Inter-populational variation in the cost of autotomy in the metallic skink (*Niveoscincus metallicus*)

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Abstract

Many species of lizard use tail autotomy to escape from potential predators. While frequency of tail loss is an unreliable indicator of predation intensity it may enable inter-populational comparisons of predation costs. This reasoning was applied to a study of the metallic skink *Niveoscincus metallicus*. A total of 368 lizards was sampled from across four populations to compare the frequency and position of tail loss and ultimately to examine whether the implications of tail autotomy differ between populations. The overall frequency of tail loss was 72%, although between populations the incidence of tail autotomy varied from 61.4% (Laughing Jack Lagoon) to 78.2% (Dynnyrne). No sexual differences were observed in the frequency of tail loss; however, the incidence of autotomy increased with age. The estimated position of tail loss did not vary between the sexes, although individuals from Dynnyrne experienced more proximal tail breaks than the other populations. This resulted in the predicted energetic cost of tail loss being significantly higher in the Dynnyrne population and, when combined with a high frequency of tail loss and relatively smaller body size, suggests that this population incurs relatively high costs as a result of autotomy. Overall, measures of tail loss in *N. metallicus* were found to be useful for examining inter-populational variation in the cost of tail autotomy.

Key words: geographic variation, predation, Scincidae, tail loss, tail regeneration, metallic skink, *Niveoscincus metallicus*

INTRODUCTION

The defensive tactic involving the autotomy of body parts in response to a predatory threat has evolved independently on numerous occasions within both invertebrates (e.g. crustaceans, cnidarians, molluscs, spiders, insects; Stasek, 1967; Robinson, Abele & Robinson, 1970; Edmunds, 1974; Roth & Roth, 1984; Klawinski & Formanowicz, 1994) and vertebrates (e.g. lizards, snakes, salamanders; Wake & Dresner, 1967; Willis, Threkeld & Carpenter, 1982; Arnold, 1988). Autotomy enables the individual to escape the grasp of the predator, the shed body portion diverting the predator's attention while the injured animal escapes (Arnold, 1988). Many lizards use tail autotomy as a defensive tactic after other strategies such as crypsis and flight have failed (see review by Arnold, 1988). The high incidence of shed tails, but not their owners, in the stomachs and crops of predators suggests that this is an effective defensive strategy (Arnold, 1988), a result that has been confirmed by staged predatory encounters within the confines of the laboratory (Congdon, Vitt & King, 1974; Dial & Fitzpatrick, 1984; Daniels, Flaherty & Simbotwe, 1986).

Consequently, some researchers have used the frequency of tail loss within a lizard population as an indicator of the intensity of predation (e.g. Pianka, 1970; Turner *et al*., 1982). However, the assumption that a positive relationship exists between the incidence of tail loss and the frequency of predation events is doubtful (see review by Jaksic & Greene, 1984). For example, in some species intraspecific aggression can confound estimates of predation activity (e.g. Vitt, Congdon, Hulse *et al*., 1974; Jennings & Thompson, 1999). More importantly, although high frequencies of tail damage may imply high levels of predation, they do not distinguish between efficient and inefficient predators. Thus, survivors may represent a relatively few fortunate escapees from efficient predators or a majority escape from inefficient predators. Predictably, Medel *et al* (1988) demonstrated experimentally that predation inefficiency results in artificially inflated estimates of tail loss frequencies.

However, the costs to individuals of autotomy and regeneration are well documented. For example, caudal autotomy in lizards may impair locomotor performance (Brown, Taylor & Gist, 1995; Martin & Avery, 1998; Downes & Shine, 2001; Chapple & Swain, 2002a), reduce

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Table 1. Potential predators of the metallic skink *Niveoscincus metallicus*. The proportion of skinks in the diet, foraging activity and predation risk are inferred from literature sources. Predation efficiency of each predator is inferred from Medel *et al*. (1988) and personal observations (see text for more details)

