# Costs associated with tail autotomy in an ambush foraging lizard, Cordylus melanotus melanotus

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Tail autotomy is a widespread method of escape among lizards and can be costly. Most studies on the effects of tail loss have focused on active foraging lizards, but few data exist for ambush foraging lizards. We investigated potential costs associated with tail autotomy in an extreme ambush foraging cordylid lizard, *Cordylus melanotus melanotus*. We induced tail autotomy in free-ranging male *Cordylus m. melanotus* and measured potential shifts in behaviour (movements, foraging behaviour, time exposed and average distance to a potential refuge), and responses to an approaching human compared to marked individuals with complete tails. Tailed and tailless lizards behaved in a similar fashion for all measured variables although power tests could not rule out the possibility of falsely accepting the null hypothesis in some cases. We also measured locomotory performance (maximum sprint speed) for tailed and tailless lizards in the lab. Locomotory performance was also not compromised by tail loss. Finally, we measured the energetic content of tails as a proportion of total energetic content using bomb calorimetry. The cost of tail autotomy was approximately 12 % of the total body energy (wet weight). Our results suggest that the major cost of tail loss in *Cordylus m. melanotus* is energetic.

Key words: tail loss, performance, antipredatory behaviour, tail energetic content, reptile.

# INTRODUCTION

Tail autotomy is a widespread method of escape among lizards (Bellairs & Bryant 1985) and occurs in 13 of 20 lizard families (Dial & Fitzpatrick 1983) (Table 1). The primary benefit is escape from predation by distracting predators to an expendable body part (Arnold 1988). Tailed lizards can be considerably more successful in escaping predators than tailless lizards (Dial & Fitzpatrick 1983), suggesting an immediate cost in the form of increased predation risk. Furthermore, a novel experimental study demonstrated that behaviour shifts following tail loss in the skink Lampropholis guichenoti, in addition to compromised locomotory performance, resulted in higher predation rates by a snake predator (Downes & Shine 2001). Costs of tail loss include impaired locomotory function (Punzo 1982; Arnold 1988; Brown et al. 1995); increased vulnerability to predators (Arnold 1988; Downes & Shine 2001); decrease in social status (Fox & Rostker 1982; Brown et al. 1995); decreased reproductive capacity (Daniels 1983; Arnold 1988; Brown et al. 1995;); loss of caudal fat reserves (Arnold 1988; Brown et al. 1995) and decreased thermoregulatory capacities

<sup>†</sup>Author for correspondence. E-mail: suem@gecko.biol.wits.ac.za <sup>‡</sup>E-mail: martin@gecko.biol.wits.ac.za (Perez-Mellado *et al.* 1997). Since the effects of tail loss are potentially costly, it follows that a lizard should compensate by altering its behaviour to reduce these effects. Lizards without tails alter their behaviour in various ways, including restricting their use of microhabitats, decreasing their distance to refuges while basking, foraging on abundant, easily captured prey, decreasing general activity levels (Martín & Salvador 1997), and increased probability of fleeing a predator (Downes & Shine 2001).

Tail loss may also affect locomotory performance (Table 1). In lizards that run bipedally, the tail can be used as a counterbalance during running (Ballinger et al. 1979; Daniels 1983) and tail loss may result in a decreased ability for predator escape until the tail has regenerated (Daniels 1983). Conversely, in lizards that run on all four limbs, the tail has little function in locomotion and locomotor performance may be enhanced by tail loss. The quadrupedal gecko Phyllodactylus marmoratus nearly doubles its speed following autotomy (Daniels 1983). Hence, where the tail plays no obvious role in locomotion, the lizard may show increased ability for predator avoidance by running faster after losing its tail (Daniels 1983). Formanowicz et al. (1990) demonstrated that

