

Jettisoning Ballast or Fuel? Caudal Autotomy and Locomotory Energetics of the Cape Dwarf Gecko *Lygodactylus capensis* (Gekkonidae)

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ABSTRACT

Many lizard species will shed their tail as a defensive response (e.g., to escape a putative predator or aggressive conspecific). This caudal autotomy incurs a number of costs as a result of loss of the tail itself, loss of resources (i.e., stored in the tail or due to the cost of regeneration), and altered behavior. Few studies have examined the metabolic costs of caudal autotomy. A previous study demonstrated that geckos can move faster after tail loss as a result of reduced weight or friction with the substrate; however, there are no data for the effects of caudal autotomy on locomotory energetics. We examined the effect of tail loss on locomotory costs in the Cape dwarf gecko *Lygodactylus capensis* (~0.9 g) using a novel method for collecting data on small lizards, a method previously used for arthropods. We measured CO₂ production during 5–10 min of exhaustive exercise (in response to stimulus) and during a 45-min recovery period. During exercise, we measured speed (for each meter moved) as well as total distance traveled. Contrary to our expectations, tailless geckos overall expended less effort in escape running, moving both slower and for a shorter distance, compared with when they were intact. Tailless geckos also exhibited lower excess CO₂ production (CO₂ production in excess of normal resting metabolic rate) during exercising. This may be

due to reduced metabolically active tissue (tails represent 8.7% of their initial body mass). An alternative suggestion is that a change in energy substrate use may take place after tail loss. This is an intriguing finding that warrants future biochemical investigation before we can predict the relative costs of tail loss that lizards might experience under natural conditions.

Introduction

Tail autotomy is very common among geckos (Gekkonidae), which will readily sacrifice their tail in defense and then regenerate a new one. For example, 65%–74% of *Coleonyx variegatus* (Parker 1972; Vitt et al. 1977), 68%–80% of *Coleonyx brevis* (Dial and Fitzpatrick 1981), and 68% of *Christinus (Phyllodactylus) marmoratus* (Daniels 1985a) in natural populations show evidence of tail regeneration. In the Cape dwarf gecko *Lygodactylus capensis* (Smith 1849), animals autotomize their tails with very little provocation, and 57% of the population sampled ($n = 39$) on the University of Pretoria campus demonstrate signs of tail regeneration (Medger et al. 2008).

On loss of their tail, lizards may incur a number of costs (reviewed in Arnold 1984, 1988; Bateman and Fleming 2008). Many lizard species demonstrate a decrease in running speed following autotomy (Pond 1978; Ballinger et al. 1979; Punzo 1982; Formanowicz et al. 1990; Martin and Avery 1998; Downes and Shine 2001; Chapple and Swain 2002b; Shine 2003; Cooper et al. 2004; Lin and Ji 2005). Compromised escape speed is not a universal phenomenon, however, and some animals are not slowed by tail loss (Daniels 1983, 1985b; Huey et al. 1990; Brown et al. 1995; McConnachie and Whiting 2003; Lin and Ji 2005). In fact, *Christinus marmoratus* geckos (Daniels 1983) and *Podarcis muralis* lacertids (Brown et al. 1995) become significantly faster in escape over horizontal surfaces after loss of their tail. Brown et al. (1995) interpret the lizards' faster responses as reflecting differences in antipredator strategies. For the geckos, however, it was suggested that, since they store fat in their tails, they are lighter and experience reduced friction with the substrate after tail loss (Daniels 1983).

To our knowledge, there has been no examination of how tail autotomy affects the metabolic costs incurred during locomotion in lizards. Given that some geckos are faster tailless compared with intact, we predict a lower cost of locomotion after caudal autotomy. Increased mobility postautotomy may therefore be a positive benefit for geckos, compensating for the loss of fat reserves. We tested our prediction by examination

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of the costs of locomotion in the diurnally active Cape dwarf gecko, *Lygodactylus capensis*, in intact animals and then after they had autotomized their tails. As far as we are aware, this is the first study to examine locomotory energetics in such a small lizard (~0.9 g).

Methods

Study Animals

Sixteen adult Cape dwarf geckos *Lygodactylus capensis* (Gekkonidae) were captured by hand from the Pretoria campus gardens at the University of Pretoria, South Africa. Each individual was intact and showed no evidence of previous tail autotomy; no gravid females were included. Animals were housed individually in 2-L clear plastic jars including perching branches under a natural lighting regime and immediately adjacent to a fluorescent lamp (as an additional UV light source). The room was relatively stable for temperature at around 20°–25°C (matching a natural temperature range for the time of year). Water was available ad lib., and the geckos were fed daily with ants, termites, or cricket nymphs dusted with vitamin powder. Animals were held in captivity at least 2 wk before experimentation and were released at site of capture 1 wk after the experiments.

Experimental Setup

In this study, we examined CO₂ production as a measure of energy expenditure during exercising for intact and autotomized geckos. We employed a “running tube” as a respirometry chamber, along which geckos ran back and forth at their own varying speed. Such an apparatus has been used successfully for the study of invertebrate locomotion (Fleming and Bateman 2007 and references therein). The running tube consisted of a 1-m length of glass tubing (internal diameter = 40 mm) with a wax base. The wax base allowed the geckos a flat surface for running and occupied approximately one-third of the internal volume; this reduced the final gas volume of the tube to about 800 mL.