Potential predator	% skinks in diet	Foraging activity	Presumed efficiency	Predation risk	Source
Reptiles					
White-lipped snake *Drysdalia coronoides* (WLS)	89	Diurnal	Moderate	High	Shine (1981)
Tiger snake *Notechis ater* (TS)	7.3	Diurnal	Moderate	Low-Moderate	Shine (1987*a*)
Lowland copperhead *Austrelaps superbus* (LC)	56	Diurnal	Moderate	Moderate	Shine (1987*b*)
Mammals					
Domestic/feral cat *Felis catus* (FC)	∼ 3–5	Diurnal–nocturnal	Low	High	Barratt (1997), Molsher *et al*. (1999), Risby *et al*. (1999)
Spotted-tail quoll *Dasyurus maculatus* (STQ)	< 1	Nocturnal	Low	Low	M. E. Jones & Barmuta (1998)
Eastern quoll *Dasyuryus viverrinus* (EQ)	13	Nocturnal	Low	Low	M. E. Jones & Barmuta (1998)
Birds					
Kookaburra *Dacelo novaeguineae* (K)	∼ 3–30	Diurnal	High	High	Legge (1999), Blomberg & Shine (2000)
Black currawong *Strepera fuliginosa* and grey currawong *S. versicolor* (C)	?	Diurnal	High	Moderate	Barrett *et al*. (2003)
Grey butcherbird (*Cracticus torquatus*) (GB)	?	Diurnal	High	Moderate	Barrett *et al*. (2003)
Brown goshawk (*Accipiter fasciatus*)	2	Diurnal	High	Low	Marchant & Higgins (1993)
Brown falcon (*Falco berigora*)	10	Diurnal	High	Low	Marchant & Higgins (1993)
Forest raven (*Corvus tasmanicus*)	?	Diurnal	High	Low	Barrett *et al*. (2003)

reproductive investment (Dial & Fitzpatrick, 1981; R. S. Wilson & Booth, 1998), restrict growth rates (Ballinger & Tinkle, 1979; Smith, 1996), diminish social status and/or mating success (Fox & Rostker, 1982; Martin & Salvador, 1993; Kaiser & Mushinsky, 1994), and reduce survival (B. S. Wilson, 1992; Niewiarowski *et al*., 1997; Fox & McCoy, 2000). Clearly, if a high percentage of individuals incur some or all of these costs there may be significant consequences for the population collectively.

Thus, although the analysis of tail loss frequency may be problematical as an index of the intensity of predation, it may still prove valuable for inter-populational comparisons of predation costs. Since individual costs of autotomy should be similar for all populations of a species, variation in the frequency and position of autotomy can be used to infer consequential differences among populations.

This reasoning was applied to a study of geographic variation in tail loss in the metallic skink *Niveoscincus metallicus*. *Niveoscincus metallicus* is a small ground-dwelling skink that is widely distributed and abundant across a range of habitats from sea level to sub-alpine environments in Tasmania and south-eastern Victoria, Australia (Melville & Swain, 1999). It was ideal for our study for a number of reasons: the biology of the species is well known, and the impact of tail loss on fat stores (Chapple & Swain, 2002*b*), reproductive output (Chapple, McCoull & Swain, 2002), locomotion (Chapple & Swain, 2002*a*; Chapple, McCoull & Swain, 2004), and thermoregulatory behaviour (Chapple & Swain, 2004)

has been studied in detail. In addition, the phylogenetic relationships between populations of the species are known (McCoull, 2001), and geographic variation in life history and behaviour has been examined (McCoull, 2001), providing detailed background knowledge with which to compare populations. Our approach was to compare the incidence of tail autotomy among four populations of *N. metallicus* using tail loss frequency, and the estimated position of tail loss. The four populations comprised two urban and two forest populations that could reasonably be expected to be subjected to the complete range of predation pressures experienced by *N. metallicus* (Tables 1 & 2). Our study addressed three specific questions:

(1) does the frequency of tail loss vary among populations of *N. metallicus*?
(2) do the patterns of breakage differ among the populations studied?
(3) what are the implications of any differences for each population?

METHODS

Study species and field sites

The metallic skink *Niveoscincus metallicus* is a small viviparous lizard (45–65 mm adult snout–vent length (SVL)) that has a wide distribution across a range of habitats from sea level to sub-alpine environments (1400 m

Table 2. Predicted abundances of the potential predators of the metallic skink *Niveoscincus metallicus* at the four field sties (inferred from M. E. Jones & Barmuta, 1998; Hutchinson, Swain & Driessen, 2001; Barrett *et al.*, 2003; pers. obs.). See Table 1 for predator codes

	Reptiles			Mammals			Birds			
Site	WLS	TS	LC	FC	STQ	EQ	K	C	GB	Other birds[a]
South Hobart	Low	Low	Low	Moderate	Absent	Absent	High	Moderate	Moderate	Low
Dynnyrne	Low	Low	Low	Extremely high	Absent	Absent	High	Moderate	Moderate	Low
Clarence Lagoon	High	High	Low	Low	Moderate	Moderate	Low	Low	Low	Low–moderate
Laughing Jack Lagoon	High	High	Low	Low	Moderate	Moderate	Low	Low	Low	Low–moderate

[a]Other birds include the brown goshawk, brown falcon and forest raven.