Family	Species	Costs <sup>‡</sup>										Reference	
		А	Т	G	S	L	Н	R	F	SS	Е		
Anguidae	Gerrhonotus multicarinatus										*	Vitt <i>et al.</i> 1977	
Gekkonidae	Lygodactylus klugei Coleonyx variegatus Coleonyx variegatus Coleonyx brevis				* * *			*	*		*	Vitt & Ballinger 1982 Congdon <i>et al.</i> 1974 Vitt <i>et al.,</i> 1977 Dial & Fitzpatrick 1981	
Iguanidae	Uta stansburiana Uta stansburiana Uta stansburiana Uta stansburiana Uta stansburiana Cophosaurus texanus Uma notata Scelophorus virgatus			*	* *	*				*		Fox & Rostker 1982 Fox et al. 1990 Wilson 1992 Niewiarowski et al. 1997 Fox & McCoy 2000 Punzo 1982 Punzo 1982 Smith 1996	
Lacertidae	Lacerta monticola Lacerta monticola Lacerta monticola Lacerta monticola Lacerta monticola Podarcis muralis Psammodromus algirus Psammodromus algirus Psammodromus algirus Psammodromus algirus	*	*			*	* *	* *	*			Martín & Salvador 1993a Martín & Salvador 1993b Martín & Salvador 1993c Martín & Salvador 1995 Martín & Salvador 1997 Brown <i>et al.</i> 1995 Salvador <i>et al.</i> 1994 Salvador <i>et al.</i> 1996 Martín & Avery 1997 Martín & Avery 1998	
Polychrotidae	Anolis				*							Schoener & Schoener 1980	
Scincidae	Scincella lateralis Scincella lateralis Eulamprus quoyii Eurmerus quoyii Eurmeces Eurmeces gilberti Eurmeces skiltonianus Mabuya heathi Lampropholis guichenoti Lygosoma laterale				* *	*		*			* *	Dial & Fitzpatrick 1983 Formanowicz <i>et al.</i> 1990 Wilson & Booth 1998 Daniels 1985 Vitt & Cooper 1986 Vitt <i>et al.</i> 1977 Vitt <i>et al.</i> 1977 Vitt 1981 Downes & Shine 2001 Clark 1971	
Teiidae	Cnemidophorus sexlineatus					*						Ballinger <i>et al.</i> 1979	

Table 1. A review of the costs of tail loss in lizards.

<sup>‡</sup>A = activity, T = thermoregulation, G = growth, S = survival, L = locomotion, H = habitat use, R = reproduction, F = foraging, SS = social status, E = energy reserves, \* = cost reported).

lizards shift their behaviour in response to tail loss in ways that may compensate for decreased locomotor performance and inability to further employ autotomy as an escape mechanism.

Previous studies of tail autotomy in lizards focused on actively foraging species (e.g., certain lacertids, scincids and teiids). The costs of tail loss, although varied, are likely different for ambush foragers. Ambush foragers have a suite of co-adapted life history traits that are different from those of widely foraging species in several important respects (Huey & Pianka 1981; Vitt 1983). First, type and amount of prey, energetic costs and reproductive biology are influenced by foraging mode (Huey & Pianka 1981). Second, predator foraging mode may also influence prey foraging mode. In some systems, ambush foragers are usually attacked by actively foraging predators (Huey & Pianka 1981); conversely, active foragers are usually attacked by ambush predators (Vitt 1983). Ambushing lizards rely mainly on crypsis to escape predation (Vitt & Congdon 1978), resulting in actively foraging predators frequently detecting them at close range. This scenario would likely provide a strong selective pressure for tail autotomy to evolve, particularly in cordylid

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lizards, which are considered to be extreme ambush foragers (Cooper *et al.* 1997). This study deals with autotomy-induced shifts in behaviour and energetic costs associated with tail loss in the cordylid *Cordylus melanotus melanotus*, a lizard confined to small rocky outcrops.

Drakensberg crag lizards (C. m. melanotus) are found in dense colonies on rocky outcrops in rolling grasslands and mountain plateaus in eastern South Africa (Branch 1998). All members of the genus Cordylus are ambush foragers (Cooper et al. 1997), and C. m. melanotus are readily visible, using rocks as vantage points. Male spacing patterns are relatively uniform, consistent with home range or specific site defence as reported by Stamps (1977) for other species. Cordylus m. melanotus exhibits well-developed sexual dimorphism such that males are larger and more colourful than females (Mouton & van Wyk 1993) and during the breeding season, males respond aggressively towards intruding rivals (Moon 2001). In addition to bright colouration, their tendency to ambush prey from vantage points makes them potentially vulnerable to a different suite of predators than those of active foragers.

