Table 5.1).

Table 5.1 The reproductive status of animals collected during each sampling period.

Month	Males (Testes Volume mm ³) (n)	Females (Reproductive Stage)
November	44.5 (8)	Embryonic Stage 30-32
s.e.	4.83	(mid-pregnancy)
February	31.8 (10)	Embryonic Stage 40
s.e.	2.78	(late-pregnancy)
March	20.1 (10)	Early Vitellogenesis
s.e.	1.54	(post-partum)

Since the procedure to remove caudal lipid estimated the dry weights, while the abdominal fat stores were measured in wet weights, the relationship between wet and dry abdominal fat weights needed to be determined. The wet weights of 15 abdominal fat bodies were recorded before each was dried as described in Section 5.2.1. Regression analysis revealed that there was a significant relationship between the wet and dry weights of fat bodies ($y = 0.813x - 0.559$; $R^2 = 0.7795$, $F_{1,14} = 45.957$, $P = 0.0001$). This relationship obtained was used to convert the wet weights of the abdominal fat bodies obtained during the dissections to dry weights to allow them to be compared to the caudal energy stores. Significant relationships between the caudal and abdominal fat stores were obtained for each comparison, except for males in

February (Table 5.2). A multiple comparison of slopes ANOVA (*post-hoc* test) revealed that there were no significant differences in this relationship between animals with complete and completely regenerated tails for each sex over the three sampling occasions.

Table 5.2 Regression equations ($y = a + bx$) between caudal (y) and abdominal fat stores (x) for males and females on each of the sampling occasions.

Time	Sex	Slope	Intercept	R ²	ANOVA		
		(b)	(a)		Df	F	P
Nov	M	3.13	-2.01	0.871	1,7	40.35	0.0007
	F	7.36	2.12	0.606	1,7	9.24	0.0228
Feb	M	0.92	30.83	0.059	1,9	0.50	0.4988
	F	9.02	-0.89	0.683	1,9	17.22	0.0032
March	M	0.49	21.12	0.538	1,7	6.98	0.0384
	F	2.85	-26.26	0.639	1,9	14.17	0.0055

The slopes of each relationship, however, were not found to be constant with the slope of the equation for females in February being significantly steeper than that for either males in February and March (Multiple comparisons of slopes ANOVA) (Figure 5.1).

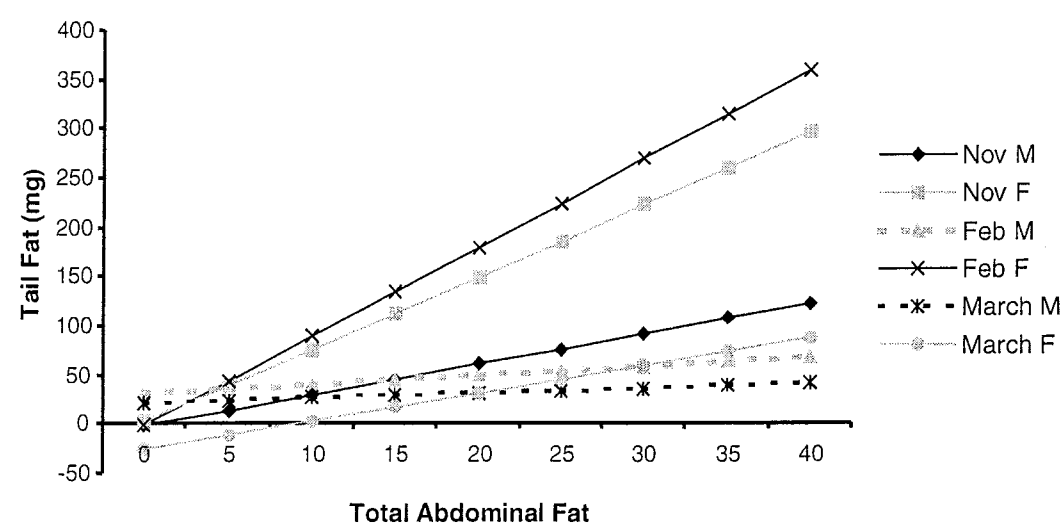


Figure 5.1 Regression lines for each sex over the three sampling occasions. Note that negative values on the graph indicate that the intercept was less than zero, possibly due to the small range of abdominal fat values distorting the regression equation.

The size of the abdominal and caudal fat reserves was found to vary between sexes and over the season (Table 5.3). Initial regression analyses for each sampling occasion revealed that caudal and abdominal fat stores were not related to SVL (>0.05 for each sex and time point). A two-way ANOVA showed that the size of abdominal fat bodies varied with time ($F_{2,55} = 38.75$; $P = 0.0001$) and between sexes ($F_{1,55} = 22.55$; $P = 0.0001$). The sex*time interaction was also significant ($F_{2,55} = 13.61$; $P = 0.0001$). Tukey's *post-hoc* test revealed that both sexes in November had smaller fat bodies than males in February and each sex in March. Males possessed significantly larger abdominal fat bodies than females in February, and these females in turn had smaller reserves than either sex in March.

Table 5.3 Dry weights (\pm s.e.) of abdominal and caudal fat stores for males and females for each of the three sampling periods November, early February and March. The proportion (\pm s.e.) of the total energetic reserves that stored in the tail is also indicated. Neither abdominal or tail fat was related to SVL.

Month	Sex	Abdominal Fat dry wt (mg)	Tail Fat Dry wt (mg)	Tail Fat as % of Total
November (n=8)	Male	6.21 ± 2.048	17.42 ± 6.872	55.61 ± 12.062
	Female	2.48 ± 0.512	20.39 ± 4.848	77.96 ± 11.239
Early February (n=10)	Male	21.97 ± 1.972	51.04 ± 7.466	67.91 ± 3.335
	Female	3.34 ± 0.719	29.21 ± 7.854	77.15 ± 9.886
March (n=10)	Male	21.75 ± 2.956	32.23 ± 3.061	60.41 ± 2.746
	Female	21.57 ± 1.830	35.21 ± 6.524	58.19 ± 3.572

A two-way ANOVA revealed that caudal fat reserves varied across time ($F_{2,55} = 5.36$; $P = 0.0078$), but not between sexes ($F_{1,55} = 1.01$; $P = 0.3195$). The interaction term was also non-significant ($F_{2,55} = 2.57$; $P = 0.0863$). A *post-hoc* Tukey's test showed that the difference across time was due to males in February possessing significantly larger tail fat reserves than either sex in November.

A two-way ANOVA showed that the total fat stores of lizards varied across time ($F_{2,55} = 10.24$; $P = 0.0002$), between the sexes ($F_{1,55} = 4.36$; $P = 0.0443$), with the interaction term also highly significant ($F_{2,55} = 5.26$; $P = 0.0085$). A *post-hoc* Tukey's test revealed that both sexes in November possessed significantly lower

amounts of total energy reserves that males in February and Females in March. Males in February also had more total fat reserves than females at the same time point. However, despite these differences, the proportional contribution of the caudal reserves to the total energetic stores did not vary between the sexes ($F_{1,55} = 2.47$; $P = 0.1223$) or across time ($F_{2,55} = 1.64$; $P = 0.2044$), with no interaction between the two factors ($F_{2,55} = 1.25$; $P = 0.2954$).

In order to determine the distribution of tail fat along the length of the tail the February and March tail samples were divided into three sections of equal length. On each sampling occasion the percentage of caudal lipid stored in the proximal third of the tail was over 90% (Table 5.4).

Log linear modeling indicated that the distribution of tail fat did not correlate with sex ($\chi^2 = 0.6995$, $df = 1$, $P = 0.7049$) or time ($\chi^2 = 0.6685$, $df = 1$, $P = 0.6685$), with no significant sex-time interaction ($\chi^2 = 5.7976$, $df = 2$, $P = 0.0551$). Similarly the percentage of dry weight in each tail section was constant between sexes ($\chi^2 = 0.0171$, $df = 1$, $P = 0.9915$) and over time ($\chi^2 = 0.0044$, $df = 1$, $P = 0.9978$), without any sex-time interaction effect ($\chi^2 = 0.0452$, $df = 2$, $P = 0.9777$).

Table 5.4 The observed fat content and dry weight by percentage (and range) of the basal, middle and distal thirds of the tail ($n = 40$). Values for each sex and month have been combined. All values represent percentages of the total fat or dry weight (mg) in each tail third.

	Tail Third		
	Proximal	Middle	Distal
	mean (range)	mean (range)	mean (range)
Tail Fat	91.7 (72.4 – 100)	8.2 (0 – 27.6)	0.1 (0 – 4.6)
Dry Wt	64.1 (56.3 – 76.4)	27.7 (19.2 – 32.4)	8.2 (4.5 – 11.8)

Assuming that caudal fat reserves are distributed randomly within the tail, the amount of tail fat stored within each region of the tail should be in accordance with the available space. The space available to store energy reserves in each tail third was estimated by the dry weight of each section (Table 5.4). On each occasion, however,

the distribution of caudal lipid in both males (Feb: $X^2 = 27.00$, $df = 2$, $P < 0.001$; March: $X^2 = 34.57$, $df = 2$, $P < 0.001$) and females (Feb: $X^2 = 43.51$, $df = 2$, $P < 0.001$; March: $X^2 = 24.22$, $df = 2$, $P < 0.001$) exhibited significant deviation from that expected from the dry weight of each tail section. Examination of the standardised residuals confirmed that this deviation was caused by a strong preference for storing fat within the proximal section of the tail (Table 5.5).

Table 5.5 Distributional preferences for fat storage expressed as standardised residuals (after Terry *et al.* 1987) based on the dry weight of each tail section and the proportion of fat stored in each section. Shaded values indicate that the distribution of caudal lipid is biased towards that section.

Month	Sex	Tail Section		
		Proximal	Middle	Distal
Feb	Male	3.14	-3.14	-2.87
	Female	3.92	-4.49	-2.76
March	Male	3.47	-3.79	-2.86
	Female	2.87	-2.88	-2.77

5.3.2 Tail regeneration rates of adults

The rate of tail regeneration was significantly faster in females than in males (Table 5.6) (1-way ANOVA: $F_{1,29} = 59.52$; $P = 0.0001$), suggesting that the energetic demands of gestation may have not been substantial.

Table 5.6 The rate of tail regeneration of males and females held in captivity for use in experiments described in Chapter 3 (\pm s.e.)

Sex	N	Rate of Tail Regeneration	
		\pm s.e.	
		(mm/week)	
Male	15	1.18	0.069
Female	15	1.78	0.034

The energetic 'cost' of replacing the tail was examined by comparing the size of abdominal fat bodies three months after the removal of the tail in experimental

animals (Table 5.7). A two-way ANCOVA revealed a significant difference between treatment groups ($F_{1,37} = 10.00$; $P = 0.0033$); however, sex ($F_{1,37} = 1.88$; $P = 0.1797$) and the treatment-sex interaction ($F_{1,37} = 2.93$; $P = 0.0961$) were found to be non-significant. A *post-hoc* Fisher's LSD test for pre-planned comparisons found that males with regenerating tails had larger abdominal fat stores than control animals ($P = 0.0014$), while there was no significant difference in the size of abdominal reserves of females ($P = 0.3007$). This increase in abdominal fat body size following autotomy, is probably due to the abdomen becoming the sole energy store, whereas tailed animals can distribute their fat reserves in both the body and tail. Snout-vent length was found to have a significant influence on abdominal fat body size ($P = 0.0037$). These animals were well fed in captivity; therefore body size appeared to influence the size of fat reserves an individual could accumulate.

Table 5.7 Wet weights of abdominal fat bodies (mg \pm s.e.) of tailed (control) and tailless (experimental) animals of each sex three months after tail autotomy. Values represent least squares means as there was a significant co-variate effect (SVL; $P = 0.0037$).

Sex	Group	N	LSMean	\pm s.e.
Abdominal Fat body size (mg)				
Male	Control	10	213.3	20.32
	Experimental	9	316.1	21.19
Female	Control	10	220.2	20.17
	Experimental	9	251.8	21.87

5.3.3 Growth and tail regeneration rates of juveniles

Juveniles assigned to both the control and experimental groups exhibited a similar increase in SVL over the eight-week period of this study (Table 5.8). A randomised complete block ANOVA showed that there was no significant difference in the growth of tailed and tailless juveniles ($F_{1,23} = 0.03$; $P = 0.8594$). Maternal size, however, had a significant influence on the growth of juveniles ($F_{1,23} = 4.85$; $P = 0.0072$).

Table 5.8 Least squares mean increase in SVL (\pm s.e.) of tailed (control) and tailless (experimental) juveniles over an eight-week period

Treatment (n = 12)	LSMean Growth (mm)	\pm s.e.
Control	1.48	0.130
Experimental	1.52	0.130

The rate of tail regeneration in juveniles (0.61 ± 0.104 mm/week) was slower than that seen in adults (Section 5.3.2). Although juveniles had regeneration rates half that of males and one-third that of females, they are approximately one-third the size of adults. Therefore, the regeneration rate appears to be quite rapid in juveniles.

5.4 DISCUSSION

5.4.1 Energetic value and fat distribution within the tail

Although the energetic impacts of caudal autotomy on processes such as growth (Congdon *et al.* 1974, Vitt *et al.* 1977, Ballinger and Tinkle 1979, Smith 1996, Niewiarowski *et al.* 1997) and reproduction (Smyth 1974, Dial and Fitzpatrick 1981, Wilson and Booth 1998) have been documented in a variety of squamate species, the value of the tail in terms of the energetic reserves it holds is poorly understood. Only a limited number of attempts have ever been made to determine the relative contribution that tail fat makes towards the total energetic reserves. The three studies that have been completed, however, highlight how valuable the tail may be and provide an explanation for the often severe energetic costs that result from tail autotomy. Thus, the percentage of the entire fat stores housed in the tail was 48.2-74.7% in the skink *Lygosoma laterale* (Clark 1971), 50% in three species of *Eumeces* skink (Vitt and Cooper 1986), and 60% in the gecko *Coleonyx brevis* (Dial and Fitzpatrick 1981). In the present study, *Niveoscincus metallicus* was found to store 55-78% of its total energy reserves in its tail, a finding consistent with these values.

This finding potentially has far reaching ramifications. It has generally been assumed that the abdominal fat bodies constitute the primary source of energetic reserves in

‘Costs’ of caudal autotomy in *Niveoscincus metallicus*

lizards. As a result most studies that have investigated the energetics of lizard behaviour, ecology and reproduction have focused exclusively on abdominal reserves (Hahn and Tinkle 1965; Brackin 1979; Castilla and Bauwens 1990; Ramirez Pinilla 1991, 1995; Diaz *et al.* 1994; Galan 1996; Martori and Aun 1997). However, this study has demonstrated that, in species such as *N. metallicus* that possess both caudal and abdominal fat reserves, the caudal reserves may represent the major energetic reserve (see also Clark 1971, Dial and Fitzpatrick 1981, Vitt and Cooper 1986). Therefore, basing conclusions about the energetic costs of seasonal processes such as reproduction and hibernation on cycles in abdominal fat stores may be unreliable as only half the picture has been obtained.

Lipids stores represent a biochemically efficient mechanism for storing energy which may be utilised for a range of purposes at a later date (Derickson 1976). Therefore, seasonal periods of fat reserve accumulation and utilisation may result in the occurrence of lipid cycles (Derickson 1974, 1976). This cycling is usually related to the animal's life-history and, consequently, may cycle in response to winter hibernation, reproduction, or both (Derickson 1976). Such cycles are generally negatively correlated with periods of hibernation and reproduction, indicating that these processes are energetically expensive (Derickson 1976). Accumulation of energy reserves may be indicative of abundant food availability or periods of intense foraging activity in preparation for hibernation or reproductive investment. However, since this study was completed over the course of the activity season for *N. metallicus* at Clarence Lagoon, only fat body cycles in relation to reproductive effort could be investigated directly.

In general the total fat stores increased between each period of sampling. Both sexes exhibited their lowest levels of energetic reserves early in the season, soon after emergence, with energy reserves increasing over the season, presumably in preparation for the next overwintering period (i.e. cycling in response to hibernation; negative correlation). Males possessed small fat stores in November, with a substantial increase in energetic reserves by February, which was maintained through to March. This increase in energy stores is inversely correlated with testicular development which decreased over the season. As a result of this negative

relationship between reproductive activity and energy reserves, spermatogenesis may be energetically costly in male *N. metallicus*. However, females laid down the majority of their fat reserves, following parturition. This indicates that either there are substantial energetic costs to pregnancy in viviparous females or that their feeding opportunities during pregnancy are limited (i.e. cycling in response to reproduction and hibernation; negative correlation). This finding supports the suggestion (Hodson 1991) that variation of energetic reserves in female *N. metallicus* is a result of reproductive effort, in relation to both vitellogenesis and placental nutrition.

Derickson (1974) has shown previously that abdominal fat is mobilised more rapidly than caudal fat. He found that although each fat store, abdominal and caudal, exhibited seasonal cycling in an iguanid, *Sceloporus graciosus*, the cycles were asynchronous with abdominal reserves being used primarily for hibernation, while caudal reserves were used for reproductive effort. However, Avery (1970) found that the lacertid, *Lacerta vivipara*, utilised both abdominal and caudal fat in the same proportion during winter hibernation (i.e. synchronous cycles).

Variation in the fat stores of *N. metallicus* was evident over the season; however, the proportional contributions of caudal and abdominal sources did not vary. Although seasonal variation in abdominal reserves was more pronounced than that observed for caudal fat stores, a significant relationship was found between the mass of fat bodies present at these two storage sites. This relationship did not vary significantly between sexes or over the course of the season, except for females in November and February (i.e. during gestation for the population studied). These differences were largely due to extremely small abdominal fat bodies. It seems likely that some factor(s) associated with gestation, such as reduced feeding rates (e.g. Schwarzkopf 1996), may have distorted the relationship. Males also had small abdominal fat stores at the time of maximum gonadal development (at least in this study), suggesting that these stores may be used in preference to caudal reserves for gamete production. In both sexes, there was a greater proportional increase in abdominal fat following maximal reproductive activity than for caudal fat. As a consequence, predicting the size of the caudal reserves using abdominal-caudal fat correlations may be unreliable during periods of reproductive activity due to preferential use of a particular energetic store.

Due to the substantial energetic value of the tail, caudal autotomy may result in the sacrifice of a significant proportion of the animal's energy reserves. The paradoxical nature of this phenomenon has been the spur for most of the work on the energetic costs of tail loss. Why do lizards store vital energetic reserves in an expendable body section? Although this question remains unanswered, several species of lizards have developed anatomical or behavioural modifications to reduce the impact of this paradox. The first adaptation present in *N. metallicus* to limit loss of energy reserves during caudal autotomy appears to be 'economy of autotomy'. Daniels (1985a) suggested that this mechanism may be important in conserving energy reserves except when the animal's future survival is at risk. Complete tail loss may occur only when it is essential for survival, as larger portions of tail act to distract predators for a longer period of time (Dial and Fitzpatrick 1983). This adaptation appears to be present in *N. metallicus*, since the tail is capable of being lost along its entire length and field populations exhibit a large degree of variation in the position of tail loss (Chapter 7).

My results suggest a second possible adaptation to limit the loss of energetic reserves: the localisation of the bulk of the caudal reserves into the proximal third of the tail; this has not previously been documented. Caudal autotomy is widely believed to represent a primitive squamate feature (Arnold 1984, 1988), which during the course of squamate evolution may have co-evolved with a range of morphological and behavioural traits (Zani 1996). The potential benefits of caudal autotomy are substantial, as evidenced by the high frequency of tail loss in many populations and the re-evolution of a homologous form of autotomy in lineages that previously lost the capacity to shed their tails (Arnold 1984, 1988). However, lizards such as *N. metallicus* appear to have turned one of their greatest assets into their achilles heel by storing fat in their tail. The preferential storage of caudal fat close to the body may allow this species to have the best of both worlds. The distributional bias acts to limit the amount of caudal energy reserves lost during autotomy, while providing a portion of tail of sufficient length to distract the predator while it escapes. Minimising the amount of fat lost during autotomy is likely to enhance future survival and, presumably, is a trait that would be positively selected for. Coupling this adaptation with economy

of autotomy provides a very effective mechanism for minimising the energetic costs of tail loss, permitting a high frequency of autotomy in this species (see Chapter 7).