Table 3. Life-history characteristics of *Niveoscincus metallicus* from Hobart and the Central Plateau of Tasmania, Australia (adapted from McCoull, 2001)

Location	Mean age (range), years	Age at maturity (years)	Mean litter size	Relative clutch mass (RCM)	Annual reproduction
Hobart	4.5 (2–9)	2	3.9	0.317	Yes
Central Plateau	7.1 (3–12)	3	3.0	0.240	Yes

a.s.l.) in Tasmania and south-eastern Victoria, Australia (Melville & Swain, 1999). It is a relatively cryptic species that occupies shaded microhabitats with medium to dense vegetation cover and thick litter (Melville & Swain, 1999). It is predominately a shuttling heliotherm and uses both rocks and logs close to the ground as basking sites (Melville & Swain, 1997). Tail autotomy is generally used as a defensive mechanism against predators only after crypsis and fleeing have failed.

Variation in the frequency and position of tail loss was examined among 4 populations of *N. metallicus*. McCoull (2001) identified 5 genetic subgroupings in *N. metallicus*; however, all 4 populations examined in this study belonged to the same subgroup. Two urban (Hobart) and 2 woodland sites (Central Plateau) were sampled during the study; however, each site varied considerably in its habitat structure and none were considered to be replicate sites. The life-history characteristics of *N. metallicus* in Hobart and on the Central Pleateau have previously been examined (McCoull, 2001; Table 3). The urban field sites, South Hobart (42°53′S, 147°18′E) and Dynnyrne (42°54′S, 147°19′E), are located in the southern suburbs of Hobart, Tasmania (altitude *c.* 50 m), with about 2–3 km separating the 2 populations. The South Hobart field site consisted of a large semi-urban backyard adjoining a patch of sclerophyll woodland. The Dynnyrne field site was a 200 m stretch of suburban street and consisted of numerous gardens along a footpath, and several domestic backyards. Domestic cats *Felis catus* are common predators of lizards in suburban areas (e.g. Barratt, 1997, 1998; this study), while birds (mostly kookaburras *Dacelo novaeguineae*) are frequently observed to attack *N. metallicus* in Hobart (R. Swain, pers. obs.; Tables 1 & 2). However, domestic cats seemed to be present in particularly high densities at the Dynnyrne site (Table 2).

The woodland sites, Clarence Lagoon (970 m; 42°04′S, 146°19′E) and Laughing Jack Lagoon (840 m; 42°10′S, 146°18′E), are located *c.* 5 km apart on the Central Plateau of Tasmania (*c.* 270 km NW of Hobart). The Clarence Lagoon site consists mainly of dry sclerophyll woodland with an understorey of low and sparse shrubs, with several patches of more enclosed mixed woodland (dry sclerophyll/semi-rainforest) and dolerite rock screes. The Laughing Jack Lagoon site is considerably more open with sclerophyll forest adjacent to a man-made dam. The site consists mostly of low and sparse shrubs and a dolerite scree slope. Avian predators are present only in low densities at the 2 Central Plateau sites (Barrett *et al.*, 2003; this study); however, snakes (white-lipped snake *Drysdalia coronoides* and tiger snake *Notechis ater*) are abundant at both sites and are believed to constitute the major predators of *N. metallicus* on the Central Plateau (Tables 1 & 2).