Measurements of CO₂ production were carried out using a flow-through respirometry system (Sable Systems TR-2 from Sable Systems, Las Vegas, NV). Air was drawn through the system, providing negative pressure throughout. We present data for CO₂ emission rather than O₂ consumption because we were measuring CO₂ emission into a large volume (the running tube), and the measurement of CO₂ production (given that the incurrent air was scrubbed of CO₂ before entry) was therefore more accurate than the measurement of a decrease in atmospheric O₂ levels. Maximum CO₂ concentrations measured averaged 55 ± 12 μmol mol⁻¹ or ppm (*n* = 12). The incurrent room-air stream was scrubbed of H₂O and CO₂ with silica gel (UniLab, Saarchem, Krugersdorp) and soda lime (UniLab), respectively; air exiting the chamber was similarly scrubbed of H₂O before entering the LiCor 6262 CO₂ analyzer. The gas analyzer was then connected to a Sable Systems subsampler pump and mass flow controller. A flow rate of approximately

270 mL min⁻¹ was maintained throughout the experiments, and temperature was stable at about 25°C. Mass air flow and CO₂ values (μmol mol⁻¹) were recorded every 0.5 s on a PC (Datacan V, Sable Systems).

Each gecko was initially tested in an “intact” trial; subsequently, each was induced to autotomize its tail by briefly suspending it from broad tweezers gripping the tail base until it shook itself free. All individuals autotomized consistently to the tail base within seconds. Two days after tail autotomy, each individual was retested. This time (2 d postautotomy) was chosen because a recent study demonstrated that 2 d after tail autotomy, plasma corticosterone levels in water skinks (*Eulamprus heatwolei*) are reduced to levels equivalent to those measured 14 d post-autotomy treatment or to levels measured in control animals (Langkilde and Shine 2006). We chose to test the same animals twice (rather than examining two different groups of control and tailless individuals) since we found a high degree of variability in individual metabolic rate, and the repeated-measures design, where individuals serve as their own control, should be the best method for standardizing such differences. Although some lizards exhibit reduced resting metabolic rate (RMR) with repeated exposure to the experimental protocol (as they presumably become accustomed to the novel process; Hare et al. 2004), we assume that while such habituation may affect RMR, it is less likely to alter locomotory energetics. Each individual was tested only two or three times using this apparatus.

We carried out initial measurements for 16 individual geckos. Because of behavioral differences in response to the experimental setup expressed by these tiny lizards (e.g., not resting on introduction to the experimental chamber, difficulties in inducing animals to turn about at each end of the chamber, wedging themselves in a corner inaccessible to the cardboard prompt; see also Hare et al. 2004), only 13 individuals yielded appropriate measurements for running speed data when tested both intact and tailless; 12 of these animals also yielded reliable respirometry data (intact and tailless).

Experiments were carried out over the middle of the day as follows: A baseline CO₂ reading was recorded. Individuals were then weighed (to 0.0001 g) and placed into the running tube. They were given at least 10 min to adjust to the chamber, during which time they were confined to one end of the running tube by blocking the tube with cotton wool. The average rate of CO₂ production (mL h⁻¹) was calculated for 5 min of this initial resting phase when CO₂ production was stable (RMR or resting \dot{V}_{CO_2}). Intact RMR was compared with tailless RMR by repeated-measures ANOVA.

After a stable RMR was recorded, the cotton wool was removed and the animal left for sufficient time for the CO₂ reading from the running tube to return to about this resting level (exposure to “un-CO₂-scrubbed” room air introduced CO₂). The gecko was then induced to move the length of the respiratory chamber by touching its back or tail with a piece of card attached to a magnet controlled by a second magnet from outside the chamber. The gecko was made to move back and forth along the length of the chamber until it was no longer

responsive to being touched with the cardboard prompt (which took 5–10 min). The time taken to move each meter was monitored with a stopwatch (to calculate speed; m s^{-1}), and the total distance and time spent exercising were recorded. Speed per meter was analyzed for the first 11 m (all animals ran at least 11 m) by ANCOVA, with speed as the dependent variable, individual ID and treatment (intact = 0, tailless = 1) as independent variables, and \log_{10} -transformed distance (meters) as a covariate. Average speed was also calculated for 5-m increments (for comparison with respiratory data, see below). Time spent moving, total distance, and overall speed were analyzed by repeated-measures ANOVA for individuals (intact and postautotomy).

Measurement of the cost of locomotion requires that animals maintain a level of exercise for sufficient time to measure metabolic rate; however, animals such as lizards (which use intermittent locomotion to effect escape) may not maintain sustained locomotion naturally (Bennett 1982). The geckos did not reach a steady state of CO_2 production during exercise under our experimental setup, and it was therefore not possible to measure active metabolic rate directly, as per published studies of locomotory energetics (see “Discussion”). We therefore analyzed a number of aspects of exercising metabolic rate traces (Fig. 1), according to Gleeson and Hancock (2001, 2002) and our own interpretation of the traces. The following five measurements were recorded. (1) Total exercising $\dot{V}\text{CO}_2$ (mL) and (2) excess exercising $\dot{V}\text{CO}_2$ (mL) were, respectively, the absolute volume of CO_2 produced and the additional amount of CO_2 (on top of RMR) over the time spent exercising. (3) Maximum $\dot{V}\text{CO}_2$ (mL h^{-1}) was the maximum CO_2 reading taken during

the experiment, inevitably measured when the animal was still exercising. (4) The excess recovery $\dot{V}\text{CO}_2$ (mL) was calculated as the production of CO_2 in excess of the expected resting $\dot{V}\text{CO}_2$. (5) The total excess $\dot{V}\text{CO}_2$ (mL) was the sum of exercise and recovery excess volumes; this value may most closely approximate the measure suggested by Gleeson and Hancock (2001) to calculate cost of transport.