5.4.2 Costs and energetics of tail regeneration

Tail regeneration is associated with intensive cellular and physiological activity (Bellairs and Bryant 1985) and, therefore, regrowing the tail following autotomy is generally considered to be energetically expensive. It is assumed that energy is likely to be diverted away from growth and reproduction in order to fuel these regenerative processes (Congdon *et al.* 1974, Vitt *et al.* 1977, Dial and Fitzpatrick 1981). Variation in the magnitude of these existing commitments, and therefore the ‘cost’ of tail loss, may result in sexual differences in the rate of tail regeneration (Congdon *et al.* 1974, Vitt 1981). In the present study, *N. metallicus* females had a significantly faster rate of tail regeneration than males. This result is surprising given that females were pregnant over the majority of the study and had a lower feeding rate (pers. obs.), while sperm production in males is generally considered to be energetically cheaper compared to female reproductive investment (e.g. Olsson *et al.* 1997).

The ‘costs’ of tail loss and regeneration, however, are not the sole determinates of the rate of tail replacement. Temperature, photoperiod and other extrinsic factors may influence the rate of tail regeneration (Turner and Tipton 1972, Ndukuba and Ramachandran 1988, Ramachandran and Ndukuba 1989, Suresh and Hiradhar 1990, Oppliger and Clobert 1997). Females over the course of pregnancy maintained temperatures that were lower than that of males, and basked more frequently than males (Chapter 4). This switch in behaviour during pregnancy may have indirectly influenced the rate of tail regeneration in females. Certainly, the lower temperatures maintained by females were closer to the optimal performance temperature of *N. metallicus* (26 °C; Melville 1998, C. McCoull, pers. comm.), so may well have been closer to the optimal temperature for tail regeneration. However, any reason for the observed difference in tail regeneration rate are purely speculative at this time.

My study attempted to test the assumption that tail regeneration is energetically expensive in lizards. However, three months after tail loss, animals that were

regenerating their tails had larger abdominal fat bodies than those with complete tails, although this difference was only significant in males. *Ad libitum* feeding of *Niveoscincus* species usually results in abdominal fat bodies several times their normal size (Olsson *et al.* 2000, present study). Animals that were regenerating their tails probably had sufficient food intake to enable caudal replacement to occur with minimal cost. Body size (SVL) was related to the weight of abdominal fat reserves; therefore since the food supply was abundant the storage space for fat reserves may have been a limiting factor. Without their primary storage area tailless lizards have to store all their energy reserves in the abdominal fat bodies, whereas tailed lizards can distribute their reserves in both the body and tail. This may have resulted in tailless lizards having larger abdominal fat reserves, but lower overall energy stores. Alternatively this increase in abdominal fat following autotomy may represent a strategy to divert energy reserves into the abdomen rather than commit them to tail regeneration. However, since the tail was replaced rapidly in both sexes over the course of the study further research is required to obtain evidence for the existence of such a strategy.

5.4.3 The impact of tail loss in neonates

Energetically, caudal autotomy at birth appeared to have no impact on newborns. Although they experience inhibited mobility following tail loss (Chapter 3), tail loss was no significant detriment to the growth rate of newborns. Clutch effects were found to be a stronger determinate of juvenile growth rate than the presence or absence of the tail. Such maternal effects are common within squamate reptiles, presumably due to differential provisioning of energy reserves during vitellogenesis and gestation and differences in the rate of energy utilisation by embryos during development. The rate of tail regeneration was rapid, with most juveniles regrowing one to two thirds of their tail over eight weeks. Therefore, since growth was uninhibited by tail loss and regeneration occurred rapidly, the energetic impact of caudal autotomy are assumed to be insignificant.

If tail loss imposed an energetic ‘cost’ to newborns, a trade-off between growth and regeneration would have been expected. Such trade-offs have been found in several

previous studies (Ballinger and Tinkle 1979, Smith 1996, Niewiarowski *et al.* 1997) but not in all (Vitt and Cooper 1986, Althoff and Thompson 1994, Van Sluys 1998, Fox and McCoy 2000). Several explanations are possible for their absence. The priorities of adults and juveniles must differ significantly, so it is possible that caudal autotomy may be energetically costly in adults, but not in juveniles. As mentioned previously, *N. metallicus* readily eats in captivity; consequently, food intake may have been sufficient to enable both growth and tail regeneration to occur uninhibited. The existence of caudal fat reserves in juvenile *N. metallicus* is yet to be established, and it is possible that neonates may lack these stores. It may well be that the only penalty imposed by tail loss in neonate *N. metallicus* is a relatively short-lived restriction on locomotory ability.

CHAPTER 6

REPRODUCTION

6.1 INTRODUCTION

The fitness of an individual is ultimately dependent on its ability to successfully reproduce and maximise its lifetime reproductive output. Morphological modifications that optimise the potential for an animal to procreate will therefore possess considerable selective advantages. The evolution of viviparity within squamate reptiles is believed to represent such an adaptation. Prolonged retention of eggs enables maternal manipulation and regulation of the embryonic environment throughout development, ensuring enhanced development and offspring viability (Shine 1985, 1995). However, such embryonic retention requires an enhanced level of reproductive investment and increases the physical burden placed upon the mother. As a result, viviparous squamates absorb several 'costs' such as reduced mobility (Shine 1980, Sinervo *et al.* 1991), an elevated metabolic rate (Beuchat and Vleck 1990, DeMarco and Guillette 1992, DeMarco 1993), modified thermoregulatory behaviour (Stewart 1984; Beuchat 1986; Schwarzkopf and Shine 1991, 1992; Brăna 1993; Daut and Andrews 1993; Tosini and Avery 1996; Andrews *et al.* 1997; Mathies and Andrews 1997), altered antipredatory behaviour (Bauwens and Thoen 1981, Schwarzkopf and Shine 1992) and a decreased food intake (Schwarzkopf 1996). Due to the extended gestation period and elevated level of reproductive investment, tail loss, with its associated loss of energetic reserves (Chapter 5), may impose some additional 'costs' upon viviparous lizards.

Most research concerning the reproductive 'costs' of tail loss has been focussed on the possibility of either a reduced vitellogenic investment due to the loss of fat reserves (i.e. reduced future reproductive potential) (Smyth 1974, Dial and Fitzpatrick 1981, Wilson and Booth 1998), or a decrease in mating opportunities of males as a result of lowered social status and reduced home range area (Fox and Rostker 1982, Fox *et al.* 1990, Martin and Salvador 1993c, Kaiser and Mushinsky 1994, Salvador *et al.* 1995, 1996). However, the potential for a proximal impact of maternal tail

autotomy on current embryonic development and the resultant offspring phenotype has not been investigated.

Niveoscincus metallicus, a viviparous skink, provides an opportunity to study the effect of caudal autotomy on current reproductive investment and offspring quality, as it is predominantly lecithotrophic with some degree of placentotrophy (Swain and Jones 1997, Jones *et al.* 1998, Thompson *et al.* 1999a). This enables tail loss, depending on its timing, to impact on the size and number of eggs during late vitellogenesis (cost to future fecundity) and the degree of placental nutrition during late pregnancy (cost to current clutch). Either of these impacts could potentially influence the reproductive output or quality and viability of the offspring. For example, tail loss prior to the commencement of, or during, vitellogenesis may retard follicular recruitment or reduce the yolk allocation to each egg.

The chorioallantoic placenta in *N. metallicus* is intermediate in complexity between simple placentae and the most complex known (Stewart and Thompson 1994). Placental transport of water, ions, amino acids, sodium, potassium, proteins and lipids has been demonstrated in this species (Swain and Jones 1997, Thompson *et al.* 1999a). It is this capability for placental nutrition that allows facultative placentotrophy to occur in this species. The presence of facultative placentotrophy is considered to constitute a strategic adaptation that provides flexibility in embryonic nutrition and optimises embryonic fitness in an unpredictable environment (Swain and Jones, in press a). However, the reduction in energy reserves due to tail loss may restrict a mother's ability to perform facultative placentotrophy, resulting in offspring smaller in weight and size.

In this chapter, two experiments were conducted to examine the proximal and future reproductive 'costs' of tail loss. Tail loss during gestation in *Niveoscincus metallicus*, prior to the onset of facultative placentotrophy, may impose a proximal (immediate) impact on the current clutch. A laboratory-based experiment was conducted to investigate the role of caudal fat and tail removal on the capacity for facultative placentotrophy. A field-based experiment was used to shed light on the impact of tail loss on future fecundity. Females with natural tail breaks were collected immediately

prior to parturition to determine whether tail autotomy prior to the start, or completion of vitellogenesis influenced clutch size or offspring characteristics. The results of these experiments were used to investigate a series of questions concerning the reproductive ‘costs’ of tail loss.

- 1) Does maternal tail loss during vitellogenesis influence future reproductive capacity?
- 2) Does caudal autotomy during late pregnancy, when facultative placentotrophy occurs, act to decrease placental nourishment to embryos, resulting in offspring of smaller size and weight?
- 3) Does maternal tail loss result in the female being exposed to different environmental conditions, impacting upon the embryonic environment and offspring phenotype?

6.2 MATERIALS AND METHODS

6.2.1 Future Reproductive Costs

Forty-three pregnant females were collected at embryonic stage 40 from Clarence Lagoon as described in Section 2.2. Dissection of females caught at the same time for use in another experiment (Section 5.2.3) confirmed that embryos were fully developed and at stage 40. Upon return to the laboratory, each female was weighed (± 0.1 mg), with measurements taken of SVL, tail length, tail break length, tail regeneration length (± 0.1 mm). Every female was given a unique toe-clip, and they were randomly housed in pairs under standard conditions until they gave birth. Females were fed twice weekly to allow them to maintain condition.

All females gave birth within two and a half weeks of arrival in the laboratory. Cages were checked twice daily for births. Newborns and their mother were removed from the cage upon birth. The sprint speed of each newborn was measured within 24 h of birth as described in Section 3.2.3. Two juveniles were chosen at random from each clutch and maintained in the laboratory under standard juvenile housing conditions to assess their growth rate. In the case of clutch sizes of two, only the growth of one

individual was measured. These juveniles were weighed (± 0.1 mg) and measured (SVL, tail length; ± 0.1 mm) within 24 h of birth and every subsequent 2 weeks for eight weeks. The remaining newborns, along with their mother, were frozen at -20°C and stored for determination of fat reserves.

Once all females had given birth, all mothers and newborns frozen for assessment of fat reserves were thawed. Each mother was re-weighed and measured and dissected as described in Section 5.2.3. The number of corpora lutea was used to confirm the clutch size of each female and confirm that no mothers had consumed any stillborns or other newborns. Abdominal and tail fat stores of females were also determined, as described in Section 5.2.1. Newborns were weighed (± 0.1 mg) and measurements taken of SVL and tail length (± 0.1 mm). They were also dissected to quantify their abdominal fat reserves.

6.2.2 The effect of tail loss on facultative placentotrophy

Niveoscincus metallicus exhibits some degree of facultative placentotrophy (Swain and Jones in press a), with maximal placental complexity and nutrient transfer occurring between embryonic stages 35 and 40 (Swain and Jones 1997). Twenty females, held in captivity for use in Chapter 4 (Section 4.2.2), were used in this experiment which investigated the effect of tail autotomy prior to the onset of facultative placentotrophy at stage 35.

Caudal autotomy was induced in 10 females, as described in Section 4.2.2.1, with the remaining 10 females acting as the control tailed group. Dissection of females collected at the same time as the animals used in this experiment (Section 5.2.1), indicated that the developing embryos had reached stage 31-32. Females were housed in pairs as described in section 4.2.2.2. Females began giving birth 5-6 weeks after arrival in the laboratory, with all births completed within 10 days. Maternal terraria were checked twice daily for newborns. Juveniles were weighed and sprinted as described in Sections 2.4 and 3.2.6.

6.2.3 Data Analysis

All data analyses were completed using the SAS System for Windows® v6.12. However, prior to the commencement of any data analysis of the animals collected in Section 6.2.1, two procedures were completed. An estimate of the initial tail length (predicted original length) was obtained for each lizard. This was achieved through the completion of a simple linear regression. Snout-vent length was regressed against tail length in animals which exhibited no signs of autotomy, that yielded an equation for predicting the original tail length (OTL) of each animal from their SVL. This original tail length was used to determine where along the length of the tail autotomy occurred (break index = break length/OTL) and the size of the present tail in relation to its original length (index of recovery = current tail length/OTL).

A correlation matrix was obtained for all the maternal and juvenile characteristics recorded to reduce the number of variables. Eliminating correlated factors reduces the possibility of multicollinearity (a violation of the assumptions of sequential regression; Tabachnick and Fidell 1989). All juvenile characteristics were clutch averages. When two variables were highly correlated ($|r| > 0.7$), only the one most relevant for the purposes of the experiment was retained. For example, SVL and weight were correlated, so only SVL was used as a measure of size in the study. This is because mass, especially in small lizards, may reflect changes in recent nutritional history rather than change in body size (Dunham 1978). The selected variables were used to investigate whether: a) the timing of tail loss influences either clutch size or juvenile morphology (1-way ANCOVA); or b) tail length (or location of break) is related to offspring phenotype (Sequential Regression).

The forty-three animals collected during late pregnancy (Section 5.2.1) were assigned to one of four groups, each containing approximately 10 individuals. The formation of these groups was done on the basis of two factors: a) the break index (see Chapter 5); and b) the length of the regenerated tail (Figure 6.1). Low break indices were indicative of proximate tail breaks, while high indices suggested more distal tail breaks, and regenerated tails smaller in length indicated more recent tail autotomy.

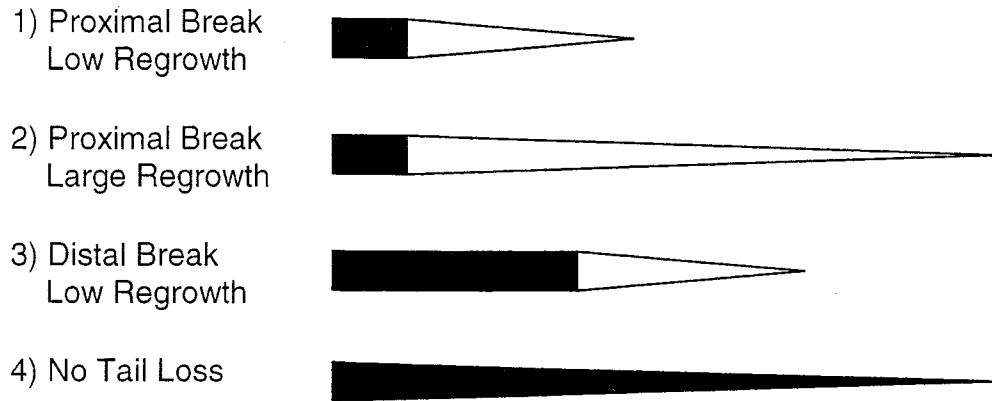


Figure 6.1 Criteria for assigning lizards into one of four groups on the basis of the location of tail break and tail regeneration. Black indicates the unbroken portion of tail and white indicates the regenerated tail section.

Group 1 lizards were animals with both proximal tail loss (i.e. fat loss) and limited tail regeneration ($n = 10$). Lizards in group 2 exhibited proximal tail breaks with tails that were almost completely regenerated (control for regeneration; $n = 8$). Animals assigned to Group 3 had evidence of breaks in the distal portions of their tail, with a small amount of tail regeneration (control for fat loss; $n = 14$). Group 4 lizards exhibited no signs of previous tail loss (control for fat loss and regeneration; $n = 10$).

The formation of these groups relied on two assumptions. The first was that the rate of tail regeneration was constant across each of the three groups that exhibited tail loss. The rate of tail regeneration was estimated using the regeneration rates observed in the laboratory (Section 5.3.2) as a guide. Since animals in the laboratory were fed *ad libitum* and able to bask for 10 h per day every day, the rate of tail regeneration was assumed to be 50-60% of that observed in the laboratory. At Clarence Lagoon the weather is extremely unpredictable (Section 2.1) and lizards, over their activity season, are likely to average no more than 3-4 days per week when they are able to be active and bask. Taking these factors into account the timing of tail loss in groups 1 and 3 was estimated to be immediately prior to or during vitellogenesis, but before emergence and ovulation. Tail loss in group 2 was estimated to have occurred in the previous activity season, during the previous gestation, since tail regeneration was nearing completion.

The second assumption was that animals that lost their tail in the proximal third should experience a substantial level of fat loss, since this is the major area of energetic reserves (Chapter 5). However, animals with tail loss of any description were assumed to suffer an energetic cost of regeneration, through the diversion of energy reserves from reproduction into the regeneration process (e.g. Congdon *et al.* 1974, Vitt *et al.* 1977, Dial and Fitzpatrick 1981). On the basis of these assumptions the four groups were deemed to allow the determination of whether the loss of tail fat or the diversion of energetic reserves, or both, are responsible for any decrease in reproductive investment, current or future.

Differences between these four groups in terms of clutch size and offspring morphology were analysed using a one-way ANCOVA design with maternal size as the co-variate. For each offspring trait the following sequence was conducted. Firstly, the significance of the co-variate was tested. If not significant, the analysis became a 1-way ANOVA; however, when significant the analysis continued. The assumption that each treatment had identical group regression slopes was tested by assessing the significance of the treatment*co-variate interaction. In every instance this assumption was met, allowing the analysis to continue. The linearity of the relationship between the offspring trait (dependent variable) and maternal size (co-variate) was evaluated by examining a plot of the residuals versus the co-variate and assessing the normality of residuals. This assumption was met for each offspring trait. Finally the independence of residual variances and the response variable was assessed by examining a plot of residuals versus predicted values and comparison of the variances of residuals among groups. *Post-hoc* HSD (when ANOVA) or LSD (when ANCOVA) tests were used to investigate treatment differences.

The influence of maternal tail length on offspring phenotype was assessed using sequential regression. Initially maternal SVL was regressed against each juvenile characteristic separately. For each analysis two additional maternal factors were added one at a time, first clutch size, then total maternal fat, to determine whether they significantly improved the model. Once a baseline relationship was obtained that contained one or more of these factors, tail loss was then added to determine whether maternal tail size improved the relationship already established. A significant

improvement indicated that the size of a mother's tail had an influence on her offspring's phenotype or sprint speed. This analysis was completed for each of the five juvenile characteristics investigated in the study.

The impact of tail loss on facultative placentotrophy in late gestation was analysed using either a 1-way ANCOVA or ANOVA, depending on the significance of the covariate (SVL). The analysis was conducted as described above for the field study.

6.3 RESULTS

6.3.1 Future Reproductive Costs

Ten of the 43 pregnant females collected lacked any evidence of caudal autotomy. A regression analysis completed on these animals yielded a significant relationship between SVL and tail length ($R^2 = 0.7321$; $F_{1,9} = 32.792$, $P = 0.0001$). This equation was used to predict the original tail lengths of the remaining animals that displayed signs of previous tail loss. The break index of each animal was calculated using this regression equation (see Section 6.2.3).

The level of reproductive investment of females in each of the four groups differed significantly (Table 6.1). Average clutch size varied significantly between the four groups (ANCOVA: $F_{3,37} = 3.81$, $P = 0.0178$). Groups 2 and 4 had substantially larger clutch sizes than groups 1 and 3. A *post-hoc* LSD test revealed that these differences were significant. However, the relative clutch mass (RCM; clutch mass/maternal mass) of each group did not differ significantly (ANOVA: $F_{3,38} = 1.90$, $P = 0.1458$). Since groups 2 and 4 had substantially higher clutch sizes, but RCM was constant between groups, mothers from groups 1 and 3 probably gave birth to a smaller number of larger offspring (see Table 6.2).

These two analyses show that within the four groups there are two distinct pairs, 1-3 and 2-4. The separation of these groups appears to be on the basis of recency of tail loss (i.e. groups 1 and 3 both have recent tail loss and regeneration), rather than the location of tail break and associated loss of fat stores.

Table 6.1 Average clutch sizes and relative clutch masses (RCM; combined clutch mass/*post-partum* maternal mass) for females assigned to each of the four groups. Group 1 = proximal tail loss, little regeneration; Group 2 = proximal tail loss, complete regeneration; Group 3 = distal tail loss, little regeneration; and Group 4 = no tail loss. The asterisk indicates that the co-variate SVL was not significant; therefore actual means are shown and the analysis is a 1-way ANOVA.

Offspring Trait	Group	lsmean	s.e.	ANCOVA		
				df	F	P
Clutch Size	1	2.88	0.192	3, 37	3.81	0.0178
	2	3.48	0.218			
	3	2.82	0.162			
	4	3.49	0.191			
RCM*	1	0.25	0.019	3, 38	1.90	0.1458
	2	0.29	0.022			
	3	0.23	0.149			
	4	0.26	0.017			

Juvenile phenotype, growth and locomotory performance at birth all differed between the four groups (Table 6.2). Thus, average SVL was significantly different (ANOVA: $F_{3,38} = 5.77$, $P = 0.0024$), with groups 1-3 and 2-4 again separating out. Groups 1 and 3 produced larger offspring than either groups 2 or 4, but a *post-hoc* Tukey's HSD test revealed that only group 3 juveniles were significantly larger than those from groups 2 and 4. The average tail length of juveniles also differed significantly between groups (ANOVA: $F_{3,38} = 3.26$, $P = 0.0319$). Juveniles born to females in group 3 had larger tails than those from other groups, with group 4 newborns possessing the shortest tails of any group. A *post-hoc* Tukey's HSD test showed that the tail length of group 3 juveniles exceeded that of group 4 juveniles only.