Collection and measurement of animals

Our 4 populations were sampled between December 1999 and January 2000. Lizards were collected randomly by noosing or hand. Measurements of SVL (± 0.1 mm) and total tail length (TL; ± 0.1 mm) were taken of each lizard. Lizards larger than 45 mm SVL were considered to be sexually mature adults (Swain & Jones, 1994; S. M. Jones & Swain, 1996). The presence of any previous tail loss was recorded, with measurements taken of the length of remaining tail (BL (break length): distance from vent to point of tail break ± 0.1 mm). Regenerated tails in *N. metallicus* have a different colour and scale pattern to the original tail portion, enabling easy identification and providing a permanent record of previous tail loss. The sex of each lizard was determined by eversion of hemipenes in males. Female reproductive status was assessed by abdominal palpation. Sampling at each field site corresponded with late pregnancy in females and virtually all mature females in each population were pregnant. Once the necessary measurements were taken each individual was given a temporary non-toxic paint mark to prevent recapture and was released at the site of

Table 4. Variation in sex ratio between populations of *Niveoscincus metallicus*. Chi-squared tests were used to determine if the observed sex ratio in each population deviated from a 1:1 ratio

Site	n	Male	Female	Ratio (M:F)	χ^2	d.f.	P
South Hobart	66	38	28	1.36:1	1.51	1	NS
Dynnyrne	101	54	47	1.15:1	0.49	1	NS
Clarence Lagoon	100	62	38	1.63:1	5.76	1	0.021
Laughing Jack Lagoon	101	47	54	0.87:1	0.48	1	NS
Overall	368	201	167	1.20:1	3.14	1	NS

capture. The visual paint marks remained on the animals for the duration of the sampling period and were lost by the next moult.

Data analysis

Site and sexual differences in SVL and the position of tail loss (break index) were investigated using analysis of variance (ANOVA). Where significant interactions were found to exist, the main effects were examined by treating each site–sex combination as a group and performing ANOVA (group as factor) post-hoc tests. Chi-squared goodness-of-fit tests were used to test whether the sex ratio at each population deviated from the expected 1:1 ratio. *G*-tests were used to compare tail loss frequencies (and break index frequencies) between sites, sexes and groups.

For each animal that exhibited evidence of previous tail loss, an estimate was made of its original tail length (OTL). This was achieved through the completion of a linear regression of SVL against tail length in lizards that exhibited no signs of autotomy (i.e. complete original tails). This produced an equation for predicting the OTL of each animal from its SVL. Analysis of covariance (ANCOVA) was used to determine if the regression equation was constant between the sexes. The calculated OTL was then used to estimate the position along the length of the tail at which autotomy had occurred; from this a break index was calculated (break length/OTL; 0 indicating proximal breaks and 1 indicating distal breaks). However, since a regression equation was used to predict the original tail length and the tail base (break length) may elongate during tail regeneration (Tinkle, 1967), our break index represents an approximation of the position where the original tail autotomy event occurred.

RESULTS

Sexual and morphological variation

A total of 368 lizards (66 South Hobart; 101 Dynnyrne; 100 Clarence Lagoon; 101 Laughing Jack Lagoon) was sampled across the four field sites during the study. The sex ratio within each population did not differ significantly from a 1:1 ratio, except for Clarence Lagoon where there was a male-biased sample (Table 4). However, sex ratio did not differ among field sites ($G = 5.16$, d.f. = 3, $P = 0.160$).

Adult body size differed significantly among the four populations (Table 5), with a significant interaction between SVL and sex (ANOVA: $F_{3,322} = 4.15$, $P = 0.007$). Post-hoc analysis (Tukey's HSD) revealed that these differences were because both sexes from Dynnyrne were smaller than females from South Hobart, Dynnyrne females were smaller than either sex from Clarence Lagoon, and females from Laughing Jack Lagoon were smaller than females from both Clarence Lagoon and South Hobart.

Measures of tail loss

Most *N. metallicus* sampled during the study exhibited evidence of previous tail loss (265 of 368; 72%). Overall there were significant population differences in the frequency of tail loss ($G = 9.38$, d.f. = 3, $P = 0.025$; Table 6), with the lowest incidence at Laughing Jack Lagoon (61.4%), and the highest incidences at Dynnyrne and Clarence Lagoon (78.2% and 78%, respectively; Table 6). Within populations males and females showed similar levels of tail loss (0.6–7.6% difference for each site; Table 6), while between populations males differed significantly ($G = 8.51$, d.f. = 3, $P = 0.037$), but females ($G = 4.0$, d.f. = 3, $P = 0.261$) or juveniles ($G = 0.23$, d.f. = 2, $P = 0.889$) did not. However, the difference between populations for males was not significant after Bonferroni correction. There was generally a lower incidence of tail loss in juveniles with approximately half of all juveniles sampled exhibiting evidence of previous tail loss, except at South Hobart where only one juvenile was caught (Table 3).