Each metabolic trait was tested separately as a dependent factor. These data included no outliers (all residuals were within ± 2.8 SDs of the mean, the critical value for a Grubb’s test with $n = 24$; the Grubb’s test is based on the Z ratio; Zar 1999). The analysis of metabolic parameters in intact and tailless geckos exposed a quandary regarding analysis of the effect of autotomy on energetic costs of locomotion. Inclusion of mass-specific measurements ($\text{mL h}^{-1} \text{g}^{-1}$) resulted in analyses where body mass contributed significantly to the analysis but treatment did not. However, since body mass was significantly altered by the removal of tails, autotomy treatment and the change in body mass are, in effect, autocorrelated. We therefore used absolute rate values (mL h^{-1}) for our metabolic measurements and included body mass in the analyses in order to control for the effects of body size.

Each metabolic trait was tested separately as a dependent factor in a mixed-model ANOVA for the 12 individuals that had been measured both intact and tailless. Treatment (intact or tailless) was entered as a fixed effect, while individual ID was included as a random effect to take into account the repeated measures (intact and autotomized) recorded for each individual. Three measures of body size were initially included as covariates to take into account relative metabolic rates (body

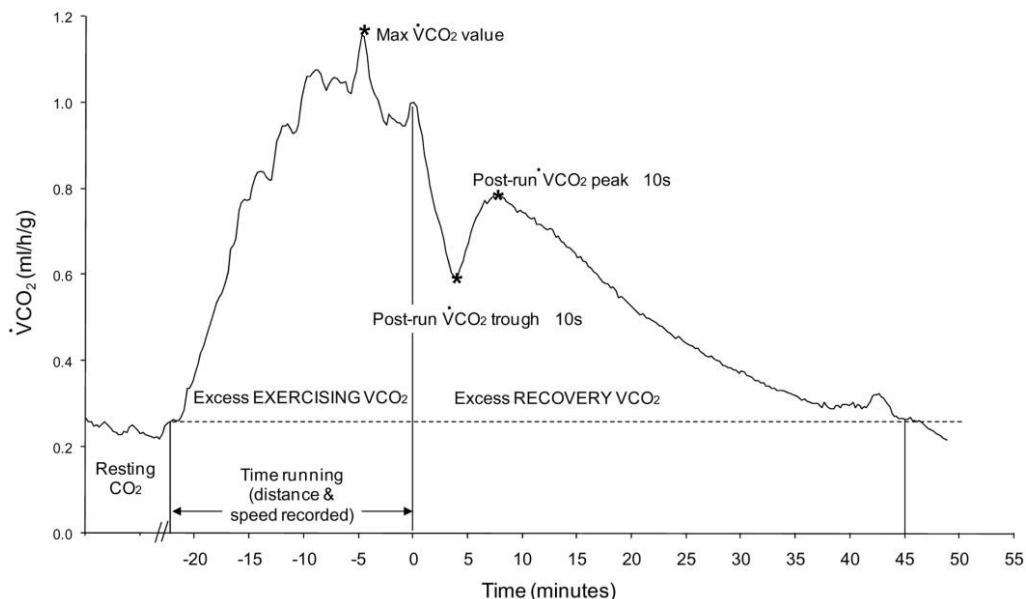


Figure 1. Example of carbon dioxide production ($\dot{V}\text{CO}_2$) in an intact 0.79 g *Lygodactylus capensis*. Resting metabolic rate was measured, then the animal was induced to exercise, running 22 m in 710 s. CO_2 production was recorded for a further 45 min after cessation of exercising. Measurements used in multiple regression analyses are labeled. The horizontal dashed line indicates the average value predicted from resting $\dot{V}\text{CO}_2$ values. All CO_2 produced above this value was considered excess (sensu Gleeson and Hancock 2001). Vertical lines represent (1) the onset of exercise, (2) the end of exercise, and (3) the end of the 45-min postexercise recovery period.

mass [g], snout vent length [mm], tail as a proportion of body length [%]); the final analyses include only intact body mass, since all three measures indicated the same patterns. RMR (mL h^{-1}) was included as a covariate in order to account for individual differences in metabolism, while the time spent exercising (s) and exercising speed (m s^{-1} ; overall, 1–5 m, 5–10 m, and 10–15 m) were included as covariates to capture differences in effort expended during exercising (distance moved had been used to calculate overall speed and therefore was not included in the analyses). The sex of animals (determined by presence of preanal pores) was included in models initially but was removed from final analyses since this factor did not influence any measure of metabolic rate.

Ethical Note

Animals were not anesthetized for the autotomy so that tail separation would occur at natural fracture planes with minimal trauma, postautotomy physiological recuperative processes would function normally, and the force/stimulus required to induce autotomy would be minimized (Arnold 1984). We also note that a large percentage of the natural population we examined demonstrated evidence of previous tail autotomy. Furthermore, a recent study in the skink *Eulamprus heatwolei* has shown that while tail autotomy causes an increase in plasma corticosterone levels, this is transitory (<2 h) and comparable to many other events, such as exposure to an unfamiliar enclosure or to a heterospecific lizard (Langkilde and Shine 2006).

Data

All data are given as means \pm 1 SD. The critical level for statistical analyses was set at $\alpha < 0.05$, and statistical analyses were carried out using Statistica (ver. 8.0; StatSoft 2007).