The objectives of this study were (1) to examine shifts in behaviour due to tail loss (i) movements, foraging behaviour, time exposed and average distance to a potential refuge; (ii) antipredatory behaviour; and (iii) locomotory ability; and, (2) to determine the energetic cost of tail loss.

# **MATERIALS & METHODS**

#### Study area

Fieldwork was conducted at Suikerbosrand Nature Reserve (SNR), approximately 40 km southeast of Johannesburg (26°27′–26°34′S, 28°09′– 28°21′E; 1800 m a.s.l.), during April/May 2000. The reserve is a grassland biome, specifically Bankenveld, and is dominated by *Eragrostis*, *Hyparrhenia*, *Themeda* and *Setaria* species (Panagos 1999).

*Cordylus m. melanotus* are restricted to the rocky ridges of SNR and were therefore readily located. Lizards were noosed or caught by hand. Only sexually mature individuals were used because juvenile growth patterns could be influenced by tail autotomy (Althoff & Thompson 1994). To control for the influence of sex, only males were used; also, males are more conspicuous than females and likely experience different selective pressures. All individuals exceeding a snout-vent length (SVL) of 80 mm were considered sexually mature (Mouton & van Wyk 1993). We never witnessed any predation events, but likely predators include mongooses, raptors (e.g. rock kestrels, *Falco tinnunculus*) and certain snakes (e.g. puff adders, *Bitis arietans*; rinkhals, *Hemachatus haemachatus*; mole snakes, *Pseudaspis cana*).

## Morphology and allocation of lizards to treatments

For each lizard, SVL, total tail length, whether the tail was broken or complete, length of regenerated tail (if tail had been broken previously), head length, head width, presence and position of scars, mass, location and the number of mites on the lizard's body were recorded. Snout-vent length and tail measurements were taken with a ruler to the nearest mm. Head measurements were taken with digital callipers to the nearest 0.01 mm. Mass was measured to the nearest 0.01 g. Twenty-one individuals in the field study were randomly selected and their tail length manipulated. This consisted of pinching the lizards' tails with forceps while releasing the body above a bucket. Approximately two-thirds of the tail was removed to standardize the approximate cost of tail loss between individuals.

## Shifts in behaviour

Activity and mobility. All lizards were permanently marked by toe clipping and temporarily marked with colour-coded plastic ties, fitted as collars, for visual identification. Activity and behaviour were assessed using focal animal sampling. Lizards were classified as 'moving', 'feeding' (Martín & Salvador 1997) and 'stationary'. We followed Martín & Salvador's (1997) convention of classifying lizards as 'moving', 'feeding', or 'stationary'. Individual lizards were observed continuously for 15 min when they were encountered in the field. During focal animal sampling, we recorded the time lizards were concealed from view; we visually estimated the distance of the lizard to its nearest potential refuge four times during each focal (0, 5, 10 and 15 min; to nearest cm). We also recorded all movements >10 cm and considered a movement terminated if a lizard remained still for at least 2 s. We then calculated the number of moves per minute (MPM) and percentage time moving (PTM) for tailed and tailless lizards. Although MPM is less useful than PTM for describing foraging mode and is often correlated with PTM; Cooper et al. (2001) have advocated reporting both values. MPM allows measurement of frequency of movement, which is an important way animals vary foraging behaviour (Cooper *et al.* 2001). The number of prey capture attempts was also noted.

Antipredatory behaviour. The same marked lizards observed using focal sampling were also used to investigate whether the tailed and tailless lizards reacted differently to a potential threat (an approaching human). Twenty lizards (11 tailless and nine tailed) were approached to measure antipredatory response. Lizards were approached from approximately 30 m, which exceeded the minimum distance at which they would react and escape. All approaches were conducted by the same individual (S.M.). When the lizard moved in excess of 10 cm, a marker was dropped. S.M. stopped at the lizard's initial location and dropped a second marker. After 5 s, the lizard's final destination was scored (visible in the open or concealed in a crevice) and indicated with a third marker. Approach distance was the distance between the first and second markers, measured to the nearest 5 cm. Flight distance was the distance between the second and third markers, measured to the nearest 5 cm. The temperature was also recorded (in the shade approximately 10 cm above the ground using a mercury thermometer) during each trial because lizards may have been compensating for low temperatures instead of lost tails. The temperature at which experimental and control trials were conducted was not significantly different (Z = 0.23, P = 0.82, n = 20, Table 2), suggesting that thermal conditions were approximately the same for both groups. We further examined antipredatory behaviour in tailed and tailless lizards using data recorded during focal animal sampling. We recorded time exposed (s), time in crevice (s), time partially exposed (s), and mean distance to the nearest potential refuge (cm). Lizards were scored as being in the crevice (when completely concealed), exposed in the open (when the entire