To examine size-related variation in autotomy, three size classes were chosen: sub-adult juveniles plus two arbitrarily selected adult groupings (Table 7). These size classes showed no differences between sites (size class I: $G = 0.23$, d.f. = 2, $P = 0.889$; size class II: $G = 6.70$,

Table 5. Mean snout–vent length of adult *Niveoscincus metallicus* (> 45 mm SVL) at the four field sites. Values are means ± SE with sample sizes in parentheses

Site	Male	Female	Overall
South Hobart	52.5 ± 0.64 (37)	54.6 ± 0.68 (28)	53.4 ± 0.48 (65)
Dynnyrne	52.1 ± 0.58 (45)	51.2 ± 0.56 (39)	51.7 ± 0.40 (84)
Clarence Lagoon	53.7 ± 0.44 (55)	53.7 ± 0.46 (36)	53.7 ± 0.32 (91)
Laughing Jack Lagoon	52.9 ± 0.60 (43)	51.0 ± 0.56 (47)	51.9 ± 0.42 (90)

Table 6. Frequency of tail autotomy in four populations of *Niveoscincus metallicus*. Values indicate the percentage (%) of animals that exhibited evidence of tail loss with sample sizes in parentheses

Site	Male	Female	Juvenile	Total
South Hobart	67.6 (37)	71.4 (28)	100 (1)	69.7 (66)
Dynnyrne	82.2 (45)	84.6 (39)	52.9 (17)	78.2 (101)
Clarence Lagoon	80.0 (55)	80.6 (36)	55.6 (9)	78.0 (100)
Laughing Jack Lagoon	60.5 (43)	68.1 (47)	45.5 (11)	61.4 (101)

Table 7. Variation in the frequency of tail loss between different size classes of *Niveoscincus metallicus* in four populations. Values indicate the percentage (%) of animals that exhibited evidence of tail loss with sample sizes in parentheses

Site		Size class (mm)		
		I < 45	II 45–52.5	III > 52.5
South Hobart	Male	100 (1)	61.11 (18)	73.68 (19)
	Female	0 (0)	55.56 (9)	78.95 (19)
	Total	100 (1)	59.26 (27)	76.32 (38)
Dynnyrne	Male	66.67 (9)	80.00 (25)	85.00 (20)
	Female	37.5 (8)	79.17 (24)	93.33 (15)
	Total	52.94 (17)	79.59 (49)	88.57 (35)
Clarence Lagoon	Male	57.14 (7)	89.47 (19)	75.00 (36)
	Female	50.00 (2)	66.67 (12)	87.50 (24)
	Total	55.56 (9)	80.65 (31)	80.00 (60)
Laughing Jack Lagoon	Male	25.00 (4)	55.00 (20)	60.87 (23)
	Female	57.14 (7)	67.74 (31)	68.75 (16)
	Total	45.45 (11)	62.75 (51)	64.10 (39)

d.f. = 3, $P = 0.082$; size class III: $G = 6.69$, d.f. = 3, $P = 0.082$), but collectively, larger animals showed significantly more evidence of tail damage compared to the remainder of the population ($G = 38.3$, d.f. = 3, $P \leq 0.005$).

Position of tail loss

Regression analysis of all animals that showed no evidence of previous tail loss revealed a significant relationship between SVL and tail length. Since this relationship was consistent between the two sexes (ANCOVA: $F_{1,97} = 0.59$, $P = 0.444$) an overall regression relationship was calculated (TL = $1.098 * \text{SVL} + 12.97$, $R^2 = 0.59$, $F_{1,100} = 145.11$, $P < 0.0001$). This regression equation was used

to predict the original tail length (OTL) of each animal and calculate the break index.

The break index (i.e. estimated point of tail loss) varied among populations (ANOVA: $F_{3,257} = 8.13$, $P = 0.0001$) but not between the sexes (ANOVA: $F_{1,257} = 1.80$, $P = 0.181$). Post-hoc analysis (Tukey's HSD) revealed that lizards from Dynnyrne had more proximal breaks than animals from other sites.