Table 6.2 Juvenile morphological characteristics, sprint speed, and growth over 8 weeks for juveniles from mothers assigned to one of four groups. Means were calculated from clutch averages for each mother within a group. The co-variate was non-significant for all analyses; therefore ANOVA was used.

Offspring	Group	Means	s.e.	ANOVA		
Trait				df	<i>F</i>	<i>P</i>
SVL (mm)	1	23.34	0.196	3, 38	5.77	0.0024
	2	22.82	0.216			
	3	23.55	0.128			
	4	22.79	0.117			
Tail Length (mm)	1	26.19	0.328	3, 38	3.26	0.0319
	2	26.47	0.780			
	3	27.38	0.334			
	4	25.71	0.247			
Fat Stores (mg)	1	2.37	0.445	3, 38	0.54	0.6584
	2	2.33	0.311			
	3	2.49	0.236			
	4	1.97	0.222			
Sprint Speed (m sec ⁻¹)	1	0.36	0.011	3, 38	0.65	0.5889
	2	0.39	0.018			
	3	0.38	0.011			
	4	0.38	0.017			
Growth (mm)	1	1.38	0.127	3, 35	1.84	0.1578
	2	1.81	0.213			
	3	1.31	0.144			
	4	1.49	0.108			

The locomotory performance of juveniles at birth showed no differences (Table 6.2) (ANOVA: $F_{3,38} = 0.65$, $P = 0.5889$). Likewise, there were no differences in abdominal fat stores at birth ($F_{3,38} = 0.54$, $P = 0.6584$) or the rate of growth over the first eight weeks ($F_{3,38} = 1.84$, $P = 0.1578$). Although juveniles from group 4 had substantially lower levels of abdominal fat at birth (17-21% less) than the other three groups. Presumably the high level of variability led to this result being non-significant.

Although animals with evidence of tail loss during vitellogenesis (Groups 1 and 3) had significantly smaller clutch sizes, the ‘quality’ of their offspring was not adversely affected. In fact, for some traits their young were ‘better’. These juveniles had slightly larger abdominal fat bodies at birth (ns), trivially lower growth rates (ns) and similar locomotory abilities to those from larger clutches (i.e. Groups 2 and 4).

6.3.2 Tail length and offspring phenotype

Maternal tail length was investigated as a possible influence on juvenile phenotype using sequential regression. Juvenile size (SVL) was not related to maternal SVL ($R^2 = 0.0157$; $F_{3,40} = 0.638$, $P = 0.4290$). The addition of clutch size, however, significantly improved the regression model (Model: $R^2 = 0.1902$; $F_{3,39} = 4.581$, $P = 0.0163$; Significance of Addition: $F_{1,39} = 8.406$, $P < 0.01$). Adding maternal fat stores (Significance of Addition: $F_{1,38} = 2.55$, $P > 0.10$), tail length ($F_{1,38} = 0.26$, $P > 0.50$) and break index ($F_{1,38} = 1.15$, $P > 0.25$) failed to improve the model. A combination of clutch size and maternal size (mainly clutch size) was therefore the only factors that were significantly related to juvenile size (final model listed above).

The tail length of juveniles was not influenced by maternal size SVL ($R^2 = 0.0083$; $F_{3,40} = 0.337$, $P = 0.5651$), but the addition of clutch size (Model: $R^2 = 0.1488$; $F_{3,39} = 3.41$, $P = 0.0432$; Significance of Addition: $F_{1,39} = 6.434$, $P < 0.025$) and maternal fat reserves (Model: $R^2 = 0.2947$; $F_{3,38} = 5.292$, $P = 0.0038$; Significance of Addition: $F_{1,38} = 7.858$, $P < 0.01$), in turn, each significantly improved the model. Adding maternal tail length (Significance of Addition: $F_{1,37} = 0.361$, $P > 0.50$) or break index ($F_{1,37} = 1.932$, $P > 0.10$) to this baseline model failed to result in a significant

improvement. The final model therefore was that for SVL, clutch size and maternal fat size (listed above).

Juvenile abdominal fat mass at birth was not related to maternal SVL ($R^2 = 0.0087$; $F_{3,40} = 0.349$, $P = 0.5579$), but again clutch size significantly improved the regression model (Model: $R^2 = 0.2370$; $F_{3,39} = 6.056$, $P = 0.0051$; Significance of Addition: $F_{1,39} = 11.669$, $P < 0.005$). The addition of maternal fat stores (Significance of Addition: $F_{1,38} = 1.429$, $P > 0.10$), tail length ($F_{1,38} = 0.232$, $P > 0.50$) and break index ($F_{1,38} = 0.044$, $P > 0.75$) were all unable to significantly improve the model. Clutch size therefore seems to be the major determinate of juvenile fat body size (final model listed above).

Juvenile sprint speed and growth rate were not related to any of the five maternal characteristics. In no cases did maternal tail length or the break position correlate with any aspect of juvenile phenotype, performance or growth.

6.3.3 The effect of tail loss on facultative placentotrophy

Eighteen pregnant females, ten tailed (control) and eight tailless (experimental) animals, were used for this experiment. The co-variate maternal size was only found to be significant for clutch size and sprint speed; therefore the analysis turned into a 1-way ANOVA.

Table 6.3 Least squares means (\pm s.e.) for each clutch size and six offspring traits for intact (n=10) and tailless females (n=8). * Indicates that the co-variate (maternal size) was not significant; therefore arithmetic means and ANOVA statistics are presented.

Offspring Trait	Group	Lsmean	s.e.	ANCOVA		
				df	F	P
SVL * (mm)	Control	22.8	0.21	1,17	1.12	0.3046
	Experimental	22.4	0.35			
Weight * (mg)	Control	229.5	6.95	1,17	0.53	0.4749
	Experimental	220.5	10.63			
Tail Length * (mm)	Control	27.1	0.44	1,17	3.20	0.0927
	Experimental	26.0	0.40			
RTL *	Control	1.19	0.010	1,17	3.27	0.0893
	Experimental	1.16	0.009			
Total Length * (mm)	Control	49.9	0.64	1,17	2.43	0.1388
	Experimental	48.5	0.72			
Clutch Size	Control	3.0	0.20	1,17	2.00	0.1776
	Experimental	3.5	0.22			
Sprint Speed (m sec ⁻¹)	Control	0.31	0.018	1,17	0.49	0.4954
	Experimental	0.33	0.020			

The combination of the absence of the tail and energetic requirements of regenerating the tail failed to have any significant effect on juvenile traits or clutch size in experimental animals (Table 6.3). Females in the experimental group gave birth to offspring that were not significantly smaller in SVL, tail length, relative tail length, total length or weight than those born to tailed females. Clutch size and sprint speeds at birth were also similar in both groups. However, the analysis revealed that larger females, regardless of the treatment group to which they were assigned, produced

larger clutches ($F_{1,17} = 34.57$; $P = 0.0001$) with offspring with slower sprint speeds ($F_{1,17} = 5.60$; $P = 0.0319$).

6.4 DISCUSSION

It is difficult to draw any unambiguous conclusions about the findings of some sections of this chapter. The choice and assignment of females to groups was done on the basis of the results obtained previously in Chapter 5 and literature findings. Most previous studies have assumed that decreased reproductive investment during vitellogenesis is the result of either the loss of tail fat during autotomy (Smyth 1974, Wilson and Booth 1998) or the diversion of energy to fuel the process of caudal regeneration (Congdon *et al.* 1974, Vitt *et al.* 1977, Dial and Fitzpatrick 1981). However, the relative importance of each of these energetic costs has never been investigated. The formation of the four groups in this study provided a situation similar to a Factorial ANOVA, allowing the interaction between these two factors to be investigated. Group 1 was presumed to have suffered fat loss during vitellogenesis and to have been involved in the diversion of reserves to tail regeneration during this reproductive period (+ and +, respectively). Group 3 (– +) presumably also lost their tails during vitellogenesis, but the location of the break indicates that no fat was lost; however, diversion of energy to regeneration must have occurred during this period. Group 2 (– –) had effectively recovered from old tail loss and therefore acted as a control for the trauma of tail loss and recovery. Finally, group 4 (– –) exhibited no signs of tail autotomy and served as a control for both loss of tail fat and energy diversion. The nature of tail loss meant that a group with no diversion of energy to tail regeneration but loss of caudal fat (+ –) was not possible. Allocation of animals to these groups was made *post-hoc* and therefore relied on two main assumptions as described in Section 5.2.3.

The assumption that lizards with tail autotomy in the proximal section of the tail lost a substantial portion of their energetic reserves since this is the major site of fat storage (Chapter 5) is probably quite safe. However, the assumption that the timing of autotomy could be estimated from the regenerated length of tail and knowledge of laboratory regeneration rates involved further assumptions. The rate of regeneration

was known for animals in the laboratory, but these animals were fed *ad libitum* and had access to 10 h of basking light every day. I estimated that, at Clarence Lagoon they would only be able to bask for half this amount of time per week. Consequently, the laboratory rate of tail regeneration was arbitrarily adjusted to provide an estimate of recovery under field conditions. The fact that this provided a very clear separation of groups may indicate that my estimate was reasonable. However, the large number of assumptions involved means that this section of my work should be viewed as a preliminary approach designed to provide ideas for future, more rigorous work.

The timing of tail loss may have a profound influence on reproductive investment and success in *N. metallicus*. This species has two major periods of reproductive investment, vitellogenesis (Jones *et al.* 1998, Thompson *et al.* 1999a) and late gestation (i.e. placental nourishment; Swain and Jones 1997, in press a). However, this species remains primarily lecithotrophic, with placental nutritional supplying only supplementary resources (Jones *et al.* 1998, Swain and Jones, in press a). Autotomy during vitellogenesis, therefore, is likely to have a more profound effect on current reproductive investment. The present study investigated this hypothesis by investigating the impact of tail loss during both vitellogenesis (results from Section 5.3.1) and late gestation (Section 5.3.3). However, since clutch size was found to be influenced by tail loss during vitellogenesis (Section 5.3.1), the resultant size and phenotype of the offspring from each group have to be considered in the context of future reproductive costs (i.e. impact while making reproductive decisions for future clutch), rather than current reproductive costs (i.e. investment in clutch following determination of clutch size, e.g. during gestation). The current reproductive costs of autotomy (Section 5.3.3) will therefore be considered separately.

Caudal autotomy while decisions of reproductive investment are being made (i.e. vitellogenesis; Section 5.3.1), regardless of its location along the length of the tail, was found to significantly decrease clutch size (i.e. reproductive investment). The reduction in clutch size in females that lost distal portions of their tail (i.e. did not lose their caudal reserves) suggests that the diversion of energetic reserves away from reproductive effort may be the primary cause of this reduced investment. Rerouting of energy reserves to fuel tail regeneration has been demonstrated in a number of

species (Congdon *et al.* 1974, Vitt *et al.* 1977, Dial and Fitzpatrick 1981). It was suggested in Chapter 5 that the energy for reproductive investment may come primarily from abdominal stores rather than caudal fat stores. This was because caudal fat stores increased in females over the course of gestation, while abdominal stores remained low in this period but increased dramatically following parturition. The evidence now presented suggests that abdominal stores may also be the primary source of energy reserves to fuel tail regeneration. The relative availability of abdominal versus tail fat stores, and the functions that are served by these sources, clearly warrants further investigation.

It is interesting to note that in those cases where tail loss has been presumed to decrease clutch size by direct reduction of caudal fat, the species involved possess only tail fat reserves (e.g. Symth 1974, Wilson and Booth 1998). In these species, therefore, caudal fat reserves are the only source of stored energy for reproduction (Doughty and Shine 1998). Consequently, the loss of these reserves is more likely to have a significant impact on reproductive investment during vitellogenesis.

The major determinant of reproductive output in lizards has been shown to be energetic reserves accumulated more than 12 months previously (Doughty and Shine 1998). In the present study, *N. metallicus* that committed to smaller clutch sizes (Groups 1 and 3) as an apparent response to the diversion of stored energy into tail regeneration, produced young that were superior to those from mothers with larger clutches (Groups 2 and 4). These mothers may have been able to invest more into their individual young. Offspring from smaller clutches had equal growth rates and sprint speeds, but slightly larger fat reserves. However, these individuals were significantly larger in size, and in one instance, they had substantially longer tails. Fox and McCoy (2000) have also reported that offspring from mothers with tail loss are substantially larger than those from tailed mothers. They suggested that this was as a result of tailless females ‘making the best of a bad situation’ by investing more into the current clutch, although they implied that this could be at the detriment of future clutches. However, as far as current fecundity is concerned, it appears that when females are faced with energetic restrictions during vitellogenesis they may be able to trade-off a reduction in clutch size by improving the quality of the young they

do produce. Whether they achieve this by producing a smaller number of larger eggs or by increasing the amount of placental transfer during gestation, or through employing both strategies, presents an interesting question that is worth consideration.

Regardless of the clutch size, food intake during gestation may influence the resultant size of the offspring (Doughty and Shine 1998). Swain and Jones (in press a) found that placental nourishment (i.e. facultative placentotrophy) in *N. metallicus* is unable to compensate for poor yolk supply. It seems unlikely therefore that the animals in groups 1 and 3 committed to fewer and smaller eggs and made up the difference during gestation. However, they may have produced a smaller number of eggs that were better resourced than those from groups 2 and 4, resulting in larger young. In this experiment, at least, reproductive investment during vitellogenesis appeared to be the primary determinate of juvenile phenotype, rather than placental nourishment (i.e. facultative placentotrophy) during gestation.

However, is the production of young that are slightly larger (2 mm) with longer tails (1-2 mm) really beneficial to offspring survival and fitness? Shine and Downes (1999) found that the highly placentotrophic skink, *Pseudemoia pagenstecheri*, when exposed to the scent of a predator during gestation, produced young that had significantly longer tails. This increase in tail length equated to 2-3 mm. Longer tails are usually associated with more successful escape from predators (Arnold 1988), but whether such a small increase in juvenile tail length would significantly enhance survival is uncertain. However, juveniles that are larger at birth may also have larger abdominal fat bodies or faster growth rates (Swain and Jones, in press b), although neither was significant in the present study. Consequently it can only be assumed that animals that are larger at birth, or that have longer tails, are of higher 'quality' and therefore better equipped for survival.

The preceding sections have discussed the impact of tail loss during vitellogenesis; however, caudal autotomy during gestation, after reproductive investment decisions have already been made, represents a separate area of investigation (i.e. current costs). Although, placental nutrition during gestation has been demonstrated in some instances to enhance offspring size and 'quality' (Swain and Jones, in press a), the

preceding discussions concluded that facultative placentotrophy was not the likely mechanism for the observed increased quality of juveniles from small clutches. However, a second experiment (Section 5.3.3) that involved removal of the tail, and its stored fat, prior to the onset of maximal placental transfer was used to verify this conclusion by investigating whether the size of fat reserves are likely to be a limiting factor in the provision of placental nutrition during gestation.

Reproduction is generally seen to be energetically expensive in squamate reptiles (Dial and Fitzpatrick 1981, Vitt and Cooper 1986, Doughty and Shine 1998, Chapter 5). However, the reduction of energetic reserves during tail autotomy failed to have any observable impact on offspring size or sprint speed in *N. metallicus*. This result suggests that placental transfer proceeded uninhibited by tail autotomy, with developing embryos from both tailed and tailless mother presumably receiving equivalent levels of nourishment during gestation (assuming that original follicle size did not differ between groups). There are several possible explanations for the absence of any current reproductive cost.

It was shown in Chapter 5 that the animals held in the laboratory had abdominal fat bodies up to 5 times larger than those found in natural populations. It is likely therefore that the abdominal energy reserves were sufficient to supply the necessary levels of placental nourishment. However, as mentioned previously, most energetic reserves used in reproduction in *N. metallicus* may come from the abdominal stores. The loss of caudal fat, therefore, may be of lesser importance for reproductive effort. Viviparous lizards may decrease their food intake during pregnancy (Schwarzkopf 1996); however, food intake during gestation may influence the size of offspring (Doughty and Shine 1998). Some authors have suggested that food intake may be increased as a result of tail loss to make up the energy shortfall that results from the reduction in caudal reserves (e.g. Dial and Fitzpatrick 1981). *Niveoscincus metallicus* may have been able to increase its food intake enable it to supply placental nourishment to its developing embryos while still achieving rapid tail regeneration (Chapter 5). The final possibility is that reproduction after the initial investment during vitellogenesis (see above) is not energetically costly. Wapstra and Swain (in prep) found that abdominal fat reserves in *N. ocellatus* increased during gestation,

which suggests that placental nutritional may not be energetically expensive. Thompson *et al.* (1999a) recently investigated the compositional changes of ovulated eggs and newborns of *N. metallicus*. Although they found that there was evidence of substantial placental transfer of ions and organic material, this supplementary nourishment was significantly less than species with some degree of obligate placentotrophy (Thompson *et al.* 1999b, c). The relatively small amount of water, ions, and organic matter that crosses the placenta might not be costly for the mother to provide. Consequently, the reduction of caudal fat stores might not impose a major restriction on the ability of a mother to supply placental nourishment. Caudal autotomy during gestation, therefore, does not appear to significantly restrict placental nutrition or impose any reproductive 'cost' on the current reproductive effort.

In *Niveoscincus metallicus* the length of an individual's tail can influence its mobility (Chapter 3) and basking site selection (see Chapter 7). Consequently the environment that an animal is exposed to may be modified due to this restricted movement and behavioural compensation. Such modification of behaviour may alter the embryonic environment during gestation. The thermal and nutritional environment that the mother is exposed to during gestation may have a substantial influence on gestation length and the phenotype of her offspring (Beuchat 1988, Schwarzkopf and Shine 1991, Shine and Harlow 1993, Mathies and Andrews 1997, Sorci and Clobert 1997, Shine and Downes 1999, Swain and Jones in press b, Wapstra in press). However, although tailless *N. metallicus* may modify their behaviour towards crypsis, presumably to limit their risk of predation (Chapter 7), this change in environment during gestation was not found to adversely affect the phenotype of their offspring. Tail length did not significantly improve the sequential regression model for any offspring trait that was recorded.

Most of the offspring phenotypic plasticity found as a result of the maternal environment are in relation to thermal conditions (see above). However, the thermoregulatory characteristics of tailless females were similar to that of tailed females during gestation (Chapter 4). Although *N. metallicus* may alter its basking site selection due to tail loss, caudal autotomy does not affect the manner or characteristics of its thermoregulatory behaviour. Swain and Jones (in press b) found

that the thermal environment of *N. metallicus* during gestation had a substantial impact on offspring phenotype, an effect that could not be compensated for through nutritionally favourable conditions. Thus, the maternal thermal environment during gestation appears to be the major source of phenotypic plasticity (or environmental effects) in squamate reptiles. Consequently, as *N. metallicus* does not alter its thermoregulatory behaviour in response to tail loss (Chapter 4), phenotypic plasticity is unlikely to result even if the individual adopts a cryptic existence or is exposed to a modified environment, since the embryo's thermal environment remains constant.

CHAPTER 7

TAIL LOSS FREQUENCY AND BASKING SITE SELECTION

7.1 INTRODUCTION

7.1.1 Tail loss and survival

It is generally accepted that the fundamental basis of caudal autotomy in lizards is to enable the individual to survive predatory encounters (Arnold 1988). However, although this defensive strategy ensures the immediate survival of the animal, previous chapters have highlighted how the absence of the tail may inflict immediate or long-term ‘costs’ on the animal. Consequently, the probability of future survival may be diminished. However, this work, and the majority of the published research, has involved laboratory-based investigations of locomotion, reproduction, energetics and behaviour. Relatively few studies have taken a holistic approach towards the effect of tail autotomy on the animal’s subsequent survival under natural conditions. All of the four field studies completed to date have involved the iguanid *Uta stansburiana* (Wilson 1992, Althoff and Thompson 1994, Niewiarowski *et al.* 1997, Fox and McCoy 2000). Although in three of these studies a reduced probability of survival was reported (Wilson 1992, Niewiarowski *et al.* 1997, Fox and McCoy 2000), tail autotomy was not always detrimental to an individual’s chance of survival (Althoff and Thompson 1994).