**Table 2**. Descriptive statistics from antipredatory behaviour trials. Mean  $\pm$  standard error, range in brackets (n = 20, 11 tailless, nine tailed).

	Tailless	Tailed
Approach distance (cm)	106 ± 157 (37–219)	117 ± 18 (63–258)
Flight distance (cm)	23 ± 3 (10–50)	29 ± 9 (2–9)
Temperature (°C)	13.36 ± 0.79 (12–19)	13.78 ± 1.02 (12–20)

animal was in the open) or partially exposed (when their hindquarters were concealed in the crevice, but the rest of the body was clearly exposed).

Performance. To measure the effects of tail loss on locomotory performance, tail lengths of half the study animals (n = 10) were manipulated in the same manner as the field study. The lizards were housed at a constant temperature ( $26 \pm 1$  °C) with a L:D regime of 12:12 for at least 24 h before the study and were provided with food (Tenebrio larvae) and water ad libitum. None of the lizards were toe clipped in case this affected their running speed (Dodd 1993). Lizards were run on a 2 m racetrack, 20 cm wide; first, horizontal with a rubber substrate, and second, at a 45° angle with a sandpaper substrate in a temperature controlled room (26  $\pm$ 1 °C). Preferred body temperature for C. m. melanotus was unknown at the time of the study, so we used the average temperature at SNR for that time of year. Sprint speed was measured on the angled track because the lizards were observed to traverse near-vertical rock faces in the field; a sandpaper substratum was used because traction was lost on the rubber. Eight photocells, at 25 cm intervals and connected to a computer (Chart ver. 3.5, Maclab<sup>®</sup> System, ADInstruments) that calculated elapsed time between 'broken' cells, were used to measure sprint speed. A dark pillowcase was draped over the end of the racetrack to provide a refuge toward which the lizards ran. Each lizard was run four times on the horizontal track and four times on the angled track, with at least 24 h between measures. The maximum speed over 25 cm was recorded for each lizard over the four trials on each track (Irschick & Losos 1998). The maximum speeds of tailed and tailless lizards were compared for both tracks using Wilcoxon rank sum tests. Because not all lizards were captured at once, we tested for an influence of duration of captivity on performance.

The number of days spent in captivity was not significantly different between tailed and tailless lizards when run on the horizontal track (tailed:  $120 \pm 5$  days, tailless:  $124 \pm 5$  days; Z = 0.36, P = 0.71, n = 17), nor when run on the angled track (tailed:  $132 \pm 4$  days, tailless:  $139 \pm 5$  days; Z = 1.59, P = 0.11). Also, the duration in captivity prior to racing did not affect performance for all lizards combined (horizontal track:  $r_s = -0.31$ , P > 0.05, n = 17; angled track:  $r_s = -0.16$ , P > 0.05, n = 17).

The body size of the lizards in the experimental and control groups were not significantly differ-

	Tailless	Tailed	Test for significant difference
Mass (g)	49.90 ± 3.39	57.44 ± 2.42	Z = 1.59,
	(31.5–65.7)	(46.6–66.3)	P = 0.11
SVL (mm)	118 ± 2	125 ± 1	Z = 1.64,
	(105–129)	(117–130)	P = 0.10
Mites	1 ± 0.4	1 ± 0.5	$\chi_1^2 = 0.012,$
	(0-4)	(0–3)	P > 0.5

**Table 3**. Descriptive statistics for lizards used in performance trials. Mean  $\pm$  standard error, range in brackets (n = 17, 9 tailless, 8 tailed).

ent (Table 3). The difference in the number of mites found on the lizards in the two groups was also not significant (Table 3).