Results

The geckos measured for this study weighed 0.91 ± 0.23 g when intact, compared with 0.83 ± 0.22 g postautotomy ($n = 13$). Their tails therefore contributed 8.7% of their initial (intact) body mass. Males and females did not differ significantly in either mass (males: 0.86 ± 0.18 g, $n = 7$; females: 1.02 ± 0.32 g, $n = 6$; t -test: $t_{10} = -1.08$, $P = 0.304$) or snout-vent length (males: 65.7 ± 5.3 mm; females: 62.3 ± 5.3 mm; $t_{10} = 1.11$, $P = 0.291$). We note also that sex was never a significant factor affecting any measurement recorded (data not shown).

Endurance and Speed

The geckos initially moved rapidly in response to stimulus, averaging speeds of 0.180 ± 0.061 m s^{-1} over the first meter (Fig. 2). However, this effort was not maintained, and speed fell exponentially until they achieved only 0.039 ± 0.021 m s^{-1} in their tenth meter and an average of 0.023 m s^{-1} after 10 m. Over the first 3 m, tailless geckos were slightly (not statistically

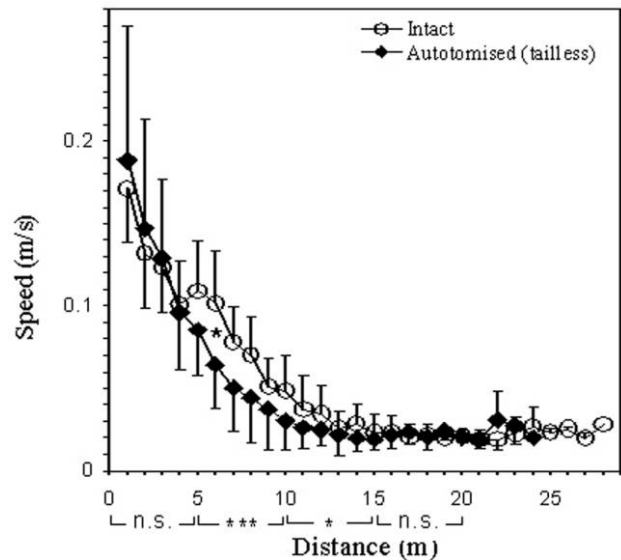


Figure 2. Speed over distance for 13 *Lygodactylus capensis* measured with intact tails and then 2 d later post-tail autotomy. Asterisks under the X-axis indicate significant differences between intact and autotomized states for 5-m intervals (repeated-measures ANOVA); *n.s.*, not significant at $P < 0.05$; *one asterisk*, $P < 0.05$; *three asterisks*, $P < 0.001$. Only the values for the sixth meter were significantly different between intact and tailless animals (repeated-measures ANOVA of speed each meter over the first 11 m; *one asterisk*, $P < 0.05$). Values are means \pm 1 SD.

significantly) faster (compared with intact measurements; $F_{1,12} = 2.25$, $P = 0.159$; Fig. 2); however, the speed of tailless geckos dropped quickly, and they were slower on the whole (Fig. 2). ANCOVA analysis indicated significant differences in speed between individuals ($F_{12,259} = 5.11$, $P < 0.001$) and treatments ($F_{1,259} = 9.19$, $P = 0.003$) once distance had been taken into account (as a covariate in the analysis).

There was no difference in the amount of time that geckos exercised when tailless compared with intact (Fig. 3a; $F_{1,12} = 0.06$, $P = 0.818$). However, because of their slower overall speed when tailless ($F_{1,12} = 5.48$, $P = 0.037$), they covered a shorter distance postautotomy compared with when intact (Fig. 3b; $F_{1,12} = 7.14$, $P = 0.020$).

Because individual behavioral differences made multiple trials necessary for some animals to ensure capture of all measurements, we had to repeat intact experimental trials for six individuals. We could therefore analyze this data to determine whether the decreases in exercise speed and distance observed postautotomy were an artifact of animals becoming habituated to stimulus (prodding with a piece of cardboard). We recorded no significant change on successive exposure to the experimental setup for time exercising (Wilcoxon matched pairs test; $Z_{n=6} = 0.11$, $P = 0.917$), distance ran ($Z_{n=6} = 1.48$, $P = 0.138$), and overall speed ($Z_{n=6} = 1.36$, $P = 0.173$) in these animals, confirming the observation that sprint speed is a highly repeatable trait (Huey and Dunham 1987). This suggests that the differences in speed between intact and tailless individuals were unlikely to be an artifact of them becoming accustomed