The observation that the ‘costs’ of caudal autotomy do not always culminate in a diminished probability of survival in nature suggests that either these costs may not be as important as laboratory studies suggest, or that morphological and/or behavioural modifications exist to enhance the chance of survival. Depletion of energetic reserves (i.e. starvation) and predation are the two major factors that need to be overcome in order to survive after tail autotomy. Limiting the amount of fat lost through either morphological or behavioural modification (see Chapter 5) may minimise the energetic costs of autotomy. However, the reduction in locomotory abilities through

tail loss (Chapter 3) may leave lizards more susceptible to predation. Tail autotomy has been reported to affect an individual's habitat use (Martin and Salvador 1992, 1993a,b, 1995, 1997, Salvador *et al.* 1995, 1996), defensive behaviour (Daniels *et al.* 1986, Martin and Salvador 1993a,b, Martin and Avery 1998), thermoregulatory behaviour (Martin and Salvador 1993a) and foraging behaviour (Martin and Salvador 1993b, Martin and Avery 1997). These impacts of caudal autotomy are generally the result of the tailless individual adopting a more cryptic existence (e.g. Martin and Salvador 1993a). Crypsis has been reported to be an effective defensive mechanism; for example, Schwarzkopf and Shine (1992) demonstrated experimentally that gravid female skinks, *Eulamprus tympanum*, which adopt crypsis due to locomotory impairment, are no more susceptible to predation than non-pregnant females. Their results suggest that the vulnerability of an animal to predation is determined by the predator's probability of detecting potential prey rather than the probability of prey capture once it has been detected. Tailless lizards that adopt a cryptic lifestyle may therefore be no more susceptible to predation than tailed lizards.

7.1.2 Frequency of tail loss

The frequency of tail loss within populations of lizards has long been regarded as an indicator of the intensity of predation that exists in the population. It is generally assumed that a positive relationship exists; that is, high incidences of tail loss are associated with more frequent predation events (Turner *et al.* 1982). The validity of this assumption, however, has often been questioned (Schoener and Schoener 1980, Jaksic and Busack 1984, Jaksic and Greene 1984). The inefficiency of predators (Medel *et al.* 1988) and the presence of intraspecific aggression (Vitt *et al.* 1974, Jennings and Thompson 1999) may invalidate this assumption. Intraspecific aggression is not prevalent amongst *Niveoscincus metallicus* (R. Swain, pers. comm.; pers. obs.); however, the inefficiency of predation is a concern to any study of tail autotomy. Efficient predators do not allow their prey to escape; therefore little or no evidence of tail loss will be evident in their prey populations. Staged encounters in the laboratory show that attacks directed towards the head and body are usually fatal; however, those focused towards the tail often result in the lizard escaping through tail

autotomy (Dial and Fitzpatrick 1984, Daniels *et al.* 1986). The frequency of tail loss in a population, therefore, may be partially the result of inefficient predation.

Regardless of the causes of tail loss, many natural populations exhibit high frequencies of tail autotomy. This frequency may vary between habitats (Brown and Ruby 1977, Perez-Mellado *et al.* 1997), age groups (Brown and Ruby 1977, Turner *et al.* 1982), sexes (Brown and Ruby 1977, Smith 1996, Fox *et al.* 1998), species (Bellairs and Bryant 1985), and with the ease with which the tail is lost (Bustard 1968). These differences are believed to reflect variation in the costs associated with tail autotomy (Arnold 1988). Consequently, the expectation is that, through the investigation of tail loss frequency, some inference may be made concerning the costs of caudal autotomy.

This chapter investigates the frequency and nature of tail loss among four populations of *Niveoscincus metallicus*. This species inhabits a wide range of habitats from sea level to alpine environments (1415 m; C. McCoull pers. comm.). The four populations selected represent the distributional extremes of the species: two lowland urban sites and two high altitude woodland sites. Behavioural differences (C. McCoull pers. comm.), and presumably predation differences (i.e. intensity/efficiency), may be evident between populations of *N. metallicus*; therefore the frequency of tail loss may also differ. The insights gained in the preceding laboratory experiments concerning the ‘costs’ of caudal autotomy (Chapters 3-6), will be utilised to explain the differences observed between the sexes and populations in regard to the frequency and nature of tail loss.

Each field site was intensively sampled during summer 1999/2000 to coincide with late pregnancy in females. The frequency of tail loss, along with the location of the break along the length of the tail, was documented in all captured animals. The habitat in which each individual was captured and the animal’s basking behaviour were also recorded to determine whether tailless lizards alter their behaviour towards crypsis. Two questions were investigated in the process of completing this study.

- 1) Does the frequency or position of tail loss differ between populations? If so, can this be related to differences in either predation intensity or efficiency?
- 2) Do tailless lizards alter their behaviour towards crypsis by basking closer to cover?

7.2 MATERIALS AND METHODS

7.2.1 Field site descriptions

7.2.1.1 Urban sites

The urban field sites, South Hobart and Dynnyrne, are located in the southern suburbs of Hobart, approximately 4 km from the city center. Each field site is located just above sea level. These field sites consisted primarily of urban gardens with small remnant patches of dry sclerophyll forests (Figure 7.1). The urban gardens provided a multitude of different habitats, providing habitat structures such as garden sleepers, abundant and thick vegetation, woodpiles, rock piles and boulders, fence lines, compost heaps and cement paths and driveways (Figure 7.1). *Niveoscincus metallicus* was observed to inhabit most areas within these urban gardens, seemingly well adapted to life among a wide range of man-made structures. Average daily temperatures in cool temperate habitats within Tasmania are usually 15-21 °C in summer, with daily temperatures normally above 7 °C in winter (Rawlinson 1974). Water was abundant at each site due to the presence of man made ponds and frequent use of sprinklers. Annual rainfall is generally below 100 mm. Both field sites experience constant human disturbance.

7.2.1.2 Central Plateau Sites

Both of the Central Plateau sites, Clarence Lagoon (1000 m a.s.l.) and Laughing Jack Lagoon (840 m a.s.l.), are situated at high altitude. At this altitude no months are frost free (Jackson 1981) and glazing storms are possible throughout the year. Snow is possible year round. The severe climatic conditions upon the Central Plateau affect the height and form of the vegetation present. The two field localities chosen in this study are both primarily high altitude woodland sites (Figure 7.2). However, a range



Figure 7.1 Urban field sites. a) - c) Variety of habitat types present at the South Hobart field site. d) - f) Range of microhabitats available for *N. metallicus* at the Dynnyrne field site.



a)



b)



c)

Figure 7.2 Central Plateau field sites. a), b) Clarence Lagoon habitat types, and c) Laughing Jack Lagoon field site.

of microhabitats is available at Clarence Lagoon (Section 2.1). Each consists mainly of dry sclerophyll forest with an understorey consisting for the most part of low and sparse shrubs. Eucalyptus species dominate these forests, resulting in a thick and deep layer of litter made mainly of eucalyptus debris. The canopy cover is usually less than 30%, allowing a substantial amount of light to filter through to the understorey. The understorey made be up to 1.5 m in height, but may be absent where dolerite boulder fields break through. Dolerite rock formations are characteristic of many areas on the Central Plateau. Human disturbance at both sites is minimal.

7.2.2 Collection and measurement of animals and habitat characteristics

During the course of intensive field sampling at the four field sites, a total of 368 lizards were collected, weighed, measured and then released. The field sites (Section 7.2.1), were chosen as they represented the opposing climatic extremes of *N. metallicus*. These two habitat types, urban gardens (Section 7.2.1.1) and high altitude woodland (Section 7.2.1.2), exhibit considerably different microhabitats, weather, potential predators and presumably predation intensities and efficiencies. The urban sites were assumed to have a high level of domestic cat and bird predation, while the two Central Plateau populations were believed to have a high density of snakes, but a lower intensity of bird predation.

Field sampling was conducted at the urban sites in late December to early January, with sampling at the high altitude sites completed during mid to late January. Due to the differences in the timing of reproductive events at each site (see Figure 1.2), the sampling periods in each habitat corresponded to late pregnancy in females and near maximal gonadal development in males (Section 5.3.1). Lizards were collected while basking by noosing, as described in Section 2.2. Each lizard was weighed (± 0.1 g) and measurements taken of SVL, total length, total tail length, tail break length and tail regeneration length (± 0.1 mm). Sex was determined by eversion of the hemipenes. Reproductive status was assessed in females through palpation. Each individual was marked with white liquid paper on the non-autotomised portion of the tail for visual identification, before being released at the site of capture. These marks

were to avoid recapture and no attempt was made to recapture these animals. These visual tags remained on the animals for the duration of the sampling period, but were lost at the next moult.

A number of basking site characteristics were recorded for each animal, in order to compare the basking and defensive behaviour of lizards with differing degrees of tail loss. The following basking characteristics were recorded:

1. basking surface (BS): boulder, rock, ground, small branch or log;
2. percentage shade (PS);
3. height of basking surface (BH): measured in metres above ground;
4. distance to nearest cover (CD): measured in metres;
5. degree of cover (DC): measured on a scale of 1-5 (1 = low, 5 = high);
6. type of cover (TC): boulder, rock, ground, small branch or log;
7. height of cover (HC): measured in metres above ground; and
8. distance to nearest vegetation (DV): measured in metres.

7.2.3 Data analysis

Analyses were performed using the SAS System for Windows® v6.12, except for a principal component analysis (PCA) which was performed using SYSTAT for PC v8.0. Initial determination of the deviation of the sex ratio at each location from the expected 1:1 ratio was tested using chi-squared analysis. Site differences in relation to size (SVL) and relative tail length (tail length/SVL) were analysed using two-way Analysis of Variance (ANOVA). Visual inspection of group standard deviations versus group means was used to assess the homogeneity of variances. Normality of data distribution was examined with a plot of estimated versus predicted residual values. Differences in tail loss frequency between populations were analysed using log-linear modeling.

The original tail length of animals that had experienced tail loss was predicted using regression analysis as described previously in Sections 6.2.3. A multiple comparison

of slopes ANOVA, was used to determine whether the relationship between SVL and tail length varied between sexes or across sites. The resultant regression equation was used to determine break indices and indices of recovery for each animal as described in Section 6.2.3. Differences in mean break indices between populations were analysed using a 2-way ANOVA. The assumptions of homogeneity of group variances and normality of data were assessed as reported above.

A principal components analysis (PCA) was used to reduce the eight structural and environmental characteristics of lizard basking sites to a smaller number of uncorrelated components that describe the underlying dimensions in the microhabitat data (FACTOR procedure of SYSTAT, Wilkinson *et al.* 1992). The principal components were extracted from the correlation matrix of the raw data, which was used since the scales of each variable differed (Tabachnick and Fidell 1989). Data were not transformed prior to the analysis; thus, the assumption of linearity may have been violated (James and McCulloch 1990). However, departure from linearity is not usually great enough to invalidate a PCA (Pimentel 1979). The number of principal components used in the analysis was determined using a scree test of eigenvalues plotted against factors. PC axes were named by the correlations of the original variables to the PC; correlations with absolute values greater than 0.5 were considered significant (Tabachnick and Fidell 1989).

A multivariate analysis of variance (MANOVA) was performed on the PC scores for each site to determine whether these scores were constant between sites. A series of separate MANOVAs were then completed to determine whether PC scores varied in accordance with the animal's relative tail length, break index or recovery index (each expressed as categories). Relative tail length (tail length/SVL) was expressed in five categories (1 = relative tail lengths less than 0.3; 2 = 0.31-0.6; 3 = 0.61- 0.9; 4 = 0.91-1.2; and 5 = over 1.2). Break index was expressed as one of six categories where 1 = break indices less than 0.2 (i.e. proximal breaks); 2 = 0.21-0.4; 3 = 0.41-0.6; 4 = 0.61-0.8; 5 = 0.8-1.0; and 6 = animals with no tail loss. The index of recovery was also expressed in five categories similar to those for the break index; however, category 1 indicated low recovery (indices less than 0.2) through to category 5 that included animals with complete original or regenerated tails (values 0.8-1.0). Category 6

identified animals with no previous tail loss. Where significant differences were found to exist in the MANOVA, individual Factorial ANOVAs were undertaken to determine whether the influence of the tail trait for the PC was constant across the four sites.

7.3 RESULTS

7.3.1 Sexual and morphological variation between populations

Between 66 and 101 animals were caught at each of the four field sites (Table 7.1). The sex ratio in each population did appear to vary (Table 7.1). However, Clarence Lagoon was the only location where the sex ratio differed significantly from the expected 1:1 ratio ($X^2 = 5.76$, $df = 1$, $P < 0.025$).

Table 7.1 Site differences in sex ratios. The deviation of the ratio from 1:1 was tested for each population using chi-squared tests. Total sample size is indicated in parentheses. CL = Clarence Lagoon, LJL = Laughing Jack Lagoon.

Site	Male	Female	Ratio M:F (n)	X^2	df	P
Sth Hobart	38	28	1.357 (66)	1.515	1	> 0.100
Dynnyrne	54	47	1.149 (101)	0.485	1	> 0.100
CL	62	38	1.632 (100)	5.760	1	< 0.025
LJL	47	54	0.870 (101)	0.485	1	> 0.100
Total	201	167	1.204 (368)	3.141	1	> 0.050

Both SVL and relative tail length differed between populations (Table 7.2). A two-way ANOVA revealed that there was a significant difference in SVL between sites ($F_{3,367} = 10.15$, $P = 0.0001$). However, no sexual dimorphism in size (SVL) was evident between the sexes ($F_{1,367} = 0.01$, $P = 0.9366$). A significant site-sex interaction was evident ($F_{3,367} = 2.84$, $P = 0.0378$). Tukey's *post-hoc* HSD test revealed that males and females from Dynnyrne were smaller in size than females from South Hobart, while the Dynnyrne females were also shorter in length than either sex from Clarence Lagoon. Females from Laughing Jack Lagoon were shorter in SVL than females from Clarence Lagoon and South Hobart.

A two-way ANOVA showed that the relative tail length varied with both site ($F_{3,367} = 13.85$, $P = 0.0001$) and sex ($F_{1,367} = 6.99$, $P = 0.0086$). However, the site-sex interaction was not found to be significant ($F_{3,367} = 0.26$, $P = 0.8545$). A *post-hoc* Tukey's HSD test revealed that males had significantly higher relative tail lengths than females. The test also revealed that animals from South Hobart had relatively shorter tails than males from Clarence Lagoon, while, on average, individuals from Laughing Jack Lagoon and Clarence Lagoon males possessed tails that were larger than animals from Dynnyrne.

Table 7.2 Summary of site differences in SVL and relative tail length (RTL). The means (\pm s.e.) for SVL are for adult lizards only (over 45 mm SVL). Sample sizes (n) are presented in parentheses.

Site	Males	s.e.	Females	s.e.	Overall	s.e.
Size (SVL)						
Sth Hobart	52.5 (37)	0.64	54.6 (28)	0.68	53.4 (65)	0.48
Dynnyrne	52.1 (45)	0.58	51.2 (39)	0.55	51.7 (84)	0.40
CL	53.7 (55)	0.44	53.7 (36)	0.46	53.7 (91)	0.32
LJL	52.9 (43)	0.60	51.0 (47)	0.56	51.9 (90)	0.42
Total	52.9 (180)	0.28	52.4 (150)	0.31	52.6 (330)	0.21
RTL						
Sth Hobart	1.0 (38)	0.06	1.0 (28)	0.07	1.0 (66)	0.04
Dynnyrne	1.0 (54)	0.05	0.9 (47)	0.05	0.9 (101)	0.04
CL	1.2 (62)	0.03	1.1 (38)	0.04	1.1 (100)	0.03
LJL	1.2 (47)	0.03	1.2 (54)	0.03	1.2 (101)	0.02
Total	1.1 (201)	0.02	1.0 (167)	0.03	1.1 (368)	0.02

7.3.2 The frequency and position of tail autotomy

The frequency of tail loss differed between each field site (Table 7.3). However, only slight sexual differences were evident in the frequency of tail loss. The lowest frequency of tail loss was observed at Laughing Jack Lagoon (Male-Female; 60-68%), with tail loss slightly more common at South Hobart (68-71%). Dynnyrne (82-85%) and Clarence Lagoon (80-81%) both exhibited high frequencies of tail autotomy. Approximately half of all juveniles collected at each site displayed signs of tail loss, with the exception of South Hobart where only a single individual was caught. Log-linear modeling revealed that the frequency of tail loss was significantly

different between sites ($X^2 = 10.802$, $df = 3$, $P = 0.0128$); however, no sexual differences existed ($X^2 = 0.3074$, $df = 1$, $P = 0.5793$). Likewise, the interaction term was also non-significant ($X^2 = 0.1863$, $df = 3$, $P = 0.9798$).

Table 7.3 Frequency (%) of tail loss for each population. Tail loss frequency is indicated for males, females and juveniles. The overall frequency of autotomy is presented. Sample sizes (n) are indicated in parentheses.

Sex	Field		Site	
	Sth Hobart	Dynnyrne	CL	LJL
Male	67.5 (37)	82.2 (45)	80.0 (55)	60.5 (43)
Female	71.3 (28)	84.6 (39)	80.6 (36)	68.1 (47)
Juvenile	100 (1)	52.9 (17)	55.6 (9)	45.5 (11)
Overall	69.7 (66)	78.2 (101)	78.0 (100)	62.4 (101)

A number of animals exhibited no visual evidence of previous tail loss. Regression analysis of these individuals revealed a significant relationship between SVL and tail length. A multiple comparison of slopes ANOVA revealed that the slope of each regression equation was constant between sexes and across all sites; therefore an overall regression relationship was calculated ($y = 1.071x + 14.16$; $R^2 = 0.570$, $F_{1,100} = 132.53$, $P < 0.0001$). This relationship was used to predict the original tail length of each animal that had experienced tail loss. The predicted original tail length of each animal was utilised to calculate two separate indices of tail autotomy: the position of tail break (break index) and the relative tail length compared to the original (index of recovery) (see Section 6.2.3).

The position of the tail break appeared to differ between sites but not sexes (Table 7.4; results presented in frequency of breaks in each tail third). A two-way ANOVA confirmed that site ($F_{3,265} = 10.32$, $P = 0.0001$) but not sexual ($F_{1,265} = 0.67$, $P = 0.4147$) differences existed. Consequently, the combined data for each site were also calculated (Table 7.4). No interaction was evident ($F_{3,265} = 0.42$, $P = 0.7412$). A *post-hoc* Tukey's HSD test revealed that animals caught at Dynnyrne had significantly more tail breaks closer to the base of the tail than either sex at the two high altitude populations.

Table 7.4 Sexual distribution in the position where tail breaks occur (break indices). The frequency of tail breaks that occurred within the proximal (break indices 0-0.33), middle (0.34-0.67) and distal (0.68-1.0) portions of the tail are presented.

Site	N	Position of Break		
		Proximal	Middle	Distal
Males				
Sth Hobart	25	40.0	36.0	24.0
Dynnyrne	37	56.8	24.3	18.9
CL	44	29.6	38.6	31.8
LJL	26	34.6	26.9	38.5
Females				
Sth Hobart	20	40.0	30.0	30.0
Dynnyrne	33	69.7	24.2	0.1
CL	29	31.0	44.8	24.2
LJL	32	37.5	31.3	31.2
Overall				
Sth Hobart	45	40.0	33.0	27.0
Dynnyrne	70	60.7	26.6	12.7
CL	73	29.5	43.6	26.9
LJL	58	34.9	33.3	31.8

7.3.3 Habitat structure and Basking Behaviour

A principal component analysis was completed to identify the basking preferences of each of the four field populations. The principal component analysis that incorporated three factors accounted for 68.5% of the variance of the raw data (Table 7.5, Figure 7.3). The first PC described a strong positive correlation between both the distance to cover and vegetation, basking height and the height of cover. Thus PC1 described a basking location dependent on the height above the ground and the proximity of refuge, with low scores represent basking sites close to the ground and refuge. The second PC revealed a strong positive correlation between the basking surface and type of cover. High PC2 scores represented vegetation or logs and low PC2 scores indicated rocks. The third PC yielded a strong positive correlation between the percentage shade and the degree of cover. This therefore represents a gradient where low PC3 scores represent overt basking and high scores denote covert basking sites.