# Energetics

Eight lizards were randomly selected from the control group used in the performance study. These lizards were euthanased and approximately two thirds of the tail was removed. The remaining portion of the tail was also removed. The lizards' bodies were cut transversely into sections < 50 mm thick and together with the tails, freeze-dried and milled (IKA® type A10). Energy values for the bodies and tails (both parts) were analysed for energy content using a bomb calorimeter (Digital Data Systems CP500 Calorimetry Systems, Johannesburg). Ten sub-samples were bombed for each lizard body and, since a minimum of 0.5 g was needed for bombing (most accurate for equipment), only two sub-samples were bombed for each of the tail portions (limited by dry weight) for each lizard. Non-combustible mass for each sample was also recorded. Energy values were converted to values for wet weight and were corrected for the non-combustible mass.

## Statistics

All data were tested for normality and homoskedasticity before applying parametric statistics. Normal approximation and continuity corrections were applied to all Mann-Whitney and Wilcoxon rank sum tests (Analytical Software 1996) and all tests were conducted at the 5 % level of significance. Because sample sizes were limited in several cases, we conducted power tests using the program GPower (Erdfelder *et al.* 1996). Furthermore, these power tests were post hoc and given the low incidence of lizard resightings in the field, we used Cohen's (1988) standard convention for detecting a 'large' effect size (w = 0.8) (Erdfelder *et al.* 1996). Power tests were calculated for *t*-tests and adjusted for Mann-Whitney values which are 95 % as powerful as *t*-tests (Zar 1996). We did not calculate power tests for data with unequal sample size and variance because the nominal power and test statistic may deviate significantly from the real values (A. Buchner, pers. comm.).

# RESULTS

# Allocation of lizards to treatments

Morphological measures and number of mites of tailed and tailless lizards observed in the field were not significantly different (Table 4). Of the 42 marked lizards in the field, 53 focals were recorded for 26 lizards of which 13 were tailless and 13 were tailed. All focals were the full 15 min duration and between one and three focals were recorded for each lizard.

# Shifts in behaviour

#### Activity and mobility

MPM and PTM were not significantly different between tailed and tailless lizards (Table 5; MPM: Z = 0.82, P = 0.40, n = 26, power = 0.48; PTM: Z = 0.46, P = 0.64, n = 26, power = 0.48). Only two prey capture attempts, by two different lizards (one tailless, one tailed), were observed during the focals (795 min).

# Antipredatory behaviour

Both approach and flight distances were not significantly different between the experimental and control groups (approach: Z = 0.34, P = 0.73, n = 20, power = 0.38; flight: Z = 0, P = 1, n = 20; Table 2). In all but one case, the lizards' final destinations were crevices; one control lizard remained in the open. After fleeing, 17 lizards were completely concealed within their refuges (crevices); one experimental and two control lizards were visible within their crevices.

Measurement	Tailless	Tailed	Test for significant difference			
Tail length	132 ± 3	125 ± 6	Z = 0.41,			
	(106–160)	(58–173)	P = 0.68			
SVL	118 ± 1	113 ± 2	Z = 1.13,			
	(108–129)	(88–125)	P = 0.26			
Head length	32.41 ± 1.04	31.56 ± 0.79	Z = 0.28,			
	(27.36–36.12)	(23.83–35.93)	P = 0.78			
Head width	26.52 ± 0.92	25.78 ± 1.06	Z = 0.41,			
	(19.51–31.09)	(19.20–30.10)	P = 0.68			
Mass	46.69 ± 2.18	41.96 ± 3.54	Z = 0.77,			
	(31.50–56.90)	(12.60–59)	P = 0.44			
Mites	2 ± 0.5	2 ± 0.6	$\chi_1^2 = 0.12,$			
	(0–6)	(0–10)	P > 0.5			

**Table 4**. Descriptive statistics for lizard body size and mean number of mites for lizards observed in the field study. Mean  $\pm$  standard error, length measured in mm and mass in g, range in brackets.