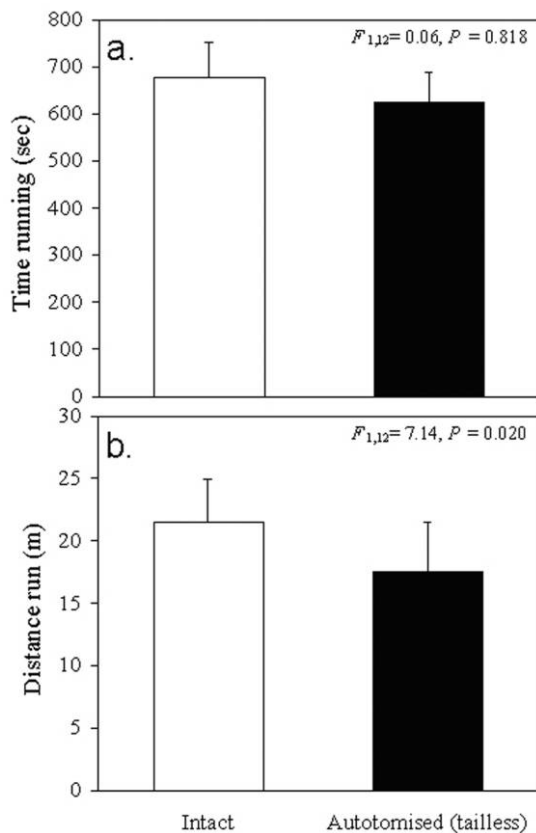


Figure 3. Time exercising (a) and distance covered (b) for 13 *Lygodactylus capensis* measured intact and then 2 d later post-tail autotomy. The results of repeated-measures ANOVA are given for each graph. Values are means \pm 1 SD.

to the prompt, lending greater weight to the possibility of physiological differences between intact and tailless animals (rather than behavioral differences only in response to stimulus).

RMR

We obtained reliable, consistent RMR data (measured over at least 10 min for intact and autotomized states) for eight individuals since most other individuals would not remain stationary for such a long time. Repeated-measures ANOVA of the absolute resting $\dot{V}CO_2$ values for these animals indicated that there was no significant difference postautotomy ($F_{1,11} = 0.008$, $P = 0.932$), with an average of 0.21 ± 0.05 mL h⁻¹ when intact compared with 0.20 ± 0.06 mL h⁻¹ postautotomy. Mass-specific resting $\dot{V}CO_2$ postautotomy (0.24 ± 0.05 mL h⁻¹ g⁻¹) was not different from measurements recorded when the animals were intact (0.23 ± 0.08 mL h⁻¹ g⁻¹; $F_{1,11} = 1.14$, $P = 0.741$).

Metabolic Costs of Activity

The total and excess volumes of CO₂ produced during exercising were directly related to overall speed during exercising

(Table 1; Fig. 4a) and the autotomy treatment (Table 1; Fig. 4b); in addition to the reduced effort tailless animals put into exercising (in terms of speed and distance covered), tailless animals also produced lower levels of CO₂ during exercising compared with when they were intact. The other metabolic measurements recorded were not informative with regard to the effect of autotomy on locomotory energetics, with no significant relationship found with the autotomy treatment (Table 1). Peak rate of CO₂ production (maximum $\dot{V}CO_2$), excess $\dot{V}CO_2$ production during the 45-min recovery period, and total excess CO₂ production (measured during both exercise and recovery periods) were affected by body mass and overall speed; maximum $\dot{V}CO_2$ was also related to the time spent exercising. RMR affected all calculated values of excess $\dot{V}CO_2$ production.

Discussion

We predicted that *Lygodactylus capensis* would become faster after loss of their tails as a result of reduced friction with the substrate or reduced body mass, as for *Christinus marmoratus* geckos (Daniels 1983). Contrary to our expectations, we found that, in addition to being slower, tailless *L. capensis* also have reduced stamina, covering a shorter distance compared with when intact. Although initial burst speed may be most important for predator avoidance, reduced stamina may alter behavior that could compromise fitness in other ways (discussed further in “Conclusions”). In addition to their exercise speed, tailless *L. capensis* demonstrated significantly lower excess exercising $\dot{V}CO_2$ compared with when they were intact. This suggests that tailless animals demonstrate reduced metabolic expenditure during exhaustive locomotion (which may be linked to their reduced metabolically active body tissue; tails are about 8.7% of intact body mass and are highly muscular) or altered energy substrate use. We discuss these findings in the context of the impact of tail autotomy on locomotory performance (speed and stamina) and metabolic costs (both resting and active metabolic rates) as well as the ecological relevance of exhaustive (as opposed to brief, intermittent) running.

Tail Autotomy Reduces Locomotion Performance in *Lygodactylus capensis*

Speed. For many lizard species, a decrease in locomotor performance postautotomy has been demonstrated. Tail autotomy results in a 12%–42% decrease in sprint speed for representatives of five lizard families: Teiidae (Ballinger et al. 1979), Iguanidae (Punzo 1982), Phrynosomatidae, (Punzo 1982), Lacertidae (Martin and Avery 1998), and Scincidae (Formanowicz et al. 1990; Downes and Shine 2001; Chapple and Swain 2002b; Shine 2003). However, not all data suggest a detrimental effect of tail autotomy on speed (Daniels 1985b; Huey et al. 1990; Brown et al. 1995; McConnachie and Whiting 2003). To date, only two gecko species have been tested, both over very short distances. *Christinus marmoratus* (~3.6 g) store large reserves of fat in their tails and are almost twice as fast tailless compared with intact when tested over short distances (10–30-cm sprints)

4 d postautotomy (Daniels 1983). More recently, Medger et al. (2008) demonstrated no significant differences in maximum escape speed for *L. capensis* (1.1 g) tested over ~0.5 m horizontal surfaces (although tailless animals were significantly slower when tested over vertical surfaces). In this study, we found that tailless *L. capensis* were not faster than when they were intact over the first 5 m of our trials, although they became slower than intact animals over longer distances (5–10 m and 10–15 m). Tailless geckos may be faster over very short sprints than when intact as a result of reduced body mass or reduced friction with the substrate they are running over (Daniels 1983); however, metabolic constraints may affect their subsequent stamina, and they are certainly not faster over longer distances (such as those tested in this study).