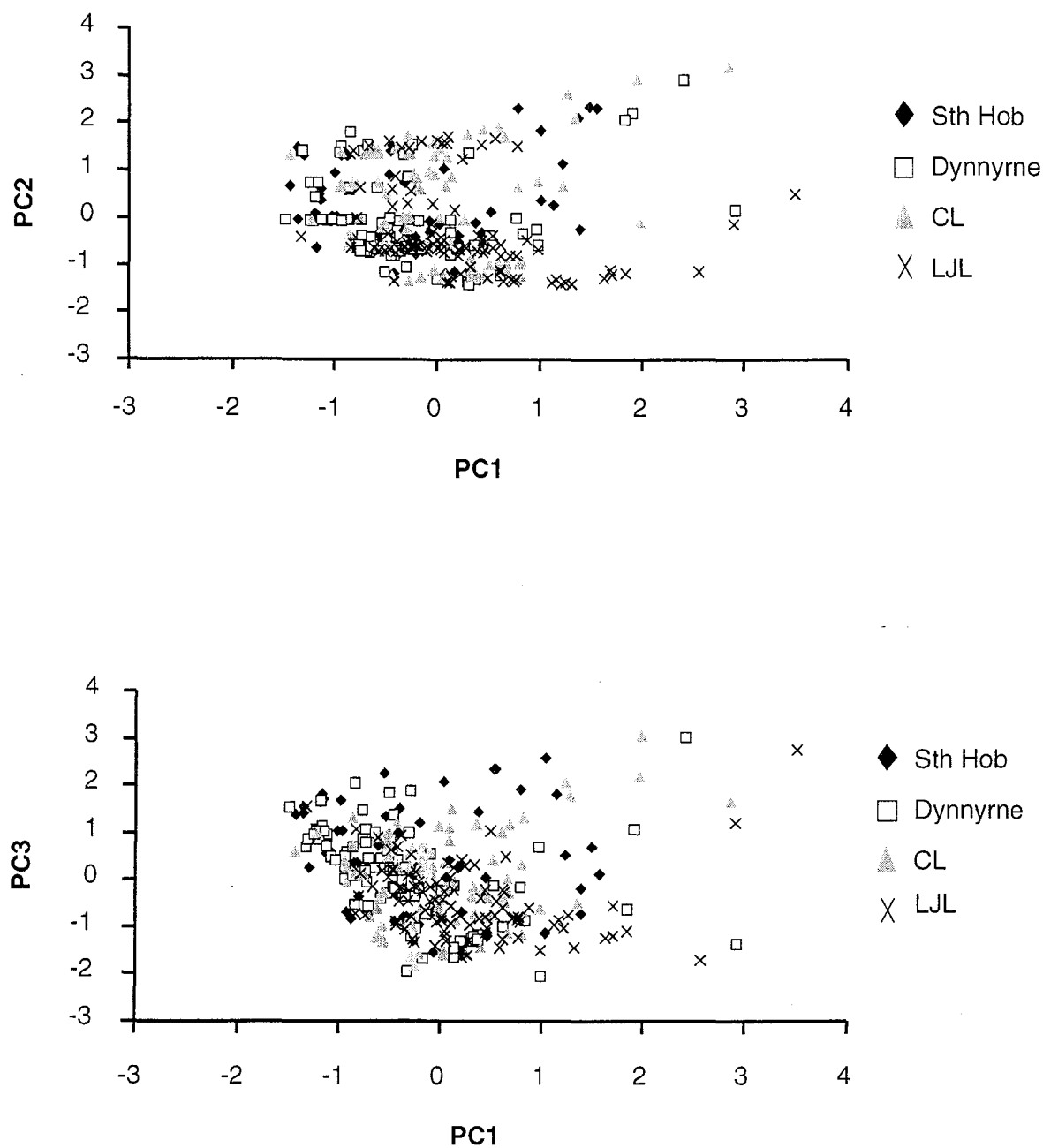


Figure 7.3 Plot of first three principal components (PC1 v PC2, PC1 v PC3) for each of the four field sites. CL = Clarence Lagoon, LJL = Laughing Jack Lagoon.

Table 7.5 Correlations of original environmental variables with the first three PC scores for each of the four field sites.

Correlations with		PC 1	PC 2	PC 3
PCs		CD 0.630 HC 0.719	TC 0.910	PS 0.695
		DV 0.606 BH 0.669	BS 0.902	DC 0.653
Percent of Variance		27.84	23.74	16.92
Group	n	Score	Score	Score
Sth Hobart	63	-0.252 ± 0.1004	0.270 ± 0.1151	0.409 ± 0.1390
Dynnyrne	97	-0.226 ± 0.1233	-0.098 ± 0.0871	0.166 ± 0.0975
CL	100	-0.002 ± 0.0682	0.232 ± 0.1141	-0.033 ± 0.0961
LJL	101	0.376 ± 0.1040	-0.305 ± 0.0935	-0.383 ± 0.0870

A multivariate analysis of variance (MANOVA) indicated that the basking site PC scores for each site differed on all three PCs (Table 7.5). On PC 1 mean scores varied significantly across sites ($F_{3,360} = 8.22$, $P = 0.0001$). Tukey's HSD *post-hoc* test revealed that animals at Laughing Jack Lagoon selected basking sites that were relatively high off the ground and further from refuge sites than those from other populations. On PC 2 mean scores also varied significantly between populations ($F_{3,360} = 7.12$, $P = 0.0001$). Tukey's HSD *post-hoc* test indicated that individuals at Laughing Jack Lagoon selected basking sites on rocks and boulders, whereas animals in South Hobart and Clarence Lagoon preferred to bask on logs and vegetation. On PC 3 each site was shown to have significantly different mean scores ($F_{3,360} = 10.08$, $P = 0.0001$). Tukey's HSD *post-hoc* test revealed that animals at Laughing Jack Lagoon basked more overtly than at either of the two urban localities, while individuals at Clarence Lagoon only basked more overtly than individuals at South Hobart. Thus, *N. metallicus* at the two high altitude sites basked more overtly than those at urban sites; however, animals at Laughing Jack Lagoon preferred to bask more on rocks and further from cover than the other three populations.

The relative tail length of animals did not influence either the mean scores for either PC 1 ($F_{4,360} = 1.17$, $P = 0.3240$) or PC 2 ($F_{4,360} = 0.77$, $P = 0.5463$); however, it had a significant influence on PC 3 ($F_{4,360} = 2.85$, $P = 0.0240$). Tukey's *post-hoc* test showed that this difference on PC 3 was due to animals with original or completely

regenerated tails (groups 5 and 6) basking more overtly than animals with relative tail lengths between 0.6-0.9 (i.e. category 3). A two-way ANOVA revealed this was consistent across all sites (interaction: $F_{12, 360} = 0.97, P = 0.4735$).

The location of previous tail breaks (break index) failed to influence the means scores of PC 1 ($F_{5,360} = 2.14, P = 0.0497$) or PC 2 ($F_{5,360} = 0.66, P = 0.6516$); however, it had a significant influence on PC 3 ($F_{5,360} = 3.92, P = 0.0018$). For PC 3 Tukey's *post-hoc* HSD test showed that animals with complete original tails (category 6) basked more overtly than animals with tail break indices between 0.2-0.6 (categories 2 and 3). A two-way ANOVA showed this difference was constant across all sites (interaction: $F_{15,360} = 1.01, P = 0.4484$).

The size of the tail in proportion to its original length (recovery index) influenced mean scores for PC 1 ($F_{5, 360} = 2.97, P = 0.0121$) and PC 3 ($F_{5,360} = 2.70, P = 0.0208$), but not PC 2 ($F_{5,360} = 0.87, P = 0.5032$). Tukey's HSD *post-hoc* test showed that for PC 1 the difference was due to animals with tail recovery indices between 0.8-1.0 (category 5) basking higher and further from refuge than animals with recovery indexes between 0.6-0.8 (Category 4). For PC 3, the difference was due to animals with original tails (category 6; no break) basking more openly than animals with tail recovery indexes between 0.4 and 0.8 (categories 3 and 4). The differences for each PC were consistent across all four site (two-way ANOVA: PC 1 interaction: $F_{15,360} = 1.23, P = 0.2454$; PC 3 interaction: $F_{15,360} = 1.19, P = 0.2785$).

These results demonstrate, therefore, that animals with shorter tails (RTL and recovery index) tended to bask closer to cover and the ground (PC1) and/or more cryptically (PC3) than animals with complete or completely regenerated tails. Individuals that had lost larger portions of tail (i.e. low break indices) also selected more cryptic basking locations (PC3). Tail length, therefore, appears to influence the selection of basking sites in *N. metallicus*.

7.4 DISCUSSION

7.4.1 Frequency and position of tail autotomy

Sexual differences in the frequency of tail loss are generally considered to represent contrasting ‘costs’ of caudal autotomy in males and females (Arnold 1988, Fox *et al.* 1998). Although several authors have reported differing frequencies of tail loss between males and females (Vitt *et al.* 1974, Brown and Ruby 1977, Vitt and Ballinger 1982, Vitt 1983, Smith 1996), few have attempted to relate these differences back to any disparate costs of autotomy (e.g. Fox *et al.* 1998). However, the preceding chapters have extensively investigated ‘costs’ of caudal autotomy in both sexes, thereby, providing an opportunity to test this assumption.

Locomotory performance (Chapter 3) was the only area where there were significant sexual differences in the costs of tail loss. However, in females, tail loss during vitellogenesis was found to have a significant impact on reproductive output (Chapter 6). Although the reproductive costs of autotomy were not investigated in males, previous authors have demonstrated that tail loss may have a similar impact on their reproductive output (i.e. mating success; Fox and Rostker 1982, Fox *et al.* 1990, Martin and Salvador 1993c, Kaiser and Mushinsky 1994, Salvador *et al.* 1995, 1996). In *N. metallicus*, therefore, there is little sexual variation in the costs of tail loss, so it may be hypothesised that the frequency of tail loss between the sexes in natural populations should be comparable. Indeed, no sexual differences in the frequency of tail loss were found in this study. The assumption that the frequency of tail loss reflects the inherent costs of autotomy may, therefore, hold true for *N. metallicus*.

It was demonstrated in Chapter 5 that the majority of the energetic reserves of *N. metallicus* are located within the proximal third of the tail. Simple examination of the frequency of tail loss may therefore be inadequate for investigating the relative cost of autotomy in this species. As the partitioning of caudal reserves within the tail was found to be equivalent in each sex (Chapter 5), sexual differences in the location of autotomy (i.e. break index) should point towards disparate costs of tail loss. However, in the present study the frequency of males and females with tail breaks

within each third of the tail was not significantly different. This is despite the presence of the hemipenes and associated musculature constraining the position where tail loss may occur in males (Barbadillo *et al.* 1995). Consequently, caudal autotomy does not appear to be more costly in one sex. However, both the frequency of tail loss and position of tail loss differed significantly between populations, indicating that the costs of caudal autotomy may vary between populations rather than sexes.

The frequency of tail loss has previously been shown to vary between conspecific populations at different altitudes (Brown and Ruby 1977). Large altitudinal differences were deliberately incorporated into the selection of sites for this study of *N. metallicus*. Although temperature, a factor that differs significantly between altitudes, may influence the ease with which tail loss occurs (Bustard 1968), variation in the frequency of tail loss between populations is generally believed to be the result of qualitative or quantitative differences in predation (e.g. Perez-Mellado *et al.* 1997). In my study I made the *a priori* assumption that predation pressure at the low (urban) and high altitude (Central Plateau) sites differed significantly. *Niveoscincus metallicus* is subject to both aerial (birds) and ground (snakes, native and introduced cats) predation. Overall predation intensity was expected to be greater at the urban localities because of a large number of bird predators and a high density of domestic cats. Fewer of these predators are likely to be present on the Central Plateau. Although birds are common their density is relatively lower. Snakes are, however, present in larger numbers but their frequency of predation on *N. metallicus* was assumed to be significantly lower than that of cats and birds.

In *N. metallicus* the frequency of tail loss was found to differ between populations at different altitudes; however, there was a similar level of variation between the two populations at each altitude. The frequency of tail loss was high at Dynnyrne and Clarence Lagoon (80-84%), but relatively low at South Hobart and Laughing Jack Lagoon (60-71%). The type of predator or predation intensity, therefore, did not appear to influence the incidence of autotomy. However, several other studies have indicated that tail breaks may also represent the frequency of intraspecific aggression (Vitt *et al.* 1974, Jennings and Thompson 1999) or inefficient predators (Jaksic and Busack 1984, Jaksic and Greene 1984). It has been demonstrated experimentally that

inefficiency of predation attempts (i.e. attack on tail not body) may inflate the frequency of animals with tail breaks within a population (Daniels 1985a, Cooper and Vitt 1985, Medel *et al.* 1988). The position where the tail is broken (break index) may provide some indication of predation efficiency as some species of lizard (including *N. metallicus*; Section 7.3.2) exhibit 'economy of autotomy' (e.g. Daniels 1985a).

Medel *et al.* (1988) found that the efficiency of an avian predator when catching three different species of lizard was greater than that of reptilian predators (i.e. snakes). Urban sites, therefore, would be expected to exhibit lower frequencies of tail loss due to more efficient predation upon them. However, domestic cats are intensive predators of *N. metallicus* at urban localities (R. Swain, pers. comm.; pers. obs.) and several predatory encounters involving cats were observed at Dynnyrne. Cats are efficient hunters of *N. metallicus* within urban gardens; however, once they successfully capture a lizard they tend to play with it rather than consume it. These observations, along with anecdotal evidence from local residents, suggests that a large proportion of lizards caught by domestic cats escape via tail autotomy. In the three observed encounters the lizard successfully escaped after shedding half to two-thirds of its tail. This 'inefficiency' of domestic cats at Dynnyrne may explain the high frequency of tail loss and proximal breaks at this locality. The lower tail loss frequency at South Hobart is probably the result of a lower density of cats (pers. obs.) associated with a much lower housing density.

Predation efficiency may be able to explain the higher frequency of tail loss and proximal tail breaks at Dynnyrne; however, an alternative explanation is required to comprehend the high frequency of tail loss at Clarence Lagoon. Tail loss in lizards occurs through fracture planes within the caudal vertebrae (Bellairs and Bryant 1985). However, since a cartilaginous rod, and not vertebrae, support the regenerated tail, subsequent tail loss is only possible through the remaining autotomous caudal vertebrae. Repeated tail autotomy will therefore result in more proximal break indices. The age of an animal will therefore influence the break index. Likewise, the age-structure of a population will influence the frequency of tail loss (e.g. Vitt and Ballinger 1982, Turner *et al.* 1982). The life span of *Niveoscincus metallicus* at

Clarence Lagoon, and presumably Laughing Jack Lagoon, may be 5-6 years longer than animals at Hobart (C. McCoull, unpublished data), so the frequency of predatory encounters per year may be greater at lower altitudes. However, the greater age of individuals at Clarence Lagoon means that they are more likely to have had a predatory encounter that resulted in tail loss. Thus, the frequency of predatory encounters at Dynnyrne may be considerably higher than at any of the other sites to result in such a high frequency of tail loss and proximal breaks. The reason, however, for the higher frequency of tail loss at Clarence may be due to the sampling of a larger number of older (i.e. larger SVL and higher probability of tail loss) animals compared to Laughing Jack Lagoon (Table 7.2).

Just as sexual differences in the frequency and position of tail loss may indicate variation in the costs of caudal autotomy, differences between populations may also represent disparate levels of costs. If the above reasoning is correct and animals at lower elevations have predatory encounters that result in autotomy more frequently, the relative tail length (tail length/SVL) of these animals would be expected to be lower. Indeed, animals from South Hobart and Dynnyrne had significantly lower relative tail lengths. An increased frequency of predatory events is the most likely cause of this decrease tail length, as no difference was found in the relative tail lengths of animals with complete tails between sites (Section 7.3.2). Animals at urban sites may therefore experience tail loss more regularly and spend more of their life regenerating portions of their tail than animals from other sites. It was suggested in Chapter 6 that tail regeneration may be energetically expensive through the presumed diversion of energy away from reproductive investment. The costs of caudal autotomy therefore may be higher at lower altitudes. However, as over 60% of animals at each population, except Dynnyrne, lost their tail within the middle or proximal third, loss of fat reserves may have been minimal in most cases. Most animals at Dynnyrne, however, appear to have experienced reduction of fat reserves and, due to the apparent high frequency of predatory events, these lizards may spend most of their life with short regenerating tails and diminished levels of mobility.

The frequency and position of tail loss are believed to have co-evolved in lizards, with tail loss frequency negatively related to break index (Zani 1996). However, in *N.*

metallicus there appears to be both a high frequency of tail loss and moderate (~30%) to high (~70%) frequency of proximally located tail breaks. Caudal autotomy is a plesiomorphic characteristic in squamate reptiles (Arnold 1988) and its evolution has been found to be correlated with caudal musculature (Russell and Bauer 1992, Barbadillo *et al.* 1995, Zani 1996) and locomotory performance (Zani 1996). However, the evolutionary origins of caudal fat storage are unknown. Greer (1986) has suggested that abdominal fat is also a plesiomorphic feature in lizards. He has reported that abdominal fat stores have been lost almost entirely from one lineage of skinks (*Sphenomorphus* group of Subfamily Lygosominae). These species now rely solely on caudal fat reserves. Although no clear evidence is currently available, it is most likely that the primitive squamate ancestor possessed both abdominal and caudal fat stores. The most parsimonious explanation is that abdominal fat stores were lost, leaving the caudal fat as the sole reserves, rather than the loss of body, and the development of caudal stores being independent events. It is likely therefore that both tail loss and break index have co-evolved with caudal fat bodies. The concentration of tail fat in the proximal section of the tail (Chapter 5) and the low frequency of proximal breaks (present chapter) may represent the end result of such co-evolution. The preferential loss of more distal tail segments in *N. metallicus* may therefore represent an adaptive strategy to limit the energetic 'costs' of autotomy (Chapters 5 and 6) while allowing the animal to retain the survival benefit obtained from tail loss.

7.4.2 The effect of tail loss on basking site selection

Niveoscincus metallicus is a ground dwelling skink, usually cryptic in nature that inhabits the majority of available habitat types from sea level to the alpine treeline (Melville and Swain 1999b). Until recently most studies on the habitat use of *N. metallicus* have focused either on a single population (Melville 1994, Melville and Swain 1997a) or have provided only qualitative and generalised habitat descriptions (Rawlinson 1974, Hutchinson *et al.* 1989). However, McCoull (in prep) has recently completed a more comprehensive study of microhabitat utilisation of *N. metallicus* and has demonstrated that there is some degree of altitudinal variation in this behaviour. The present study has also shown that the basking site selection of *N. metallicus* varies considerably between populations. However, the altitudinal

variation reported by McCoull (in prep) was found to be less distinctive when urban and high altitude sites were compared.

Although individuals from higher altitudes were found to bask more overtly than those at lower elevations, a result also found by McCoull (in prep), significant differences in the basking behaviour of high altitude lizards were found. *Niveoscincus metallicus* at urban localities were found to select shaded basking sites that were located in thicker vegetation. However, individuals from Laughing Jack Lagoon differed from those at the three other populations, including Clarence Lagoon, by preferring to bask more on rocks and boulders that were higher above the ground and further from refuge. *Niveoscincus metallicus* clearly exhibits flexibility in its use of microhabitats across its range (McCoull in prep, present study).

The inter-population variation in basking site selection does not appear to be responsible for the differences in tail loss frequency between sites. Although the predation pressure and efficiency, as evidenced by similar break indexes and relative tail lengths, was similar at both localities the selection of basking sites that were further from refuges did not increase the incidence of tail loss in individuals from Laughing Jack Lagoon. In fact these animals had the lowest tail loss frequency of any population. Likewise, the relatively cryptic basking of individuals at urban localities did not decrease the incidence of tail loss; however, it is unknown whether the frequency of tail loss would be higher if it was not for this covert basking. Differences in basking site selection therefore may be the result of alternative strategies to regulate body temperature under the disparate thermal climates at high and low altitude (McCoull in prep).

Running is the primary defensive mechanism in *N. metallicus* as it is small in size and lacks any alternative defense such as aggression; however, caudal autotomy is generally seen as the 'last ditch' effort to escape once caught. Following tail loss, therefore, running is the only remaining escape mechanism available to the animal. It was demonstrated in Chapter 3 that tail autotomy in *N. metallicus* decreases mobility and agility. Under natural conditions autotomy may result in an increased probability of predation. This chapter has shown that *N. metallicus* selects basking locations on

the basis of their height and proximity to refugia, the type of basking substrate, and the degree of shade and vegetative cover. Tailless lizards may therefore modify their basking preferences by selecting locations that are closer to refugia (compensation for decreased locomotion) or more cryptically located (i.e. limit detection) to limit their chances of predation. My study did indeed find that animals with either shorter tails (RTL or index of recovery) or more proximal breaks basked closer to cover and preferentially chose more sheltered sites. *Niveoscincus metallicus* therefore appears to switch its habitat use following tail loss towards crypsis.