Lizards spent approximately 92 % of their time exposed. Mean total time exposed between tailed and tailless groups was not significantly different (Z = 0.31, P = 0.76, power = 0.48). Mean distance to the nearest potential refuge between the experimental and control groups was not significantly different (equal variance,  $t_{24} = -0.60$ , P = 0.56;  $F_{12} = 1.08$ , P = 0.45, power = 0.48; Table 5).

# Performance

The maximum speed over 25 cm for tailless lizards was not significantly different to that of tailed lizards for both the horizontal track or the angled track (horizontal: tailed:  $2.21 \pm 0.17$  m/s, tailless:  $1.94 \pm 0.28$  m/s; Z = 0.59, P = 0.55, n = 17; angled: tailed:  $2.17 \pm 0.33$  m/s, tailless:  $1.79 \pm 0.33$ 

**Table 5**. Descriptive statistics from focal animal sampling during the field study. Mean  $\pm$  standard error, time measured in s and distance in cm, range in brackets (n = 26, 13 tailless, 13 tailed).

	Tailless	Tailed
Percent time moving	0.0009 ± 0.0004 (0-0.00005)	0.001 ± 0.0004 (0-0.005)
Moves per minute	0.04 ± 0.01 (0-0.12)	0.08 ± 0.02 (0-0.25)
Time exposed	774 ± 71 (0–900)	776 ± 46 (450–900)
Time in crevice	49 ± 32 (0-316.50)	33 ± 21 (0–270)
Time part exposed	69 ± 69 (0-900)	70 ± 46 (0-450)
Distance to refuge	12 ± 2 (0-26)	10 ± 2 (6–30)

0.20 m/s; *Z* = 1.16, *P* = 0.24, *n* = 17; power = 0.32 for both).

# Energetics

The mean total energy of whole lizards was 57.78 J/mg dry weight (DW) and 416.26 J/mg wet weight (WW) (Table 6). The whole tail constituted 12.05 % of the total WW energy and 30.02 % of the total DW energy. The total percentages of water and non-combustible mass were 65.98  $\pm$  1.66 % and 13.47  $\pm$  0.68 %, respectively.

## DISCUSSION

There have been numerous studies of the costs associated with tail loss in lizards (Table 1). These studies have focused mainly on widely foraging species in Europe and North America. Costs of tail loss lie predominantly in locomotory abilities and survival (in terms of increased predation risk). These two factors may be linked. If a lizard suffers impaired locomotory ability, it is less likely to escape a predator (Downes & Shine 2001). Also, a lizard would be unable to distract a predator without a tail to autotomize; lizards therefore may compensate behaviourally to offset an increased predation risk (Formanowicz et al. 1990). Reduced reproduction also appears to be a common cost to tail loss. Tail loss can interrupt any step in the reproductive process from access to mates to reproductive output. This may, in turn, be linked to social status (e.g. Fox & Rostker 1982; Fox et al. 1990) and possibly even habitat use (e.g. Salvador et al. 1994; Salvador et al. 1996; Martín & Salvador 1997).

Tail loss did not affect activity levels, movement

Table 6.	Wet and o	dry weight	energy	values	and	per	cent	ages	s of t	otal ene	ergy	for the	three	e portior	ns of lizar	d. N	lean :	±
standarc	l error (n	= 8, tailed	l). Tail '	1/3 and	l tail	2/3	are	the	first	(closest	t to	body)	and s	second	portions	of t	he tai	Ι,
respectiv	/ely.																	

	Dry	/ weight	Wet weight				
	J/mg	% of total energy	J/mg	% of total energy			
Body	23.08 ± 0.32	39.95	366.11 ± 8.99	87.95			
Tail 1/3	$18.40 \pm 0.33$	31.84	22.42 ± 0.85	5.39			
Tail 2/3	16.29 ± 0.28	28.21	27.73 ± 1.49	6.66			
Mean total	57.78	100	416.26	100			

patterns, amount of time exposed, nor the distance to the nearest potential refuge in C. m. melanotus. Activity in lizards is often a function of sex, age and reproductive condition (e.g. Fitch 1989; Rodda 1992). In Sceloporus virgatus, the highest activity occurs during the breeding season when males are active for longer periods and move further than during the non-breeding season. In Lacerta monticola (an active forager) tail loss did not have any effects on time budget, except when males are devoted to moving, and this was suggested to influence mate searching (Martín & Salvador 1997). Since this study was conducted in late autumn (i.e. out of breeding season), the lizards' activity may have been reduced and therefore may have masked real differences related to mate searching in the breeding season.