In *N. metallicus* substantial energy reserves (55–75% total) are held in the form of caudal fat; 90% of these reserves are held in the proximal third of the tail, 10% in the middle third, and there is no caudal fat in the distal third (Chapple & Swain, 2002a). Thus, only those animals that experience autotomy in the proximal and middle thirds of the tail incur loss of energy reserves, and only those with proximal breaks suffer major losses. To examine differences in the cost of predation in our test populations the distribution of tail breaks within each third of the tail was determined for each population (Table 8). At no site were there sexual differences in the location of tail breaks ($P > 0.9$ for each site). When the distribution of proximal breaks was analysed there was a significant difference associated with site ($G = 9.34$, d.f. = 3, $P < 0.01$). It is clear from Table 8 that in the Dynnyrne population an extraordinarily high proportion of both males and females lose 90% of their caudal energy reserves.

DISCUSSION

The incidence of tail loss in the metallic skink *N. metallicus* varied considerably among the four populations (61.4–78.2%). Tail loss frequencies have previously been reported to vary between conspecific populations at different altitudes (e.g. Brown & Ruby, 1977), presumably owing to the higher levels of predation experienced by populations at lower elevations (Fox, Perea-Fox & Castro-Franco, 1994). However, no clear altitudinal pattern in the incidence of tail loss was evident in *N. metallicus*. Likewise, although sexual differences in the frequency of tail autotomy have been observed in some lizard populations (Brown & Ruby, 1977; Smith, 1996; R. S. Wilson & Booth, 1998), no sexual variation in the incidence of caudal autotomy was observed in *N. metallicus*.

The likelihood of a lizard having a predatory encounter increases with age; consequently tail loss is relatively more

Table 8. Frequency and location of autotomy in adults from four populations of *Niveoscincus metallicus*. For animals with tail breaks the location of the break has been scored as proximal (break indices 0–0.33), middle (break indices 0.34–0.67), and distal (break indices 0.68–1.0). See text for calculation of break index

Site	Male					Female				
	n	Proximal	Middle	Distal	No break	*n*	Proximal	Middle	Distal	No break
South Hobart	37	0.30	0.24	0.16	0.30	28	0.32	0.21	0.18	0.29
Dynnyrne	45	0.53	0.24	0.18	0.04	39	0.62	0.23	0.08	0.08
Clarence Lagoon	55	0.25	0.36	0.25	0.13	36	0.25	0.39	0.19	0.17
Laughing Jack Lagoon	43	0.19	0.19	0.23	0.40	47	0.26	0.28	0.23	0.23

common in larger size classes (Brown & Ruby, 1977; Turner *et al.*, 1982; R. S. Wilson & Booth, 1998). In the four populations of *N. metallicus* there was a general trend for the frequency of tail loss to increase with age and with size class, although this pattern was only significant in the Dynnyrne population.

Domestic cats are common predators of lizards in suburban areas of Australia (e.g. Barratt, 1997, 1998; this paper), while birds, mainly kookaburras, frequently attack *N. metallicus* around Hobart (R. Swain, pers. obs.; Table 2). However, domestic or feral cats are rare on the Central Plateau and avian predators are present only in low densities (Table 2). Snakes (white-lipped and tiger snakes) are abundant at the Central Plateau sites and are believed to constitute the major predators of *N. metallicus* in this area (Table 2). It has been demonstrated experimentally that inefficient predation may artificially inflate the frequency of tail breaks in a population (Medel *et al.*, 1988). Snakes, birds and cats all seem to predate upon lizards with varying efficiencies. Snakes seem to be relatively inefficient, regularly allowing their prey to escape via tail autotomy (e.g. Dial & Fitzpatrick, 1984; Cooper & Vitt, 1985; Medel *et al.*, 1988). However, avian predators may be extremely efficient predators of lizards (Medel *et al.*, 1988; Blomberg & Shine, 2000; D. G. Chapple & R. Swain, pers. obs.). Although domestic cats frequently catch *N. metallicus*, they generally tend to play with the lizard rather than consuming it, and this often results in the lizard escaping following tail autotomy (D. G. Chapple, pers. obs.). The high incidence of tail loss in the Dynnyrne population may therefore be owing to a high density of domestic cats whereas that at the Clarence Lagoon site may be attributable to a large snake population. However, lizards at Dynyrnne also show higher incidences of proximal tail breaks ($\leq$ 70%) than those from our other populations ($\leq$ 40%). *Niveoscincus metallicus* is able to lose its tail at any point along its length, but generally loses the least amount necessary to escape from predators (termed 'economy of autotomy'; Chapple & Swain, 2002*a*). Since lizards that experience repeated tail autotomy must lose their tails progressively closer to the tail base, it is probable that Dynyrnne lizards experience a particularly high rate of non-lethal or inefficient predatory attacks (i.e. from cats; Tables 1 & 2) compared to the other populations.