The Iberian Rock Lizard, *Lacerta monticola*, has also been demonstrated to modify its habitat use following tail loss (Martin and Salvador 1992, 1993a,b, 1995, 1997). However, although tailless individuals were found to use open bare ground to a lesser extent and remain closer to cover, this species does not chose cryptically located basking sites as *N. metallicus* does. Pregnant females that exhibit locomotory inhibition comparable to tailless *N. metallicus* have also been shown to modify their predator avoidance strategies (Bauwens and Thoen 1981, Cooper *et al.* 1990, Schwarzkopf and Shine 1992, Brăna 1993, Kik 1998) by switching towards crypsis, by allowing predators to approach closer, by fleeing shorter distances, and by staying closer to refuge. The modification of bask site selection by *N. metallicus* following tail autotomy may therefore be one of a suite of anti-predator tactics.

Successful predation may be divided into four main phases: detection, pursuit, subjugation and consumption (Endler 1986, Schwarzkopf and Shine 1992), with unsuccessful predation attempts resulting from the failure of any one of these steps (Vermeij 1982, Schwarzkopf and Shine 1992). Caudal autotomy works on the third phase by providing an opportunity for the lizard to escape once it has already been detected and caught. However, due to their consequently impaired mobility, they are also more likely to be caught (i.e. pursuit phase) and, since they can not autotomise a tail again until it is replaced, subjugation and consumption will occur uninhibited. Schwarzkopf and Shine (1992) suggested that in pregnant females the observed switch towards crypsis prevents this chain of events from occurring by limiting the initial detection of the animal by a potential predator. Their experimental evidence that pregnancy in a viviparous skink did not increase its vulnerability to predation

supported this reasoning. The switch towards crypsis in *N. metallicus* following tail loss may also be interpreted as an adaptive mechanism to limit its susceptibility to predation.

CHAPTER 8

GENERAL DISCUSSION

This thesis provides the first comprehensive investigation of caudal autotomy in any member of *Niveoscincus*, and one of the few such studies on an Australian lizard. It has examined the ‘cost’ of tail autotomy on locomotory performance, thermoregulation, energetics, reproduction and behaviour. Although several significant impacts were evident, this investigation has highlighted the presence of several behavioural and anatomical modifications that appear to limit the potential costs of autotomy. The ‘costs’ of caudal autotomy in *N. metallicus* were found to stem from two main sources: a reduction in mobility and the depletion of energetic reserves.

Caudal autotomy in *N. metallicus*, as in most other lizards, was found to decrease locomotory performance (e.g. Ballinger *et al.* 1979, Punzo 1982, Formanowicz *et al.* 1990, Brown *et al.* 1995). However, it preferentially inhibited terrestrial locomotion (sprinting and stamina), with little influence on arboreal locomotion. Tail loss therefore restricts this species major form of locomotion, since it is primarily a cryptic ground dwelling animal that spends most of its time moving and foraging within the soil-litter interface (Melville and Swain 1999b). Consequently, the reduced mobility that results from caudal autotomy may influence the way in which *N. metallicus* moves through and interacts with its environment. However, since several of these locomotory ‘costs’ were only transient, caudal autotomy may only represent a temporary ‘nuisance’ to the animal.

Niveoscincus metallicus is a widely foraging species that feeds opportunistically on terrestrial and aerial invertebrates (pers. obs.). The high occurrence of cryptic and hidden prey in the diet of the related species *N. ocellatus* (Wapstra and Swain 1996) also suggests that it actively searches for food. Although the foraging ability and food intake of *N. metallicus* in the laboratory was not affected (pers. obs.), its ability to forage through the dense undergrowth within its habitat for prolonged periods of time may be reduced following caudal autotomy. Several studies have indicated that modification of habitat use following tail loss (Martin and Salvador 1992, 1993a,

1995, 1997), may result in a switch in dietary preferences (Martin and Salvador 1993b). The selection of more cryptic basking locations by *N. metallicus* may therefore have nutritional consequences. *Niveoscincus metallicus* is commonly observed to feed on ants and flying insects while basking (pers. obs.). Preferential utilisation of hidden microhabitats may reduce its chances of opportunistic feeding. Consequently, the combination of a reduced ability to actively forage and the diminished potential to feed opportunistically may further decrease the condition of tailless *N. metallicus*.

Substandard individuals within a population generally experience disproportionate levels of predation (Temple 1987). Staged laboratory encounters have indicated that predators catch a higher proportion of tailless lizards (Dial and Fitzpatrick 1984, Daniels *et al.* 1986). Caudal autotomy and running are the primary escape mechanisms utilised by *N. metallicus*; therefore tailless lizards that rely solely on their inhibited mobility for escape are likely to experience high rates of predation. However, the selection of cryptic basking sites that are close to refuge by tailless lizards may represent a switch in defensive behaviour to decrease their probability of predation (e.g. Schwarzkopf and Shine 1992). Due to the diminished sprinting ability of tailless lizards they are presumably more likely to be caught if detected by a predator; however, by reducing their probability of detection (i.e. crypsis) and maintaining shorter distances to cover their chance of capture is reduced. Tailless *N. metallicus* that adopt this strategy may therefore be no more vulnerable to predation than their tailed counterparts.

The present study found that sex significantly influenced the time taken for the complete restoration of locomotory ability following caudal autotomy. Although this difference may have been the result of the faster rate of tail regeneration in females or the ‘cushioning’ effect of pregnancy, males appear to endure restricted locomotory ability for longer periods of time. The cost of caudal autotomy did not appear to differ significantly between males and females, and the frequency and position of tail loss was equivalent in both sexes. There is no indication therefore that the costs of tail loss are more severe in males; however, males appear to experience longer periods of cost. Such extended periods of locomotory costs in males may indicate that the tail

length at which maximal performance abilities are restored is greater than for females. The biomechanics of tail autotomy and recovery is deserving of further investigation to determine why there is sexual variation in the temporal impact of caudal autotomy.

Although the duration of the ‘costs’ of caudal autotomy appear to be dependent on the rate at which the tail is regenerated, there was no evidence of *N. metallicus* modifying its thermoregulatory behaviour following tail loss. The absence of such a behavioural shift may be the result of the evolutionary coupling of the thermal optima for tail regeneration and the ‘normal’ thermal preferences. However, the numerous behavioural and anatomical modifications found to be present in *N. metallicus* to reduce the impact of caudal autotomy, may mean that tail regeneration is a low priority. *Niveoscincus metallicus* was found to be capable of thermoregulatory plasticity, as the thermal preferences of females were reduced during gestation. However, Swain and Jones (in press a) have shown that the maternal thermal environment of *N. metallicus*, rather than her physical state (i.e. nutritional condition), has an overriding impact on offspring viability and phenotype. Consequently, a behavioural switch to facilitate rapid tail regeneration may have had an adverse effect on the female reproductive output. Reproductive success therefore appears to represent a higher priority in female *N. metallicus*, with normal thermoregulatory behaviour and tail regeneration constituting only minor priorities in comparison.

In squamate reptiles, the thermal environment that the developing embryos are exposed to has been shown to influence their phenotype at birth (e.g. Beuchat 1988, Shine and Downes 1999, Swain and Jones in press b, Wapstra in press). The selection of more shaded, and presumably cooler, basking sites by tailless lizards had the potential to expose developing embryos to different thermal conditions during gestation. However, tailless *N. metallicus*, by maintaining the equivalent thermoregulatory behaviour of tailed females during gestation, were able to ensure that the phenotype of their offspring was not adversely affected. *Niveoscincus metallicus*, therefore, despite suffering inhibited mobility and modifying its habitat use appears to be able to limit the survival, thermoregulatory and reproductive costs of caudal autotomy.

This study has demonstrated that caudal fat stores are the primary energetic reserve in *Niveoscincus metallicus*. However, this heavy reliance on caudal fat stores has the potential to result in severe energetic costs (e.g. Symth 1974, Congdon *et al.* 1974, Dial and Fitzpatrick 1981, Wilson and Booth 1998). The presence of a previously unreported anatomical modification, however, appears to limit the loss of energetic reserves during tail autotomy. *Niveoscincus metallicus* was found to store the majority (~90%) of its caudal reserves within the proximal third of its tail. It appears that this aggregation of caudal fat enables *N. metallicus* to readily lose its tail to escape predatory encounters. *Niveoscincus metallicus*, therefore, has developed a mechanism to allow it to reap the survival benefits of caudal autotomy, while limiting the subsequent energetic costs it imposes.

Although *N. metallicus* appears to be capable of limiting the direct loss of fat reserves when the tail is shed, there seems to be a high energetic cost of regenerating the tail. Caudal autotomy during vitellogenesis was shown to result in a significant reduction in clutch size. Although reduced clutch sizes have commonly been found to result from tail autotomy (e.g. Smyth 1974, Dial and Fitzpatrick 1981, Wilson and Booth 1998), the reduction of caudal fat has generally been considered to be the primary cause. However, the diminished level of reproductive investment in the present study was attributed to diversion of energy previously allocated to reproduction towards tail regeneration. Due to the high frequency of tail loss in *N. metallicus*, females appear to have developed an alternative reproductive strategy should they experience caudal autotomy whilst making their reproductive decisions. These females appear to adopt a strategy whereby they produce a smaller number of larger and ‘better’ quality young by provisioning more yolk to each embryo. The reproductive strategies of *N. metallicus* appear to be flexible, a trait that presumably allows them to inhabit a wide range of habitats in the unpredictable Tasmanian environment.

Caudal autotomy, however, during gestation was not found to influence the size or weight of offspring. *Niveoscincus metallicus* utilises both lecithotrophy and placentotrophy (Swain and Jones 1997, in press a; Jones *et al.* 1998; Thompson *et al.* 1999a); however, developing embryos remain primarily dependent on yolk reserves during development (Swain and Jones in press a). Tail loss in *N. metallicus*,

therefore, appears to inhibit lecithotrophy but not placentotrophy. Presumably the major reason for this discrepancy is the level of reproductive investment that occurs during each of them. Vitellogenesis provides an egg rich in lipids and energy (Jones *et al.* 1998, Thompson *et al.* 1999a), whilst placentotrophy during gestation only requires the provision of water, ions and a small amount of organic material (Thompson *et al.* 1999a). The accumulation of abdominal fat stores in *N. ocellatus* during gestation (Wapstra and Swain in prep) suggests that the provision of resources during gestation is relatively inexpensive. Consequently, it appears that placental nutrition in *N. metallicus* does not place a high energetic burden on the mother and therefore the reduction of energetic stores through caudal autotomy has little relevance to the phenotype of the current clutch.

Contrary to popular belief (e.g. Turner *et al.* 1982) the frequency of tail loss in *N. metallicus* did not appear to be related to predation pressure. However, the position of tail breaks seemed to be associated with predation efficiency, a result that has been suggested previously (Jaksic and Busack 1984, Jaksic and Greene 1984, Medel *et al.* 1988). The most interesting finding, however, was the apparent ability of *N. metallicus* to perform 'economy of autotomy'. Around 60-70% of the individuals caught during this study were found to have lost their tail beyond the proximal third where the caudal fat is stored. Zani (1996) has found that the frequency of tail loss and position where autotomy occurs has co-evolved in lizards, with tail loss frequency negatively related to break index. This situation is no more evident than in *N. metallicus* where the high frequency of autotomy appears to result from tail breaks within the distal portion of the tail. However, the aggregation of caudal fat within the proximal regions of the tail in *N. metallicus* may have been the driving force for the evolution of 'economy of autotomy' in this species, and quite possibly in the 39 species studied by Zani (1996).

The results of this study have suggested that the costs of caudal autotomy may differ between adults and juveniles. Locomotory performance was severely restricted (~50% decrease) in juveniles following autotomy; however, tail loss at birth did not restrict its growth rate. The absence of any energetic costs in juvenile may be related to the differing priorities of adults and newborns. This study has shown that survival and reproductive success are the major priorities of adult *N. metallicus*; however,

since newborns do not have any concerns in relation to reproduction their primary goal appears to be survival to reproductive maturity. Neonatal growth rate is vital to the survival of juvenile lizards as the speed with which individuals can progress through size classes and reach sexual maturity may influence their survival (Dunham 1978, Ferguson and Fox 1984, Sinervo *et al.* 1992, Sinervo and Adolph 1994), age and size at maturity (Wapstra 1998) and consequently their future reproductive success (Adolph and Porter 1996). However, tail loss in newborns, a common occurrence in *N. metallicus* (pers. obs.) has the potential to impose energetic costs and reduce their growth rate and survival. Rapid attainment of large size is particularly relevant to juvenile skinks as a greater number of predators are able to subdue and consume juveniles but not adults. For example, Vitt and Cooper (1986) have observed hatchling *Eumeces laticeps* captured in spider's webs, presumably a result of their small size. However, juvenile *N. metallicus* appear to be able to quickly pass through these vulnerable stages even after caudal autotomy. The ability therefore for tailless *N. metallicus* newborns to grow at the same rate as their tailed siblings may be an adaptation to enhance their probability of reaching sexual maturity, thus increasing their fitness.

This study has demonstrated that *N. metallicus* possesses a number of behavioural and anatomical modifications to limit the costs it incurs from caudal autotomy. The ability to autotomise the tail is an ancestral squamate characteristic (Arnold 1984, 1998) that appears to have co-evolved with morphology (Russell and Bauer 1992, Zani 1996), locomotory performance (Zani 1996, Barbadillo and Bauwens 1997) and foraging behaviour (Vitt 1983, Zani 1996). Such intimate co-evolution indicates the undeniable benefit of autotomy and the strong selection pressures to reduce the costs that result from tail loss. Indeed the ability of *N. metallicus* to store fat close to its body, minimise the length of tail lost, modify its defensive and reproductive strategies and maintain its growth rate following tail loss suggests that the survival advantage of autotomy is substantial. However, *N. metallicus* has not been able to successfully overcome the energetic costs of tail regeneration or the inhibition of locomotory performance. The presence and absence of 'costs' in *N. metallicus* appears to represent the end result of continued co-evolution and trade-offs between the costs of benefits of caudal autotomy.

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‘COSTS’ OF CAUDAL AUTOTOMY IN LIZARDS:

Does survival come at a price?

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A review of literature submitted to the School of Zoology, University of Tasmania, in partial fulfillment of the requirements for the degree of Bachelor of Science with Honours.

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1.0 INTRODUCTION

Complex and bizarre behaviours have evolved in numerous animal lineages, because they enhance the species' chances of survival. This is well illustrated by autotomy, an antipredator behaviour that involves the self-amputation of certain body parts during predatory encounters. In lizards, the process is referred to as caudal autotomy, as it involves the loss of the tail (Bellairs and Bryant 1985, Arnold 1988). Caudal autotomy can be an extremely effective defensive tactic, distracting the predator while allowing the lizard to escape.

Caudal autotomy is common among lizards; however, seven of the 20 families and many species lack the ability to perform autotomy (Dial and Fitzpatrick 1981). Evolutionary history, ontogeny and environmental conditions all appear to influence the ease and frequency of tail loss. In the majority of lizards, the tail is regenerated after autotomy. The regeneration rate and eventual length of the replacement tail is highly variable between and within lizard assemblages, a consequence of a range of factors.

While most of the early studies on the topic focused on the processes and mechanisms of tail loss, more recent studies have attempted to comprehend the reasons for such a drastic action. Researchers have investigated the costs and benefits of autotomy, primarily in four areas. Although tail loss facilitates survival of predatory attacks, it has subsequent impacts on locomotory ability, reproductive success, behaviour and prospects for future survival.

This review will attempt to assess our current understanding and knowledge of caudal autotomy in lizards. The primary focus will be on the costs and benefits of autotomy and how the magnitude of each varies both within and between species. Due to the considerable amount of published literature on the topic, I will focus on the literature from the past decade, where possible. Arnold (1984, 1988) and Bellairs and Bryant (1985) provide comprehensive reviews of caudal autotomy in lizards, summarising the literature up to the mid-1980s. These reviews have been used as a basis for the current review, with subsequent work reviewed in later sections.

2.0 TAIL LOSS IN LIZARDS

It has become evident from recent research in lizard ecology, that the strategy of caudal autotomy plays an integral role in the antipredator behaviour of many species. It may seem surprising then that the ability to perform tail autotomy has been lost or reduced within several lizard assemblages. Chameleons, agamids and platynotids have all lost the ability to lose their tail, along with several species of geckos, skinks and iguanids (Bellairs and Bryant 1985). Arnold (1984) suggested that caudal autotomy represents an ancestral feature in lizards, due to its complete absence from some groups (listed above) and its presence in *Sphenodon*, a primitive living sister taxon. Tail function appears to be a driving force in the move away from autotomy in some groups, as the majority of species lacking the ability to lose their tail possess a functionally important tail (Bellairs and Bryant 1985). For example, autotomy is absent in monitor lizards that use their heavy tails for swimming and defense, and in chameleons where the tail has a strong prehensile ability to suit their arboreal life-style (Bellairs and Bryant 1985). However, the absence of autotomy may simply be a consequence of the phylogenetic history of a species rather than an indication that autotomy is disadvantageous in the current environmental conditions (Arnold 1988).

In species that are capable of tail loss, the decision to perform caudal autotomy appears to result from the shifting balance of the costs and benefits resulting from tail loss (Arnold 1988). Escaping predatory encounters is generally the main benefit of tail loss in lizards. However, several factors influence exactly how important caudal autotomy is in facilitating escape. Arnold (1984, 1988) provided five examples of situations that might affect the benefits of tail loss:

- 1) the benefits of autotomy will be slight when predation is rare;
- 2) breaking free of a predator can only be useful if the lizard can elude further pursuit, by running from the vicinity or reaching a secure refuge; this must be achieved before the shed tail has been consumed by the predator;
- 3) autotomy may be of limited importance where the lizard has some alternative means of deterring predation, for example claws or attack with the tail;

- 4) autotomy may be more beneficial to smaller species with a limited ability to fight back than to robust larger species; and
- 5) the effectiveness of the tail as a distraction device depends on the tail being palatable and an acceptable food source to the predator; tails that are small or do not move significantly after autotomy may have a limited distraction value.

The 'costs' of tail autotomy (discussed in detail in Section 4), like the benefits, exhibit extreme variation within and between species. These fluctuating costs and benefits affect the extent and ease of tail loss, and along with the evolutionary history of each species, place constraints on how, if and when, caudal autotomy occurs.

2.1 THE PROCESS OF TAIL LOSS

The anatomical and physiological aspects of caudal autotomy have been extensively studied over the past two centuries. However, Bellairs and Bryant (1985) provide the only comprehensive review of this work. For simplicity, I will present only a generalised outline of the process of caudal autotomy in lizards, using their review as a basis.

In lizards, two forms of caudal autotomy are possible (Bellairs and Bryant 1985):

- 1) intravertebral (or 'true') autotomy- tail breakage occurs through predetermined sites of weakness, called fracture planes; each fracture plane passes through a caudal vertebrae, hence, its name intravertebral autotomy; significant caudal modifications exist, with fracture planes extending through surrounding soft tissues; and
- 2) intervertebral autotomy- the breakage point is located between caudal vertebrae. This is the type of autotomy that occurs in lizards with regenerated tails and those species where tail autotomy has evolved secondarily. No obvious caudal modifications usually exist.

Although in theory these two forms of autotomy are discrete, in practice it may be difficult to distinguish between them (Arnold 1988). Autotomy can occur through

two mechanisms: a) sheer mechanical force (i.e. tail grasped by predator); or 2) muscular force (i.e. contraction of caudal musculature) (Bellairs and Bryant 1985). The latter is often referred to as spontaneous autotomy as no force is applied. However, in most instances a combination of both mechanisms is required to achieve autotomy (Bellairs and Bryant 1985). Caudal autotomy is under some degree of neurological control, due to the muscular action required for shedding the tail. Therefore some species are capable of losing the smallest portion of tail necessary to ensure escape (Arnold 1988). This process is known as 'economy of autotomy'.

Having a tail forcibly removed by a predator could result in massive trauma in lizards, if it was not for a series of adaptations in the caudal tissues. Soft tissues such as muscles, blood vessels, nerves and the spinal cord are all modified to limit the damage during and after autotomy (Bellairs and Bryant 1985). The anterior caudal vertebrae usually lack fracture planes to prevent breakage occurring too close to vital organs near the cloaca (i.e. hemipenes in males) and major locomotory muscles such as the femur caudifemoralis (Bellairs and Bryant 1985). The functional constraint posed by the caudifemoralis muscle group may influence the patterns of caudal evolution due to its relationship with locomotory ability (Russell and Bauer 1992). The process of tail regeneration (Section 3) is primarily responsible for repairing tissue damage and limiting possible infection.