Endurance/Stamina. We found a 19% reduction in distance ran for our tailless geckos compared with when intact. These results are in line with the few other studies that have been conducted on the effect of tail autotomy on running endurance or stamina. Distances moved by *Psammotromus algirus* postautotomy are significantly shorter (Martin and Avery 1998), swimming stamina is reduced in the water skink *Eulamprus (Sphenomorphus) quoyii* postautotomy (Daniels 1985b), and female (but not male) *Niveoscincus metallicus* demonstrate a 36% decrease in endurance capacity postautotomy (Chapple and Swain 2002b).

Tail Autotomy Does Not Change RMR in Lygodactylus capensis

RMR. Energy expenditures of intact and tailless animals have been measured by various authors (Congdon et al. 1974; Vitt et al. 1977; Dial and Fitzpatrick 1981; Bellairs and Bryant 1985; Naya and Bozinovic 2006; Naya et al. 2007). It is important to bear in mind that most lizards are able to fully regenerate a lost tail (Arnold 1988). Tail regeneration is an energetically expensive process (Chapple et al. 2002); therefore, if energy expenditure is measured some time after tail loss, the effects of tail loss are compounded with regeneration costs, and these

animals are likely to demonstrate higher RMRs (compared with intact animals). For example, a 15% increase in food intake and a 26% increase in standard metabolic rate have been recorded for *Liolaemus nitidus* (Liolaemidae) autotomized 3 wk before measurement (Naya and Bozinovic 2006), a 36% increase in standard metabolic rate has been measured for *Liolaemus belli* 1 wk after autotomy (Naya et al. 2007), and a 25% increase in energy intake has been measured for tailless *Coleonyx brevis* geckos undergoing “rapid tail regeneration” (Dial and Fitzpatrick 1981). There was no difference recorded for *Coleonyx variegatus* (Congdon et al. 1974; time since autotomy unknown).

In our study, we found no significant differences in resting $\dot{V}CO_2$ measured when animals were intact or 2 d post-tail autotomy, suggesting that tail loss did not significantly change the absolute amount of metabolically active tissue mass in resting *L. capensis*. We have collected the only immediate postautotomy data for lizards recorded that we are aware of, and longitudinal studies of the metabolic rates of lizards during tail regeneration are warranted. As an aside, an interesting complication to the relationship between autotomy and metabolic rate is that lizards with increased corticosteroids (increased immediately on autotomy; Langkilde and Shine 2006) actually express lower basal metabolic rates (Miles et al. 2007).

Tail Autotomy Affects Active Metabolic Performance in Lygodactylus capensis

In this study, we have investigated the use of continuous recordings of CO_2 production in order to assess locomotory energetics. This is an experimental method that has been established for invertebrates; however, it is a novel application for lizard locomotory energetics, which effectively kept the animal moving but allowed it to self-select its pace. Tailless *L. capensis* exhibited lower CO_2 production during exercise compared with when intact, which may reflect reduced body mass, as was proposed by Daniels (1983) for *C. marmoratus*. Additionally, many lizards have actively functional tails that help the animal

Table 1: Summary of mixed-model ANOVA analyses of metabolic variables during exercise for *Lygodactylus capensis* ($n = 12$) measured intact and then 2 d later post-tail autotomy

	Effect	df Effect	Total Exercising V_{CO_2} (mL over Time)	Excess Exercising V_{CO_2} (mL)	Maximum $\dot{V}CO_2$ (mL h ⁻¹)	Excess Recovery V_{CO_2} (mL)	Total Excess V_{CO_2} Exercise + Recovery (mL)
Body mass (g)	Covariate	1	.067	.081	<.001	.006	.003
RMR (resting V_{CO_2} ; mL h ⁻¹)	Covariate	1	.773	.040	.989	.002	.001
Time exercising (s)	Covariate	1	.099	.199	.026	.725	.822
Speed (m s ⁻¹):							
Overall	Covariate	1	.002	.001	.001	.010	.002
Over 0–5 m	Covariate	1	.097	.125	.586	.527	.310
Over 5–10 m	Covariate	1	.121	.031	.284	.800	.235
Over 10–15 m	Covariate	1	.981	.837	.985	.192	.338
Individual ID	Random	11	.803	.825	.258	.193	.200
Treatment (intact vs. tailless)	Fixed	1	.011	.018	.944	.727	.136

Note. Column headings are dependent variables tested in this model. Independent factors (fixed, random, and covariates) are indicated in each row. Values are *P* values; those in bold are <.05. RMR, resting metabolic rate