The microhabitat used by an animal is important when considering how foraging mode might affect autotomy-induced shifts in behaviour. *Cordylus m. melanotus* ambush prey from rocky outcrops that normally contain several crevices. As such, they have quick and easy access to refuges and any differences between tailed and tailless lizards are likely to be subtle or only apparent during the capture-subjugation phase of predation. Recent work on antipredatory behaviour in crevice-dwelling lizards including a number of cordyliforms and two *C. melanotus*, experimentally show that these lizards exhibit a wide array of defensive behaviours in the crevice, including protection of the body by the tail (Cooper *et al.* 2000). Tailless lizards would likely be more vulnerable to predation during this phase.

The maximum speed over 25 cm on both the horizontal and angled tracks was not significantly different between the two groups. Tail loss therefore appears to have no effect on the lizards' sprinting ability. *Cordylus m. melanotus,* however, are rupicolous and therefore frequently have to traverse irregular rocky surfaces. The tail could therefore play a role as a balancing organ, especially during jumping. Standard measurement of sprint speed would not measure these effects.

The energy lost in tail autotomy in *C. m. melanotus* was approximately 12 % of the total wet weight energy and approximately 30 % of the total dry weight energy. Compared with published measures of energy loss from caudal reserves in other taxa, however, this is a relatively small energy loss. Studies have shown the energy values of tails to be in excess of 20 J/mg DW (Table 7). In addition to the loss of caudal fat reserves, however, additional energy must be expended to regenerate the tail. Therefore, the effect of energetic loss incurred during autotomy is frequently

Table 7. Comparative energy values (dry weight) of lizard bodies and tails. Values were recalculated for	: Coleonyx
<i>brevis</i> for easier comparison (nc = non-combustible mass; sample size in brackets.).	

		Body			Tail			
Species	J/mg	% water	% nc	J/mg	% water	% nc	Reference	
Mabuya heathi	19.47 (5)	70.4	_	22.04 (3)	68.0	_	Vitt 1981	
Coleonyx variegatus	24.77 (22)	73.7	16.70	26.40 (3)	25.7	9.0	Vitt et al. 1977	
Coleonyx brevis	20.92 (10)	74.3	16.9	19.33 (10)	73.6	7.6	Dial & Fitzpatrick 1981	
Eumeces skiltonianus	25.69 (13)	68.7	13.43	27.40 (3)	72.8	13.9	Vitt et al. 1977	
Eumeces gilberti	24.69 (14)	65.4	20.23	24.85 (3)	71.0	15.9	Vitt et al. 1977	
Gerrhonotus multicarinatus	25.77 (18)	69.9	15.05	26.48 (3)	71.1	23.9	Vitt et al. 1977	
Cordylus m. melanotus	23.08 (8)	67.23	9.07	17.35 (8)	56.5	15.7	This study	

underestimated because this measure is not taken into account. Loss of energetic reserves may also constrain the amount of time a male can expend on mate searching and in the case of females, how much energy she can allocate to developing offspring.

In summary, the lack of significant differences in behaviour and performance between tailed and tailless lizards is not surprising because C. m. melanotus is considered an extreme ambush forager (Cooper et al. 1997). They exhibit strong site fidelity, move relatively small amounts (time and distance) and are always relatively close to a potential refuge. Potential costs in this, and other, ambush foraging lizards lie in compromised antipredatory behaviour in the crevice (see Cooper et al. 2000), social status, survival (particularly during hibernation), growth and reproductive capacity. Tailless lizards may also increase food intake to compensate for lost reserves. (Home range size and quality are unlikely to be affected since MPM and PTM were similar for both groups and should correlate to home range size.) Although there have been a variety of studies which include the energetics of tail loss (e.g. Clark 1971; Congdon et al. 1974; Vitt et al. 1977; Dial & Fitzpatrick 1981), the functional and ultimate significance of loss of caudal fat and energy reserves is poorly understood. Direct measures of the fitness costs of tail autotomy are likely to be a fruitful avenue of research.

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