The ability for caudal autotomy has been lost several times within the evolution of lizards (Section 2.0); once it has been lost it is impossible for this ability to be redeveloped in its original form. Intervertebral autotomy seems to represent a re-evolution of tail autotomy in taxa that have previously lost the capacity for intravertebral autotomy (Arnold 1988). The ability to perform autotomy may become restricted within the lifetime of an individual. During ontogeny, there may be complete or partial fusion of the fracture planes, reducing the capacity for tail loss (Arnold 1984). Alternatively, the loss of fracture planes in the skin, along with a corresponding increase in the strength of attachment of musculature to myosepta in some species, acts to increase the force required to achieve autotomy (Arnold 1988). These mechanisms may be responsible for the decrease in the ability to perform autotomy with age that is observed in several species (Arnold 1988).

2.2 AUTOTOMY AS A DEFENSIVE STRATEGY

At first glance the strategy of caudal autotomy in lizards appears to be paradoxical, since it involves shedding a functional appendage that has a range of uses in several facets of life. However, tail autotomy seems to benefit lizards in two distinct ways (Arnold 1988):

- 1) it facilitates escape from a predator that has seized them by the tail; and/or
- 2) it allows the tail to be used as a distraction, engaging the attention of the predator while the lizard escapes.

The tail may be offered to the predator while still attached, diverting the point of attack to the tail and away from the vulnerable head and body (Daniels *et al.* 1986). Colour and markings may also enhance the attractiveness of the tail to the predator (Section 2.2.2). The shed tail usually moves vigorously for a period of time, maintaining the attention of the predator and increasing the handling time to consume the tail. Compared to the rest of the lizard, eating the shed tail may be a less nutritious meal for the predator, but it has already been secured (Arnold 1988). To the lizard, providing an entrée is preferable to becoming the main course. However, some small Australian monitor lizards (the predators) appear to take advantage of the fragile tails of some geckos and deliberately harvest them as the geckos are difficult to catch and eat whole (Arnold 1990).

2.2.1 How effective is tail autotomy?

Few who have ever attempted to catch lizards would doubt the effectiveness of caudal autotomy as a defensive mechanism. The high frequency of tails, but not their owners, in the crops and stomachs of predators highlights the value of autotomy in nature (Arnold 1988). Although not all lizards that perform autotomy manage to escape from predators, it seems that enough do to make the strategy worthwhile (Arnold 1990).

Predation events are rarely observed in the wild, making it difficult to assess the effectiveness of caudal autotomy in natural situations. However, staged encounters in the laboratory have demonstrated the effectiveness of autotomy during predatory episodes. Congdon *et al.* (1974) placed four tailed and four tailless geckos (*Coleonyx variegatus*) in a test arena with their natural predator, the spotted night snake. Over thirty trials, 37% escaped by autotomy and 63% were caught. However, no tailless lizards that were grasped managed to escape. Similar results were found by Daniels *et al.* (1986) during trials involving the Australian gecko, *Phyllodactylus marmoratus*, and a marsupial predator. Seventy-six percent of tailed lizards escaped, 62% through autotomy, and only 24% were caught. However, when tail autotomy was not a possible defensive mechanism, as in tailless lizards, 71% were caught with 29% escaping by running. In some instances, as seen in the skink *Scincella lateralis*, predators can be extremely efficient and catch every tailless lizard, whereas autotomy may be an effective strategy (73% escaped, 37% through autotomy) (Dial and Fitzpatrick 1984). These studies serve to illustrate the effectiveness of caudal autotomy and demonstrate how such a behaviour can confer an adaptive advantage.

2.2.2 Why do predators attack the tail?

The effectiveness of caudal autotomy in some lizards can be enhanced through enticing the predator to focus its attack on the tail. In some instances the tail may even be 'offered' to the predator in order to divert the attack away from the vital head and body (Arnold 1988). In order to use the tail as a decoy, the lizard must draw the attention of the predator towards it. Two major mechanisms have been adopted to achieve this: a) behaviour and tail movement, and b) tail colour or markings.

Two studies, by Daniels (1985a) and Daniels *et al.* (1986), illustrate how effective behavioural responses to predation can be in diverting the attack to the tail. In the presence of its natural predator, *Antechinus swainsonii*, the gecko *Phyllodactylus marmoratus* performed several behaviours including running, remaining motionless and vibrating the tail laterally (Daniels *et al.* 1986). These responses were effective as 70% of the attacks were directed towards the tail, allowing 62% of the animals to escape through autotomy and 14% by running. Few lizards survived when the attack

was focused towards the head or body. Attacks directed at the tail also have an increased likelihood of missing altogether, sometimes allowing escape without the need for autotomy. Postautotomy tail movement also acts to maintain the attention of the predator and allow the lizard to escape, with violently thrashing tails requiring more handling time than slowly moving tails (Dial and Fitzpatrick 1983).

A brightly coloured tail may enhance the attractiveness of a moving tail to a predator. This is exemplified by skinks in the genus *Eumeces*, where juveniles possess blue tails (tail colouration absent in adults) that appear to aid in diverting predator attacks (Cooper and Vitt 1985). The tail is thrashed laterally in response to predators, emphasizing the colour. Cooper and Vitt (1985) found that this mechanism managed to divert half of the attacks by scarlet king snakes to the tail. When the blue tail was hidden by black paint, all attacks were directed towards the body resulting in 100% mortality, showing that the blue colouration is extremely effective in attracting the attention of predators. However, the effectiveness of strong colouration as an escape strategy may in turn increase the probability of detection (Cooper and Vitt 1991).

2.2.3 Factors determining the ease of tail loss

The ease of tail loss, that is how readily the tail is lost in response to predation attempts, exhibits inter and intraspecific variation. Although inherent factors such as evolutionary history and ontogeny (Section 2.1) affect the ease with which the tail is lost, other factors also have an influence. In some instances the benefits from autotomy are high enough to warrant shedding a valuable tail. Conversely, in situations where the benefits from autotomy are low, tail loss should be avoided. Arnold (1988) proposed that the readiness of tail loss should vary depending on the value of the tail. Animals with low cost tails should lose their tails earlier in response to predators and at lower levels of tactile stimulation. However, in situations where the tail is extremely valuable (e.g. lipid storage organ) and costly to replace, autotomy should be delayed until the risk of capture without tail loss approaches certainty.

Several authors have found that a range of intrinsic and extrinsic factors may combine to influence the ease of tail loss. The force required to achieve autotomy generally

decreases with temperature; therefore the ease of tail loss should increase in response to decreasing temperature (Bellairs and Bryant 1985). This is generally the case in most lizards, except for the gecko *Gehyra variegata* where tail loss occurs with greater ease at low (4°C) and high (19-29°C) temperatures, but not intermediate temperatures (Bustard 1968). Fox *et al.* (1998) found that females autotomised their tail with greater ease than males, which may have been an indicator of the potential costs of tail loss in terms of reproduction and social status. However, depending on the sexual differences in the costs of tail loss, the situation may be reversed in other situations or species. Lizards with a previous history of caudal autotomy have been observed to relinquish their tails more readily on subsequent occasions (Fox *et al.* 1998). Perhaps this is due to the decreased value of the regenerated tail; therefore the lizard would part with it more readily. Perez-Mellado *et al.* (1997) found that the ease of tail loss was greater in continental populations than island populations due to the higher probability of predation. Data from Fox *et al.* (1994) support this conclusion. They observed that tail loss occurred more readily at low elevations with high predation than high elevations with low predation rates. Alternatively, the differences in ease of autotomy may simply be the result of different predator and attack modes, or environmental differences. Starved geckos, *Phyllodactylus marmoratus*, shed their tails more readily than fed ones, indicating that physiological state can affect the ease of autotomy (Daniels 1984). Neurological control also has an important function in determining the ease of autotomy, with conscious animals losing their tails more readily than unconscious ones (Arnold 1988). This implies that the contraction of the caudal musculature that causes tail autotomy is under active neurological control.

This final point has an important implication for the studies performed in this area, all of which were conducted in the laboratory using artificial mechanisms to achieve autotomy. The ease of autotomy measured may be a result of the laboratory conditions and not an accurate reflection of the ease of tail loss when confronted by predators in nature. However, studying the ease of caudal autotomy in field conditions would be difficult.

2.3 THE FREQUENCY OF TAIL LOSS

Haldane and Huxley (1927, cited Arnold 1988) believed that the high frequency of broken and regenerated tails in many populations illustrated the effectiveness of caudal autotomy. Most authors consider the frequency of tail loss to be an indication of the predation intensity within a population, with each lost or regenerated tail evidence of a predatory event (Arnold 1988). Consequently, several studies have attempted to utilise tail loss data to obtain a measure of predation intensity. These studies have discovered that several factors may affect the frequency of autotomy in lizard populations. Bellairs and Bryant (1985) listed six factors that influence the prevalence of tail loss:

- 1) the habits and habitat of the species (Vitt 1983, Arnold 1984);
- 2) the readiness with which the tail is shed (see Section 2.2.3);
- 3) frequency of intraspecific aggression (Vitt *et al.* 1974);
- 4) prevalence of different types of predators;
- 5) age and sex of the individual (Turner *et al.* 1982, Vitt and Ballinger 1982); and
- 6) longevity of the species.

The frequency of tail autotomy within a species is generally determined using field observational or mark-recapture studies. Laboratory studies can also assess the proportion of individuals that autotomise their tail during staged encounters. In the case of field studies, collecting bias may artificially affect the prevalence of tail loss and tails may also be lost in the process (Arnold 1988). Some studies (Vitt and Cooper 1986) have determined tail loss frequencies from preserved museum specimens. However, population estimates of tail break frequency may be unreliable using this method as museums usually prefer to collect intact animals and the tail may have been lost during collection or post-mortem handling (Arnold 1984).

The occurrence of tail loss in lizards can be highly variable, ranging from no autotomy to 80-90% tail loss within a population. Males tend to have higher rates of tail autotomy than females, as observed in *Sceloporus virgatus* (Smith 1996) and the gecko *Lygodactylus klugei* (Vitt and Ballinger 1982). This is generally attributed to

differences in activity and behaviour, with males usually covering greater distances to forage, making them more susceptible to predation. Age (and size) can also have an effect on the prevalence of tail loss; in some instances the frequency of autotomy increases with age (Turner *et al.* 1982, Vitt and Ballinger 1982), while in others it decreases or remains constant (Smith 1996). Long-lived species usually have higher incidences of tail loss, as they are likely to encounter more predators in their life than short-lived species, with the possibility of multiple breaks. Brown and Ruby (1977) observed that in male iguanas, *Sceloporus jarrovi*, tail loss was more frequent at higher elevations.

The ecology of a species also appears to have some influence on its frequency of tail loss. Arnold (1984) documented the tail loss frequency in museum specimens of three different assemblages: European lacertids, African agamids and East Arabian lizards (skinks, geckos and lacertids). In each group tail autotomy was found to be more frequent in climbing species than in ground dwelling species, as the tail is less important in locomotion when climbing. Therefore, to obtain useful estimates of tail loss frequency, a range of factors need to be considered.

2.3.1 Is tail loss an indication of predation intensity?

It is widely assumed that the prevalence of caudal autotomy provides an approximate estimate of predation intensity within a population (Section 2.3). Generally the association between tail loss and predation is considered to be positive; more lost or regenerated tails indicates more predation events (Arnold 1988). However, how valid are these assumptions? Does the frequency of tail loss really indicate predation intensity? Are all tails lost to predators or can they be lost in some other way?

Jaksic and Greene (1984) documented tail loss frequencies of five lizard species and the presence of these species in the diets of 11 predators in central California. They found a negative correlation between the frequency of tail loss and the intensity of predation; species where tail loss was more prevalent occurred less commonly in the diet of predators. It was suggested that tail loss frequencies are more likely to reflect the inefficiencies of predators (prey attacked, but autotomised tail and got away),

rather than the intensity of predation. By this reasoning, predation intensity would be expected to be greatest in species with low frequencies of tail autotomy, as efficient predators would attack the body and not the tail. However, the authors seem to have underestimated predation intensity. Although the diets of most of the predator species were accurately known, complete data were not available for one species. It is also uncertain whether information on all predatory species was included; if not, the probability of concluding that a negative relationship existed would be increased. Turner *et al.* (1982) also found no correlation between predation and tail loss in yearling and 2 year old *Uta stansburiana*, but a positive correlation was observed in hatchlings.

Medel and colleagues (1988) provide some evidence to support Jaksic and Greene (1984). In staged laboratory encounters, they compared the predation efficiency of three predator species, a teiid lizard, snake and falcon. The falcon was found to be the most efficient predator, catching 100% of each of the three species of lizard. However, between 10-20% of lizards escaped from the teiid lizard and snake through tail autotomy. Although predation efficiencies can be artificially inflated in laboratory tests, the study does demonstrate that predator inefficiencies can affect the prevalence of tail loss. Despite this, positive relationships between tail loss frequency and predation intensity are possible in the wild (Turner *et al.* 1982).

2.3.1 Partial Tail loss

Although, in the majority of instances, caudal autotomy results from attempted predation, the tail (or portions thereof) may be lost under different circumstances. Vitt *et al.* (1974) suggested that intraspecific fighting and aggression might be responsible for tail autotomy in certain situations. They observed a population of male iguanids, *Sceloporus magister*, in the field, documenting the frequency of defensive displays and fighting. Males of this species establish and maintain territories, with fighting often resulting in scars and wounds on the legs and tail. These scars are absent in females which do not display aggression. It was found that males lost their tails four times more frequently than females. They used this information to infer that intraspecific fighting in males may be partly responsible for

the disparity in tail loss frequency. Although no experimental support is currently available, this anecdotal evidence indicates the possibility of autotomy through this process. However, intraspecific fighting in most instances would probably result in partial rather than complete tail loss.

Partial tail loss may also be the result of 'economy of autotomy' (Section 2.1), where the smallest portion of tail necessary for escape is lost. The mechanism acts to limit the costs of autotomy (i.e. caudal fat loss), while maintaining the benefit of escape from potentially fatal predatory encounters. Regeneration time (Section 3) may also be substantially reduced as there is less tail to replace, decreasing the period where inhibited locomotion and reproductive, behavioural and survival expenses is experienced. Therefore, such a mechanism appears to be adaptively advantageous (Arnold 1984). However, not all species that possess this ability make full use of it in nature, as seen in the gecko *Phyllodactylus marmoratus* (Daniels 1985a).

3.0 TAIL REGENERATION

In the majority of lizard assemblages, some degree of tail regeneration occurs after caudal autotomy. Tail regeneration is the reproduction of relatively complicated organs and structures after they have been lost through trauma or other events (Bellairs and Bryant 1985). Although most organs, such as the tail in lizards, that have the capacity for autotomy, generally possess some powers of regeneration, these two phenomena are not necessarily linked (Bellairs and Bryant 1985). This is highlighted in agamid lizards that perform intervertebral autotomy, where the shed tail may or may not be regenerated and if it is the results is a less functional tail (Arnold 1984). Defining what actually constitutes caudal regeneration can be hazardous, as the border between regenerative and reparative processes such as wound healing can become blurred (Bellairs and Bryant (1985).

3.1 THE PROCESS OF TAIL REGENERATION

As was the case with caudal autotomy, Bellairs and Bryant's (1985) review will be used as a basis for this section. The mechanisms responsible for tail regeneration in lizards are generally conserved between species, with caudal replacement achieved in three principal phases:

- a) wound healing;
- b) blastema formation; and
- c) differentiation and growth (Bellairs and Bryant 1985).

Tissue damage from tail loss is limited as a result of the mechanisms described in Section 2.1, with a minimal amount of blood loss and structural damage. Blood clotting on the tail stump forms a scab and plugs the ruptured spinal cord, while the surrounding skin rapidly contracts to cover the stump (Bellairs and Bryant 1985). Phagocytic cells, white blood cells and lymphocytes migrate to the area to limit infection and commence wound healing. A blastema, a mass of undifferentiated cells, forms under the scab, but despite intense cellular activity, regeneration of the tail does not begin for 10-15 days (latent period) (Bellairs and Bryant 1985). After this latent

period, the blastema begins to differentiate and proliferate, forming new tissues, resulting in tail elongation. Regeneration is rapid over the subsequent weeks, decreasing back towards normal somatic growth after about three months (Bellairs and Bryant 1985).

The resultant regenerated tail may be longer than the original, with enhanced lipid levels (Vitt *et al.* 1977); however in some species the replacement tail never reaches the original size (Bellairs and Bryant 1985). The regenerated tail may have a diminished value as an antipredatory device, as the lost caudal vertebrae are replaced by a cartilaginous tube. The tail may be forcibly broken, but due to the absence of fracture planes 'true' autotomy is impossible within the regenerated portion. However, future intravertebral autotomy can still occur through the remaining autotomous caudal vertebrae and the junction point of the regenerated tail. The regenerated caudal muscles are generally less organised and are attached to cartilage instead of bone. This may limit the range and force of tail movement, also diminishing the range of post-autotomous movement.

3.2 FACTORS INFLUENCING TAIL REGENERATION

Arnold (1988) proposed that the rate and extent of caudal replacement should be determined through the balance of costs and benefits of tail restitution. Tail regeneration restores a potentially valuable antipredator device, which is also important in many aspects of locomotion, behaviour, reproduction and survival (Section 4). However, doing so requires energetic and material resources that might otherwise be used for body growth and reproduction. He suggested that in situations where the potential benefits of regaining the tail outweighed the cost of doing so, caudal replacement should be rapid.

The rate and degree of caudal replacement exhibits intrinsic (i.e. phylogenetic and ontogenetic) and extrinsic (environmental) variation (Arnold 1988). Tail replacement may be achieved in as little as 4 weeks or as long as 12 months, if at all (Arnold 1984, Bellairs and Bryant 1985). Several authors have found that some degree of sexual dimorphism exists in the rate of regeneration (Congdon *et al.* 1974, Vitt *et al.* 1977,

Vitt 1981, Vitt and Ballinger 1982), with juveniles generally regenerating their tails faster than adults (Vitt *et al.* 1977). Species with functionally important tails usually divert more energy into regeneration and, therefore, regenerate their tail rapidly. Vitt *et al.* (1977) demonstrated that life history variation may affect caudal regeneration. They found that tail replacement was quicker in short-lived, early maturing species with several breeding opportunities each season, than long-lived, late maturing species with short seasonally restricted breeding seasons. It is evident, therefore, that certain intrinsic constraints are capable of influencing the rate of tail regeneration.

Several external factors have also been shown to have a major effect on regeneration performance. Regeneration rates generally increase with rising temperature, up to a certain optimum, and in some instances temperature can have a profound effect (Bellairs and Bryant 1985). Ramachandran and Ndukuba (1989) demonstrated experimentally that photoperiod can influence caudal regeneration. They found that geckos, *Hemidactylus flaviviridis*, treated with a high dose of parachlorophenylalanine (p-CPA), a chemical which restricts photoperiodic reception, exhibited lower rates of tail regeneration than untreated animals. There also appears to be an optimum light-dark (photoperiod) regime for caudal regeneration (Turner and Tipton 1972). Other chemicals such as NaF also work in a dose-dependent manner to either inhibit (high dose) or accelerate (low dose) tail regeneration (Suresh and Hiradhar 1990). External factors that impact on body condition appear to affect the rate of tail regeneration. Lack of food availability in the wild might decrease regeneration rates, as it has been shown that diet supplements in the laboratory can increase the rate of tail replacement in some species (Bellairs and Bryant 1985). Oppliger and Clobert (1997) showed that *Lacerta vivipara* with energetically costly blood parasites devoted less energy to regeneration, resulting in lower regeneration rates than unparasitised animals.

4.0 THE 'COSTS' ASSOCIATED WITH CAUDAL AUTOTOMY

Since the mid-1980s reviews by Arnold (1984, 1988) and Bryant and Bellairs (1985), much of the literature concerning caudal autotomy in lizards has focused on the costs of tail loss. In this short space of time a vast amount of literature has built up in three main areas: locomotory ability, reproduction and behaviour. However, this knowledge appears to have come at the detriment of other aspects of caudal autotomy such as physiology, anatomy, morphology, tail regeneration and endocrinology. Recent literature in these areas is scarce, with little addition to the knowledge base of the last decade. Although much of the research on the 'costs' of autotomy since these earlier reviews has extended our knowledge, its value may be limited. Most studies have focused on selected taxa, mainly iguanids in America and lacertids in western Europe, with only a limited number of researchers tackling these questions in Australia. How this research translates to Australian species of skinks and geckos (the majority of the autotomous lizards in Australia) is yet to be seen. However, several areas still need to be explored in order to fully comprehend the ramifications of tail loss in lizards. This section will review the advances in our knowledge about the costs of autotomy over the past decade.

Caudal autotomy in lizards facilitates escape from potentially fatal predatory attacks, as highlighted in previous sections. However, subsequent, and at times, massive costs are incurred in doing so. Regenerating the lost tail may be energetically expensive, consuming vital resources that would usually be directed towards body growth or reproductive effort (Martin and Avery 1997). However, behavioural compensation may allow lizards to maintain normal body temperatures (Section 4.3.3) and food intake (Section 4.3.2) to maintain metabolic rates and hasten regeneration.