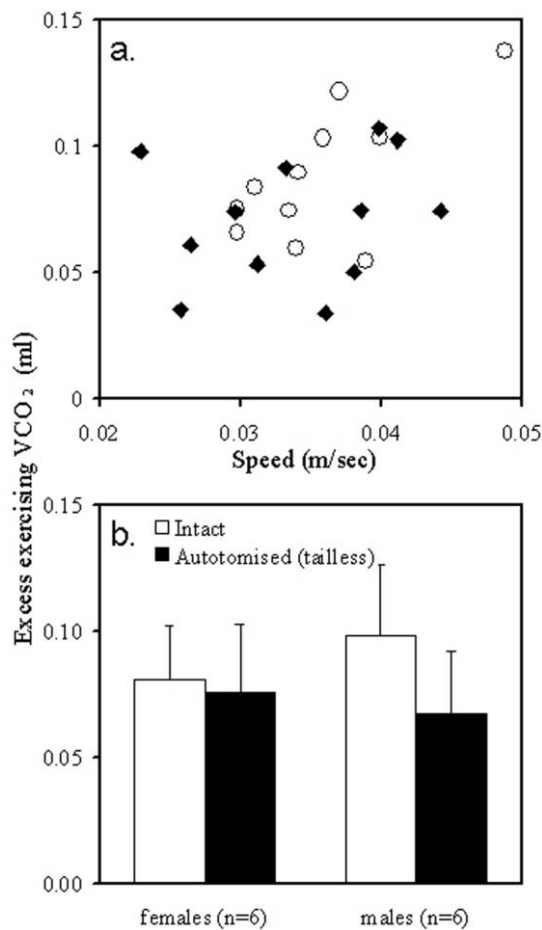


Figure 4. Excess V_{CO_2} (mL) produced during exercise for 12 *Lygodactylus capensis* measured intact (open symbols and bars) and then 2 d later post-tail autotomy (filled symbols and bars). Excess V_{CO_2} was calculated as absolute values minus resting metabolic rate V_{CO_2} . In addition to a significant affect of speed (a) on V_{CO_2} , tail autotomy resulted in reduced excess V_{CO_2} production during exercise (there was no significant effect of sex; b). Autotomized values are indicated with filled symbols and bars. In b, values are means \pm 1 SD.

to correct for the disequilibrium caused at each stride; for example, loss of stride length (Martín and Avery 1998), stability (Ballinger 1973; Daniels 1985b), and thrust or momentum (Daniels 1985b) may all be consequences of tail autotomy. The reduction in CO_2 production recorded for *L. capensis* may therefore reflect reduced mass or reduced amount of metabolically active tissue (due to loss of the tail musculature); however, these possibilities are less likely to explain why these geckos demonstrated reduced stamina. The lack of a difference in locomotion response for repeated trials on the same individuals suggests that this result is also unlikely to be due to behavioral habituation to the experimental setup. An alternative explanation is that there may be a change in substrate metabolism (i.e., reduced availability of fatty acids in the blood stream due to tail loss). We discuss this proposed mechanism in respect to what we know about reptile locomotion.

In reptiles, metabolite changes during high speed locomotion

are consistent with a pattern of fiber-type recruitment favoring fast-twitch glycolytic fibers and therefore use of glycogen (e.g., *Dipsosaurus*: Gleeson and Dalessio 1990; *Varanus*: Jayne et al. 1988); between 60% and 80% of the total ATP utilized during exercise in lizards is generated via glycolysis (Gleeson 1991). A walking pace, however, may be maintained, suggesting aerobic capacity as this reduced speed. The contribution of oxidative fibers is smaller during high speed locomotion. These differences in muscle metabolism may relate to selection of different paces by lizards. For example, two distinct voluntary speeds are recorded for *Uma scoparia*, a rarely used walk (used ~13% of observations) and a faster running pace (used ~87% of observations); only the slower pace is likely to be aerobically sustained (Jayne and Irschick 2000). The fast initial speeds expressed by *L. capensis* allowed them to cover the first meter in 6 s or the first 10 m in about 3 min; however, they kept moving at a slower pace for up to a further 8 min beyond this. Therefore, in addition to an initial burst of speed (fuelled anaerobically via glycogen and accompanied by lactate accumulation; blood lactate concentration may increase five- to 10-fold after a bout of intense activity; Bennett 1978), these animals must be undertaking low levels of aerobic metabolism to sustain further locomotion.

Unfortunately, while a large amount of research has focused on glycolysis, we know much less about substrates fueling aerobic metabolism, which presumably primarily makes up the remaining 20%–40% of ATP required during lizard locomotion. The rate of glucose uptake by active muscle is low during activity, and blood glucose concentrations are not affected by vigorous exercise (Gleeson and Dalessio 1990); the utilization of fatty acids to make up the remaining ATP required for sustained locomotion is therefore a possibility. Compared with when they were intact, tailless lizards run at similar speeds over the first 5 m (which we suggest is supported by anaerobic metabolism fuelled primarily through glycogen); however, their speed over 5–15 m (when they are more reliant on aerobic processes) is significantly reduced. In addition to the long-term metabolic cost of replacing tissue (Vitt et al. 1977; Bellairs and Bryant 1985), in the short-term lizards lose fat reserves stored in their tails (Avery 1970; Vitt et al. 1977; Dial and Fitzpatrick 1981; Daniels 1984; Daniels et al. 1986; Arnold 1988; Chapple and Swain 2002a; Chapple et al. 2002; Doughty et al. 2003). Increased pausing during escape (e.g., Martín and Avery 1998; Lin and Ji 2005) and reduced stamina (Daniels 1985b; Martín and Avery 1998; Chapple and Swain 2002b; this study) due to autotomy may reflect an energetic cost in terms of reduction in fat reserves to sustain locomotion. The role of fatty acids in exercising lizard muscle is speculative, yet it certainly warrants further investigation.