The smaller size (SVL) of Dynnyrne individuals compared to that of animals from the neighbouring South Hobart population indicates a high proportion of young animals, presumably because increased predation has reduced life expectancy. Animals in the Hobart area have a mean life span of 4.5 years (range 2–9 years) providing a reproductive life of only 2 years (McCoull, 2001; Table 3). Fecundity in *N. metallicus* is size related, and the species is an annual breeder with females generally breeding each year (S. M. Jones & Swain, 1996), so reducing life expectancy in the Dynnyrne population will have a major impact on reproductive output.

However, the high incidence of tail loss in the surviving population will have additional important consequences. *Niveoscincus metallicus* stores energy in the form of both caudal and abdominal fat with most (50–70%) being held in the tail (Chapple & Swain, 2002*a*). Abdominal stores are important for reproduction (reduced in pregnant females in *N. metallicus* (Chapple & Swain, 2002*a*), and in *N. ocellatus* (Wapstra & Swain, 2001)) suggesting that tail fat is particularly important for winter survival (see Chapple *et al.*, 2004), as in other species (e.g. Avery, 1970). Since 90% of the tail fat is located proximally, Dynnyrne animals, with their unusually high frequency of tail loss, and especially proximal tail loss, may have greater than normal difficulty maintaining condition through winter.

Even if the tail break is not associated with the loss of caudal fat, energetic resources previously allocated to growth or reproduction may be diverted to facilitate tail regeneration (Congdon *et al.*, 1974; Vitt, Congdon & Dickson, 1977; Dial & Fitzpatrick, 1981). Indeed, tail loss has been associated with reduced rates of growth (Ballinger & Tinkle, 1979; Smith, 1996) and reproductive investment (Dial & Fitzpatrick, 1981; R. S. Wilson & Booth, 1998) in lizards. In *N. metallicus* effects on reproduction may be quite subtle, but may nevertheless have a substantial population impact, especially in populations such as those at Dynyrnne and Clarence Lagoon, where tail loss is a regular occurrence. For example, litter size is reduced significantly, by an average of 17.5%, if the tail is lost during vitellogenesis, and this effect is independent of where the break occurs (Chapple *et al.*, 2002). However, when the break is accompanied by little or no loss of caudal fat (i.e. only the middle and/or distal segment of the tail is lost) females compensate for their reduced output by giving birth to significantly larger offspring (Chapple *et al.*, 2002), presumably by virtue of their capacity for facultative placentotrophy (Swain & Jones, 2000). These effects will be greatest in relatively short-lived animals such as those from the two Hobart populations; at the Laughing Jack and Clarence Lagoon sites average life expectancy is 7.1 years (range 3–12 years; McCoull, 2001), and, even allowing for the extra year taken to reach maturity, females at these sites can expect four reproductive seasons (Table 3). Reproductive consequences are not evident in animals with regenerated tails, i.e. they do not extend beyond the current reproductive season, suggesting that changes in reproductive output represent a cost of tail regeneration.

Caudal autotomy in lizards often impairs locomotor performance (Brown *et al.*, 1995; Martin & Avery, 1998; Downes & Shine, 2001) and this may also have impacts at the population level. In *Niveoscincus metallicus* reduced locomotor performance is gender specific: males exhibit reduced sprint speed and tails take longer to regenerate; females show reduced stamina (Chapple & Swain, 2002*a*). However, the locomotory impact of tail loss is short-lived and no effects were observed after 3 months. Nevertheless, populations of *N. metallicus* may experience the costs of tail loss to differing degrees and for varying periods of time. Individuals from Dynnyrne, in particular, are likely to suffer more severe impacts of autotomy; their increased regularity of tail loss and the high frequency of proximal breaks will result in more animals spending more

time regenerating their tails. This may well translate into decreased survival in the population as demonstrated with tailless lizards in other natural populations (B. S. Wilson, 1992; Niewiarowski *et al.*, 1997; Fox & McCoy, 2000). However, tail loss in *N. metallicus* does not result in modification of thermoregulatory behaviour (Chapple & Swain, 2004) and the species is generally a cryptic basker (Melville & Swain, 1997), so any changes in survivorship are unlikely to be simple consequences of increased exposure to predators.

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