The absence of a tail, however, imposes some restrictions on the capabilities of the animal. Caudal autotomy affects several areas such as locomotion (Section 4.2), reproduction (Section 4.1.2), behaviour (Section 4.3) and future survival (Section 4.4), most of which are intrinsically linked. Tail loss may reduce locomotory ability, agility and endurance, which leaves the lizard more vulnerable to future predation. No literature is currently available on the duration of these costs or the manner

(gradual, exponentially) in which these abilities return. During regeneration, behavioural compensation may occur, with modified activity levels, movement rates and microhabitat use. In some instances social status and reproductive success are also reduced as a consequence of tail loss. Although lizards can modify their behaviour to some extent to compensate for tail loss (Formanowicz *et al.* 1990), caudal autotomy may have major implications in several facets of everyday life.

4.1 ENERGETIC COSTS OF TAIL AUTOTOMY

It may seem paradoxical, but in many species of lizards that perform tail autotomy, caudal fat stores constitute a large proportion of their total energy reserves. Caudal lipid stores are a major source of energy during hibernation and episodes of severe food shortages (Avery 1970). Therefore, the loss of this auxiliary energy source through tail autotomy could dramatically decrease the probability of future survival. In laboratory conditions, Daniels (1984) showed that starved tailed lizards survived longer than their starved tailless counterparts. Some species attempt to limit the loss of caudal fat stores through 'economy of autotomy' (Section 2.3.2), or by returning to consume the shed tail (Clark 1971). Clark (1971) found that 40% of *Lygosoma laterale*, a ground-dwelling species with substantial caudal fat reserves, returned to eat their tail if it was not consumed by the predator. He suggested that this might be an adaptive mechanism to recoup energetic costs and enhance the chances of future survival. Interestingly, species without caudal fat reserves, such as iguanids, rarely cannibalise their shed tail (Clark 1971).

Caudal fat stores are not only utilised in times of nutritional stress, they also provide a significant proportion of resources to two major processes: 1) body growth (Vitt *et al.* 1977), and 2) reproduction (Dial and Fitzpatrick 1981). However, as a result of the loss of caudal fat reserves in autotomy, the remaining energy stores are required to cater for these two processes. Tail regeneration can require a vast amount of energy resources, diverting energy away body growth and reproductive processes. Costs may be incurred through decreased body growth or reduced reproductive energy allocation as a result of this energy restriction. Althoff and Thompson (1994) believe that any decrease in body growth after tail loss is a result of social interactions or decreased

home range quality, rather than a consequence of energy diversion to regeneration. This is a valid point as the decreased home range and its quality (Section 4.1.2, 4.3.2), along with behavioural modification, might decrease nutritional intake, thus limiting body growth. However, energy diversion away from body growth has been observed in a number of studies (Section 4.1.1).

4.1.1 Body Growth

Caudal autotomy may severely restrict the rate of body growth in some species. Ballinger and Tinkle's (1979) work on hatchling *Sceloporus undulatus* demonstrates the effect tail loss may have. Tailed hatchlings grew at an average of 0.56 mm per day, nearly twice that of tailless hatchlings, 0.3 mm/day. Similar growth deficiencies have been observed in tailless *Uta stansburiana* (Niewiarowski *et al.* 1997). However, under conditions of high mortality, Althoff and Thompson (1994) found that there was no difference in the growth rates of tailed and tailless *U. stansburiana*, as the tail was not a lipid storage organ. Conflicting reports of decreased body growth (Ballinger and Tinkle 1979, Niewiarowski *et al.* 1997) and unchanged body growth (Ballinger and Tinkle 1979, Vitt and Cooper 1986, Van Sluys 1998) act to confuse our understanding of the costs of tail loss on growth. However, in most instances where tail loss did not impact upon body growth, the energy requirements of caudal regeneration were relatively low. Juveniles and females generally require more energy for body growth and reproduction respectively; therefore there is a greater likelihood of inhibited growth resulting from autotomy (Bellairs and Bryant 1985). This appears to be correct, as most of the studies that reported an effect on body growth were conducted on juveniles.

4.1.2 Reproduction

Wilson and Booth (1998) experimentally demonstrated the effect of tail loss on future reproductive output in the eastern water skink, *Eulamprus quoyii*. They found that removing the tail of reproductive females immediately prior to the onset of vitellogenesis resulted in a decrease in reproductive investment, as measured by the number of vitellogenic follicles and size of ovarian follicles. The resultant clutch size

was 75% lower in tailless lizards than in tailed females. A reduction in egg number was also observed by Smyth (1974) in two other species. This may well be as a result of the decreased energy allocation to reproduction in tailless females (Dial and Fitzpatrick 1981). Dial and Fitzpatrick (1981) found that the resultant eggs can also be lower in mass and energy content compared to tailed females with full energy reserves.

Size can strongly relate to social status in lizards and the tail may play an important role in communication, courtship and intraspecific interactions. Therefore, a process such as caudal autotomy that impacts on body size and tail function can result in a number of social costs. Fox *et al.* (1990) found that tail loss reduced the social status of subadult *Uta stansburiana*. Artificial replacement of the tail restored dominance in males but not females. This result suggests that the tail is an important status-signalling badge in males, but not females. In males of other species, tail loss appears to have little significance once territories have already been established, but may initially have a role attaining territories (Kaiser and Mushinsky 1994). However, these studies have only been conducted on a limited number of species, with the effect of tail loss on other species or groups and those without dominance hierarchies largely unknown.

In semi-natural conditions, it has been observed that tail loss decreases the number of courtships and copulations in both sexes of *Lacerta monticola* (Martin and Salvador 1993a). Salvador *et al.* (1996) demonstrated that this is a result of decreased social status. Tailless male *Psammodromus algirus* have significantly smaller home range sizes than tailed males. This may be a result of decreased social status, but they suggest it may be caused by impaired locomotory and activity abilities (Section 4.2). These restrictions result in smaller home ranges being maintained, diminishing access to females. Therefore smaller home ranges may be partly responsible for the decreased number of courtships and copulations in many species. However, no genetic studies have been undertaken to determine the exact parentage of each clutch, or the success of each copulation in producing young. Genetic studies have often revealed different mating situations to those obtained through behavioural

observations (e.g. in birds- Petrie and Kempenaers 1998). Genetic studies would reveal the true effect of tail loss on reproductive success.

Caudal autotomy affects reproduction in a number of ways; however, many aspects of reproduction have not been investigated in relation to tail loss. Reproductive mode, oviparity or viviparity, may affect the magnitude of the costs of tail loss. It is currently unknown whether autotomy has a larger impact in oviparous or viviparous females. Tail loss should affect viviparous lizards to a greater extent due to their higher reproductive investment and increased time carrying young. Viviparous lizards might be heavier, and therefore already have inhibited locomotion before autotomy (Shine 1980). Tail loss would further decrease locomotory abilities and increase the predation risk. The effect of maternal caudal autotomy on offspring fitness has not been studied. Shine and Downes (1999) found that environmental conditions during the pregnancy of viviparous skinks, *Pseudemoia pagenstecheri*, influenced offspring phenotype. Tail loss might result in decreased locomotion (Section 4.2), modified behaviour (Section 4.3) and modified thermoregulatory behaviour (Section 4.3.3), exposing the pregnant female to different environmental situations. Therefore, these factors may act to alter the phenotype of offspring born to tailless mothers, affecting their fitness.

4.2 LOCOMOTION

Many authors have investigated the effect of tail loss on the locomotory abilities of lizards. The tail has been proposed as having an important role in several facets of locomotion such as:

- 1) running speed;
- 2) flight distance;
- 3) endurance;
- 4) pause frequency; and
- 5) balance (Ballinger 1973).

Several authors have reported substantial decreases in running speeds after the removal of all or portions of, the tail. Maximum speeds in tailless lizards decreased by 36% in *Cnemidophorus sexlineatus* (Ballinger *et al.* 1979), 32% in *Cophosaurus texanus* (Punzo 1982), 35% in *Scincella lateralis* (Formanowicz *et al.* 1990), and 40% in *Psammodromus algirus* (Martin and Avery 1998). All of these species are quadrupedal; there is evidence that tail loss has a more substantial effect on bipedal locomotion. Punzo (1982) found that in the bipedal lizard, *Uma notata*, tail loss decreased running speeds by 42%. However, the true effect of tail loss is uncertain due to the inconsistency of methods used in the above studies. Each study differed in the amount of tail removed, the distance over which speed was measured, the method of measuring speed, substrate type, locomotion type (quadrupedal or bipedal), type of running (maximal, flight, normal), ecology of the species and the functional importance of the tail. It is clear, however, that tail loss does impact significantly on the locomotory ability of most species.

Several hypotheses have been put forward to explain these decreases in speed, including, the tail acting as a counterbalance (Pond 1978, Punzo 1982, Arnold 1984, 1988), or as an inertial damper (Arnold 1984, 1988), or as a regulator of stride frequency (Hamley 1990). Martin and Avery (1998) supported the view of Hamley (1990), finding that tail loss reduced stride length in *Psammodromus algirus*. These factors may be less important in climbing species and those that move on rocky substrates as the tail is less important in these forms of locomotion (Arnold 1984). However, some quadrupedal lizards are capable of faster sprint speeds once the tail has been removed (Daniels 1983, Hamley 1990, Brown *et al.* 1995). It is likely that in these instances the tail does not hold an essential function during locomotion. Brown *et al.* (1995) discovered that previous tail loss might affect locomotory ability subsequent to autotomy. They found that individuals with regenerated tails prior to autotomy ran faster and longer with more agility than those with original tails, suggesting that these lizards had learned how to compensate for the absence of a tail.

The majority of the work done in this area has focused on terrestrial locomotion. Some species of lizards that are capable of caudal autotomy possess other forms of locomotion such as gliding, climbing and swimming. No literature is currently

available in relation to autotomy in gliding species; however some information is available for the other two forms of locomotion. Arnold (1984) found that the frequency of tail loss was higher in climbing species. He suggested that this was the result of the tail being less important in climbing than in terrestrial species. However, no quantitative data have been obtained to test this hypothesis. Daniels (1985*b*) conducted the only study investigating the effect of autotomy on swimming ability. He found that tail loss reduced swimming speed and stamina in the water skink, *Sphenomorphus quoyii*. Clearly, further work is required to determine the effect of autotomy on these alternative forms of locomotion.

Locomotion without a tail may be energetically or metabolically expensive, as tailless lizards have decreased levels of endurance (Daniels 1985*b*, Martin and Avery 1998). This decreased stamina appears to affect the movement patterns of tailless lizards. Martin and Avery (1998) found that tailless *Psammodromus algirus* moved smaller distances in each burst (as burst duration was constant), and increased the frequency of pauses, resulting in lower overall speeds. These factors, combined with decreased stride frequency, resulted in lower maximal and overall speeds, with shorter distances covered in escape bursts. Locomotory restraints such as these would severely diminish the ability to escape predators in tailless lizards. However, behavioural compensation may limit some of the locomotory costs of autotomy (Section 4.3).

4.3 BEHAVIOUR

The primary costs of caudal autotomy are in relation to energetic restrictions and inhibited locomotion. However, modified behaviour appears to represent a secondary cost. Tail loss diminishes the ability to move, run, grow and reproduce. These actions are vital components in most aspects of behaviour and impact on most other important ecological factors (Martin and Avery 1997). Consequently, lizards tend to exhibit behavioural modification in order to compensate for the absence of a tail. The three major areas of behaviour that are heavily impacted on are: 1) antipredator behaviour; 2) foraging ecology; and 3) thermoregulation.

4.3.1 Antipredator behaviour

Most animals have the ability to assess and behaviourally influence their risk of being preyed upon, with behavioural decisions during foraging, activity periods, social interactions and everyday life affecting the risk of predation (Lima and Dill 1990). Most lizards exhibit a range of behavioural responses when they are confronted by a predator, including flight, body, head and tail movements, biting, tail lashing, body compression, vocalisations and tail autotomy (Daniels and Heatwole 1990, Leal and Rodriguez-Robles 1995). However, most of these usual behaviours directly or indirectly involve the use of the tail. Consequently, the absence of the tail decreases the range and effectiveness of the antipredator behaviours available to a lizard. Flight by running, the major antipredator response of most species, is generally less effective due to locomotory constraints (Section 4.2). These locomotory constraints, combined with altered antipredatory behaviour due to the absence of the tail, are primarily responsible for the high levels of mortality of tailless lizards observed in laboratory encounters (Section 2.2.1).

The literature specifically relating to the behavioural modifications of antipredator responses in tailless lizards is scant. However, it has been inferred from studies on the activity levels, movements and foraging ecology of tailless lizards that many species adopt a more cryptic lifestyle in response to caudal autotomy (Section 4.2.2-4.2.4). Due to reduced escape speeds, lizards usually forage closer to vegetation cover or refuges, adopt smaller home ranges (Salvador *et al.* 1996) and are generally less active. Tailless lizards also utilise rocky substrates, where predator density may be lower, to a greater extent (Martin and Salvador 1993*b*). These modifications might act to reduce the likelihood of being detected by a predator and, if detected, enhance the probability of escape.

Since tail loss may make lizards more susceptible to predation, one of two options could be implemented to reduce this risk. Tailless lizards should either become more cryptic (as seen above) or increase their vigilance or predator detection behaviours (e.g. tongue flicks). Although it is clear that tailless lizards tend to modify their behaviour to limit their risk of predation, no authors have investigated if autotomy

results in increased vigilance. Enhanced levels of vigilance would help the lizard to avoid predator encounters or escape earlier, which may be beneficial due to the reduced array of defenses available when faced with a predator. One final area that merits investigation is the response by predators to tailless prey. Since tailless lizards seem to act and respond to predators differently, it may result in the predator attacking the situation in a different manner. If such a behavioural shift occurs with predators, it may be partly responsible for the increased attack efficiency by predators towards tailless prey.

4.3.2 Foraging ecology

Since tail loss appears to have a significant impact on locomotion, activity, movement and home range quality, it is likely that the impact on foraging ecology would be substantial. Martin and Salvador (1993b) found that tailless Iberian rock lizards, *Lacerta monticola*, foraged more extensively in rocky microhabitats where predation risk was lower, but food availability was also lower. This resulted in a less diverse diet and an increased proportion of suboptimal prey items. However, they did not sufficiently sample the available invertebrate fauna in each microhabitat, their samples consisting of a single 1-minute visual survey of a small area. More intensive sampling that takes into account temporal variation and species other than ground-dwellers would be required in order to get a valid indication of the available food resources. Therefore, their conclusion that autotomy influences foraging behaviour should be viewed with caution.

As seen in Section 4.2, tail loss causes locomotion to be more ‘stop-start’ in nature, which is generally believed to be a result of the animal adopting a more cryptic lifestyle. However, this may in fact be a tactic to increase foraging success. Avery (1993) found that this form of pause-travel movement in *Lacerta vivipara* increased the probability of prey capture compared to faster forms of locomotion. However, the reasons why tailed lizards do not do this as well are unclear.

When deciding when and how to initiate the capture of a potential prey item, animals should consider not only its profitability, but also the associated risk of predation

(Martin and Avery 1997). Martin and Avery (1997) hypothesised that tailless lizards should be more careful when deciding to capture prey for two reasons:

- 1) tailless individuals may be more vulnerable to predation when the sudden running to capture prey attracts the attention of potential predators; and
- 2) tail loss may decrease sprint speed performance and the ability to chase fast-moving prey.

They tested these hypotheses in the laboratory using the lizard, *Psammodromus algirus*. Tailless lizards were found to be slower to initiate attack (reaction time), and also ran towards the prey item at submaximal speeds. Other aspects of prey capture and detection did not differ. Their study therefore provided experimental evidence that tailless lizards delay the decision to attack, while taking into account the energetic and antipredatory considerations of prey pursuit. However, relatively little is known about the effect of tail loss on the foraging behaviour of lizards as only two studies have ever been conducted on the topic. More comprehensive studies that fully document the available food resources, foraging behaviour and diet of tailless lizards are required to fully gauge the effect of autotomy on foraging behaviour in lizards.

4.3.3 Thermoregulation

In ectothermic animals, such as lizards, thermoregulation plays an important role in the maintenance of temperature sensitive processes. Tail regeneration involves a series of complex temperature-dependent physiological processes; therefore, in order to replace the tail rapidly, thermoregulatory behaviour should act to maintain optimum body temperatures. However, despite the importance of body temperature to regeneration rate, only one study has been reported. Martin and Salvador (1993c) examined the effect of caudal autotomy on the thermoregulation capabilities of the rock lizard, *Lacerta monticola*. They found no difference between tailed and tailless lizards in time spent basking, field or selected body temperature, mean duration of basking or basking frequency. Thermoregulatory postures and heating and cooling rates were not recorded. Tailless lizards seemingly adjusted for locomotory impairment by using rocks to a greater extent; rocks are a better heat retaining

medium for thermoregulation than other substrates. They also basked closer to refuges and maintained lower morning body temperature by increasing maximal duration of basking periods. Their observations indicate that tailless lizards are able to limit the thermoregulatory costs of tail loss by modifying their behaviour in order to maintain the same thermoregulatory precision as tailed lizards.

4.4 FUTURE SURVIVAL

Previous sections have explored the costs and benefits of caudal autotomy, with various laboratory and field studies exploring the effect of each aspect separately. However, relatively few long-term studies have been completed which explore the overall survival probability of tailless lizards under natural conditions. Wilson (1992) studied seven populations of *Uta stansburiana* using mark-recapture methods and documenting the extent of tail injury. He found that lizards with incomplete tails generally suffered higher rates of mortality in the field, indicating that tail loss is positively associated with an increased risk of mortality.

However, Althoff and Thompson (1994) and Niewiarowski *et al.* (1997), despite studying the same species, found that tail loss had no effect on survivorship. Each of these studies involved mark-recapture of a large number of lizards over a number of seasons; however, different experimental methods were used. Wilson (1992) analysed natural tail loss in juveniles and adults, while Althoff and Thompson (1994) and Niewiarowski *et al.* (1997) only studied juveniles and induced tail loss. Wilson (1992) did not find that tail loss significantly reduced survival in every population, age group or sex, but in the majority of cases tail loss caused decreased survival. Niewiarowski *et al.* (1994) conducted their experiment under conditions of high mortality (up to 80% in natural populations), so any effect of tail loss may have been relatively smaller and not detected. Variation in food availability, food competition and predation intensity may explain the different results between the studies. Ferguson and Fox (1984) found that the annual fluctuation in these factors resulted in variation in the survival advantage of large juvenile *Uta stansburiana*. Therefore, the same environmental variation may be responsible for the differential impact of tail loss between the three studies.

The problem is that due to the large number of small studies that have been completed, each has focused on one aspect of tail loss in the laboratory, with few large field studies completed over a number of seasons and incorporating several aspects of caudal autotomy. Consequently, how each aspect of autotomy relates to each other aspect is not fully understood.

Therefore, the overall effect of tail loss in the wild may be different to that of the individual aspects observed in the laboratory. Alternatively, the four major modifications to reduce the costs of tail loss (Arnold 1984, listed below) may be sufficiently effective to avoid any substantial decrease in survivorship:

- 1) restriction of regeneration (no or partial tail regeneration);
- 2) consumption of the shed tail (Clark 1971);
- 3) 'economy of autotomy' (Section 2.1, 2.3.2); and
- 4) behavioural modification (Section 4).

Whatever the case, in certain situations the costs of caudal autotomy are extreme, resulting in severe impairment of function or behaviour, or both. Whether this translates into a decreased probability of survival may be dependent on the circumstances and the effectiveness of the above modifications.

5.0 SUMMARY

The aim of this review was to summarise the current knowledge and understanding of reptilian caudal autotomy. The processes of tail autotomy and caudal regeneration are extremely complex and variable; however, physiological, ecological, evolutionary and behavioural information can act to explain some of the diversity exhibited. Caudal autotomy appears to be a highly effective defensive tactic against predators. Despite the immediate and obvious advantages of tail loss, a wide range of subsequent costs are inflicted upon the animal. In situations where the potential benefits significantly outweigh the costs of tail loss, caudal autotomy becomes an adaptively advantageous strategy. However, autotomy may seriously increase the probability of future mortality and decrease reproductive success. In these circumstances, the fitness of tailless individuals will be severely diminished. Lizards can, however, modify aspects of their behaviour to limit the possible disadvantages of autotomy. Overall, the adaptive advantage of the caudal autotomy behaviour appears to be an extremely species or circumstance dependent mechanism.

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