We were interested in determining whether the metabolic cost of transport (the relationship between metabolic rate and running speed) was altered by tail autotomy in *L. capensis* and for comparison with other gecko species (e.g., Farley and Emshwiller 1996; Autumn et al. 1997, 1999; Autumn 1999; Weinstein and Full 1999; Kearney et al. 2005). However, it was not appropriate to calculate the metabolic cost of transport

(MCOT) of our geckos for three reasons. First, our geckos did not maintain a steady effort during exercising, with speed swiftly declining after the initial few meters. Second, most studies assume that the animals are exercising in a stable and primarily aerobic capacity, with negligible contribution of anaerobic energy. This is clearly not a valid assumption for reptiles that undergo extensive anaerobic metabolism (Bennett 1978). Third, the analysis of MCOT requires that all metabolic costs incurred by the animal are included. However, measuring O_2 consumption (or CO_2 production) just during locomotion, without inclusion of measurements during recovery, does not capture all of the metabolic costs associated with activity, a problem commonly encountered for animals that utilize intermittent locomotion (e.g., territorial defense and foraging behavior in many lizards; Gleeson and Hancock 2001, 2002). Calculation of MCOT clearly requires inclusion of both exercising and recovery in *L. capensis*. The measure of “cost of activity” (C_{act}) proposed by Gleeson and Hancock (2001) for both exercising and recovery phases includes a measure of the change in concentration of metabolites, which was not feasible in this study with such small animals (without killing).

Finally, some interesting patterns were revealed during recovery in *L. capensis*. A large percentage of total CO_2 production was recorded only after they had stopped moving, and for every trial carried out, individuals demonstrated a distinct decrease and then increase in CO_2 production (a postexercise \dot{V}_{CO_2} trough and then peak) after they had stopped moving (e.g., Fig. 1). We have found no similar data for other species in the literature, although most authors have generally utilized \dot{V}_{O_2} consumption as their measurement of metabolic rate. Values for the \dot{V}_{CO_2} (mL h^{-1}) averaged over ± 10 s during the post-exercise \dot{V}_{CO_2} trough and the postexercise \dot{V}_{CO_2} peak were not significantly related to any of the variables recorded in this study (i.e., autotomy, body size, exercise effort; data not shown). This postrun peak in CO_2 production is particularly intriguing. Elevated \dot{V}_{CO_2} may reflect (1) increased CO_2 production due to elevated metabolic rate, (2) a consequence of hyperventilation in response to increased demand for O_2 (i.e., increased metabolic rate during recovery as oxidative processes restore muscle stores of glycogen or creatine phosphate; Bennett 1982, p. 178; Gleeson and Hancock 2002), or (3) increased excretion of CO_2 during recovery from acid-base imbalance caused by increases in circulating lactic acid (John-Alder and Bennett 1981; Gleeson and Bennett 1982). For three lizard species (two varanids and one iguanid), Gleeson and Bennett (1982) recorded arterial blood lactate and H^+ concentrations peaking 1.5 min after terminating exercise and minimal values of plasma HCO_3^- and CO_2 levels after 5 min of recovery. The postexercise peak in CO_2 production in *L. capensis*, about 6 min (range 5–8 min) after cessation of exercise (which was coupled with an increase in ventilation rate; data not shown), may reflect removal of lactate and increase in blood pH. A similar increase in ventilation rate after cessation of exhaustive exercise has been demonstrated in *Alligator mississippiensis* (Hartzler et al. 2006).

Conclusions

We have demonstrated a significant reduction in active metabolic rate after tail autotomy in *Lygodactylus capensis*. Without a tail, these geckos were 8.7% lighter and also had less muscle tissue; both could account for significantly lower metabolic expenditure during running (i.e., excess exercising CO_2 production). However, tailless geckos also demonstrated reduced stamina during locomotion; they ran significantly slower and over a shorter distance postautotomy. Reduced stamina suggests that lack of energy reserves stored in the tail (e.g., fat) may play a significant role in the locomotory energetics of these animals; this hypothesis warrants further biochemical studies.

Naturally, many lizards remain within a short flight of refuge (Cooper 2007) and exhibit very short escape distances when disturbed (e.g., 1.4–2.4 m for intact and tailless *Holbrookia propinqua*: Cooper 2003; 0.5–1.4 m for intact and tailless *Sceloporus virgatus*: Cooper 2007). Over such short distances, tailless *L. capensis* were not compromised; however, over longer distances, tailless animals demonstrated reduced mobility or stamina/endurance. Increased locomotory costs will have marked consequences for normal daily activity patterns. For example, tailless geckos may choose to stay nearer cover (Martín and Salvador 1992; Salvador et al. 1995; Cooper 2003) or become less active (Formanowicz et al. 1990; Salvador et al. 1995; Downes and Shine 2001) or less aggressive (Fox et al. 1990; Martín and Salvador 1993b). Such altered behavior may lead to altered foraging decisions (Martín and Salvador 1993a), territoriality (Martín and Salvador 1993a; Salvador et al. 1995; many individual dwarf geckos on the University campus appear to have distinct territories; Dando 2008), and access to mates (Martín and Salvador 1993b; Salvador et al. 1995), as has been demonstrated in other lizard species. The effects of autotomy on such behavior in *L. capensis* therefore warrant investigation. Metabolic costs of tail loss also include reduced female fecundity (Smyth 1974; Wilson and Booth 1998; Chapple et al. 2002; but see Fox and McCoy 2000) or production of smaller eggs (Smyth 1974; Dial and Fitzpatrick 1981).

Finally, nocturnal gecko species have significantly lower metabolic costs of transport compared with diurnal species (e.g., Autumn et al. 1997), and studies of the response to tail autotomy between gecko species should take this into account. In contrast to this study for diurnal *L. capensis*, nocturnal *Christinus marmoratus* geckos show a near doubling of sprint speed after tail autotomy (Daniels 1983). It would therefore be valuable to compare the effects of tail autotomy on locomotory energetics for other gecko species. The inclusion of species that actively use their tail during locomotion as a counterbalance (Vitt et al. 1977) would also prove a valuable contrast to these geckos.

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